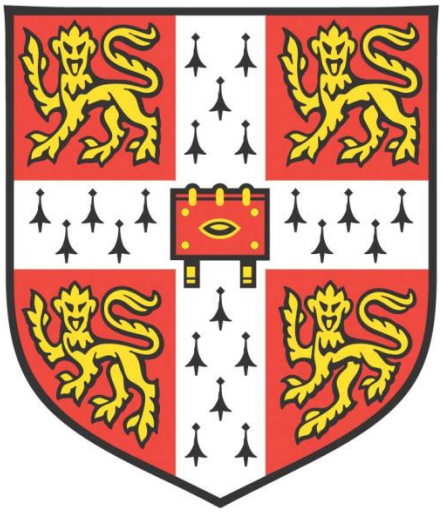
Effects of healthy ageing on the precision of episodic memory



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This thesis is submitted for the degree of Doctor of Philosophy

September 2019

Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the acknowledgments and specified in text.

It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution.

The experiments presented in Chapters 2 and 3 were reported in the paper by Saana M. Korkki, Franziska R. Richter, Priyanga Jeyarathnarajah, & Jon S. Simons (2020). Healthy ageing reduces the precision of episodic memory retrieval. *Psychology and Aging*, *35*(1), 124.

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

Acknowledgments

Firstly, I wish to thank my PhD supervisor Jon Simons. I am grateful for all the opportunities and support you have provided me over the years, enabling me to gain my confidence as a researcher. I would also like to thank all the past and present members of the Cambridge Memory Lab: Ayat Abdurahman, Rose Cooper, Jane Garrison, Deborah Green, Helena Gellersen, Priyanga Jeyarathnarajah, Simon Kwon, Franziska Richter, Sophie Schmidt, Michael Siena, Carolin Sievers, Alexandra Trelle and David Vogelsang. A special thanks to Priya and Helena for assistance with recruitment and testing of older volunteers, ensuring that the experiments described in Chapters 3 and 5 ran smoothly, and to Franka for all the invaluable guidance and advice you have provided throughout my PhD. I appreciate you always taking the time to discuss my work, and have learnt a great deal from you.

I would also like to express my gratitude to all the individuals who volunteered their time to participate in the experiments presented in this thesis, and to the Biotechnology and Biological Sciences Research Council for providing the financial support for me to undertake my PhD research. Thank you also to the staff at the Cognition and Brain Sciences Unit for assistance with the MRI scanning for the experiments presented in Chapters 4 and 5.

Last, but not least, I am very grateful to my family, my parents Saija and Jyrki, and my brother Vertti, for the unwavering support and encouragement you always have for me, and to my partner Bárður for sharing this journey with me.

Abstract

Episodic memory decline is one of the hallmarks of human cognitive ageing, but our understanding of the neurocognitive mechanisms underlying this decline remains limited. In particular, it is unclear whether healthy ageing differentially affects distinct components of episodic memory retrieval; specifically, the probability of successfully retrieving information from memory, and the quality, or precision, of the retrieved memory representations. The research reported in this PhD thesis used continuous measures of memory retrieval to dissociate these two alternative sources of age-related memory deficits and their cognitive and neural underpinnings, providing more detailed insight into the nature of age-related episodic memory decline.

Two behavioural experiments reported in Chapter 2 provided initial evidence for differential effects of healthy ageing on the success and precision of episodic memory retrieval, suggesting greater sensitivity of mnemonic precision to age-related declines. Chapter 3 assessed whether these decreases in memory precision are specific to long-term memory or may be explained by age-related decreases in the fidelity of perceptual or working memory processes. The results from this experiment demonstrated that age-related reductions in the precision of episodic memory retrieval persisted after controlling for decreases in the fidelity of perception and working memory, suggesting a predominantly long-term memory basis for this deficit.

The functional and structural magnetic resonance imaging experiments reported in Chapters 4 and 5 sought to elucidate the neural basis of age-related changes in the success and precision of episodic memory retrieval. Results from Chapter 4 revealed distinct encoding and retrieval contributions to the decreases in these two aspects of memory retrieval exhibited by older adults. At retrieval, age-related reductions in activity associated with successful memory retrieval were observed in the hippocampus, while decreases in activity underlying the precision of memory retrieval were evident in the angular gyrus. Furthermore, at encoding, age-related decreases in activity predicting both later success and precision of memory retrieval were evident in the fusiform gyrus, while prefrontal reductions were observed in the encoding activity predicting the subsequent success of memory retrieval only. In addition to these functional changes, Chapter 5 provided evidence for the role of structural integrity of

the lateral parietal cortex in individual differences in mnemonic precision across older adults.

Together, the results reported in this thesis highlight the sensitivity of memory precision to age-related cognitive decline, and suggest both distinct and common factors underlying age-related decreases in the success and precision of episodic memory retrieval.

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Chapter 1: General introduction

Healthy ageing is associated with various cognitive and neural changes most notably affecting the integrity of flexible, higher-order cognitive processes, such as the ability to learn and retain information in memory over both short and longer time scales (Park et al., 2002). In particular, episodic memory, a consciously accessible form of memory for previously experienced events bound to a specific spatio-temporal context (Tulving, 1985), exhibits pronounced declines in older age (Park et al., 2002; Rönnlund, Nyberg, Bäckman, & Nilsson, 2005). Episodic memory function typically begins to decline at around the age of 60 (Rönnlund et al., 2005; Schaie, 1994), and in many people exhibits greater age-related losses in comparison to other forms of long-term memory, such as semantic memory, the memory for general knowledge and facts (Nyberg, Bäckman, Erngrund, Olofsson, & Nilsson, 1996; Nyberg et al., 2003; Rönnlund et al., 2005), as well as non-consciously accessible forms of memory, such as priming and procedural memory (Henson et al., 2016; Nilsson, 2003; Nyberg et al., 1996). However, despite the well-known vulnerability of episodic memory to age-related decline, the specific neurocognitive mechanisms underlying this decline remain unclear. Prior studies have suggested ageing to affect both the likelihood of successful retrieval of information from memory (e.g., Cansino et al., 2018; Naveh-Benjamin, 2000), and the quality and specificity of the retrieved information (e.g., Addis, Wong, & Schacter, 2008; Koutstaal & Schacter, 1997; Trelle, Henson, Green, & Simons, 2017), but distinguishing between these two potential sources of age-related memory impairments has been difficult in previous paradigms relying on categorical measures of memory accuracy or participants' subjective ratings of retrieval quality.

To gain more detailed insight into the exact nature of episodic memory declines in older age, the research presented in the current thesis uses fine-grained, continuous measures of memory retrieval in combination with mixture modelling of participants' retrieval errors. In the four experimental chapters presented in this thesis, I use continuous measures of memory retrieval to disentangle the effects of healthy ageing on two separable aspects of episodic memory: the probability of successfully retrieving information from memory, and the quality, or precision, of the retrieved memories, as well as their cognitive and neural underpinnings. Before presenting findings from these experiments, I will here provide an overview of previous research motivating the current experiments. I will first discuss the neural basis of episodic memory and age-related

memory impairments, focusing on the medial temporal, prefrontal and parietal lobes due to their previously-demonstrated involvement in young adults in the memory paradigm employed in the current experiments, as well as being implicated in age-related episodic memory decline. I will then discuss the general pattern of age-related episodic memory changes, presenting evidence for age-related changes in memory quality. Lastly, I will review emerging evidence from younger populations demonstrating the dissociability of the success and precision of episodic memory retrieval, and conclude with an overview of the research presented in the experimental chapters of the thesis.

Neural substrates of episodic memory

Following the findings of amnesia associated with medial temporal lesions (Scoville & Milner, 1957), the role of the medial temporal lobes, and the hippocampus in particular, in forming and retaining episodic memories has been widely recognized (Eichenbaum, 2000; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Squire, 1992). During memory formation, the hippocampus is thought to play a critical role in integrating multiple event details that constitute an experience into a coherent episodic representation (Eichenbaum, Yonelinas, & Ranganath, 2007; Squire & Zola-Morgan, 1991). The role of the hippocampus in binding episodic details during encoding has been contrasted to the function of other medial temporal regions (Davachi, 2006). For instance, while the perirhinal cortex has been implicated in encoding of item information and the parahippocampal cortex in encoding of contextual attributes of previous experiences (e.g., Davachi, Mitchell, & Wagner, 2003), the hippocampus is thought to bind these elements together into a conjunctive memory representation (Komorowski, Manns, & Eichenbaum, 2009; Ranganath, 2010).

During memory acquisition, the hippocampus is also thought to allow for overlapping experiences to be represented in an orthogonalized manner via the mechanism of *pattern separation* (McClelland, McNaughton, & O'Reilly, 1995; Norman & O'Reilly, 2003). Specifically, hippocampal pattern separation enables the storage of similar inputs as distinct representations in order to avoid catastrophic interference (Norman & O'Reilly, 2003; Yassa & Stark, 2011). Pattern separation has most notably been attributed to the dentate gyrus (DG) subfield of the hippocampus (Bakker, Kirwan, Miller, & Stark, 2008; Berron et al., 2016; Leutgeb, Leutgeb, Moser, & Moser, 2007), due to the sparse

representational properties of this region (Norman & O'Reilly, 2003; Treves & Rolls, 1994). At retrieval, the hippocampus supports the recollection of previous experiences via the mechanism of *pattern completion*, enabling the recovery of a complete hippocampal memory representation in response to a partial or degraded input (McClelland et al., 1995; Norman & O'Reilly, 2003; Treves & Rolls, 1994). Following the reinstatement of the hippocampal pattern, the hippocampus is thought to facilitate reinstatement of the retrieved information in the neocortical regions originally involved in encoding the information (Danker & Anderson, 2010; McClelland et al., 1995). Consistent with this proposal, functional neuroimaging studies have demonstrated event-specific patterns of encoding activity to be reinstated in cortical regions during memory retrieval (Kuhl & Chun, 2014; Ritchey, Wing, LaBar, & Cabeza, 2013; Staresina, Henson, Kriegeskorte, & Alink, 2012; Wing, Ritchey, & Cabeza, 2015), with hippocampal retrieval activity correlating with the degree of this reinstatement (Staresina et al., 2012).

Beyond the medial temporal lobes, the lateral prefrontal cortex has been implicated in memory control processes that direct the encoding and retrieval of information in a goal-oriented manner (Eichenbaum, 2017; Fletcher & Henson, 2001; Moscovitch, 1992; Simons & Spiers, 2003). The ventrolateral and dorsolateral parts of the prefrontal cortex are thought to exhibit a degree of functional specialization during both memory encoding and retrieval (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). During encoding, the ventrolateral prefrontal cortex has been proposed to mediate the selection and elaboration of relevant information, while the dorsolateral prefrontal cortex supports the online organization of the to-be-encoded material (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). Consistent with this proposal, while ventrolateral prefrontal activations have been observed for semantic elaboration during encoding (Baker, Sanders, Maccotta, & Buckner, 2001; Otten, Henson, & Rugg, 2001), the dorsolateral prefrontal cortex is involved, in particular, in tasks requiring the formation of associations between units of information (Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Murray & Ranganath, 2007). At retrieval, the ventrolateral prefrontal cortex is thought to underlie controlled memory access via the specification of appropriate retrieval cues and the selection of goal-relevant information among competing representations (Badre & Wagner, 2007; Simons & Spiers, 2003). The dorsolateral prefrontal cortex, on the other hand, plays a role in post-retrieval monitoring and

evaluation of the retrieved content in relation to current task goals (Achim & Lepage, 2005; Dobbins, Foley, Schacter, & Wagner, 2002; Henson, Shallice, & Dolan, 1999).

The role of the lateral parietal cortex in episodic memory has also evoked growing interest in recent years (Cabeza, Ciaramelli, & Moscovitch, 2012; Moscovitch et al., 2016; Rugg & King, 2018; Wagner, Shannon, Kahn, & Buckner, 2005). The ventrolateral part of the parietal lobe, in particular the angular gyrus, typically exhibits increased activation during successful episodic memory retrieval (Rugg & Vilberg, 2013). According to attentional accounts, the ventrolateral parietal cortex may support "bottom-up" attentional processing, where salient aspects of information retrieved from memory trigger a shift in attentional focus toward the internal representation of the retrieved content (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; see also Wagner et al., 2005 for a similar proposal). In contrast, others have proposed a critical role for the lateral parietal cortex in representing or maintaining the retrieved information online during retrieval (Rugg & King, 2018; Shimamura, 2011; Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Vilberg & Rugg, 2008; Wagner et al., 2005). Specifically, the ventrolateral parietal cortex has been proposed to function as a buffer between episodic memory and executive control processes, where information retrieved from episodic memory is maintained online to inform decision making (Vilberg & Rugg, 2008; Wagner et al., 2005).

The multi-modal nature of representations maintained in the angular gyrus has been emphasized by others (Rugg & King, 2018; Shimamura, 2011). During retrieval, the angular gyrus may bind information across modality-specific cortical sites into an integrated episodic representation (Bonnici, Richter, Yazar, & Simons, 2016; Rugg & King, 2018; Shimamura, 2011; Yazar, Bergström, & Simons, 2017). The role of this region can thus be viewed as complementary to that of the hippocampus; while the hippocampus is thought to bind episodic details at encoding, and to facilitate the reinstatement of this information in cortical sites during retrieval, the angular gyrus may play a role in maintaining and representing the reinstated episodic content online until a mnemonic decision is reached. The representations maintained by the angular gyrus may, in particular, support the quality and richness of episodic remembering (Rugg & King, 2018; Simons et al., 2010). Lateral parietal lesions have been observed to be associated with reduced confidence of memory retrieval, as well as decreased frequency of subjectively 'remembering' a past event (Davidson et al., 2008; Simons et al., 2010),

leading to a proposal of this region supporting subjective aspects of episodic memory in particular (Ally, Simons, McKeever, Peers, & Budson, 2008; Simons et al., 2010; Yazar, Bergström, & Simons, 2014). In line with this proposal, neuroimaging studies have displayed activity in the angular gyrus to be associated with the subjective vividness and detail of retrieved memories in healthy adults (Bonnici et al., 2016; Kuhl & Chun, 2014; Tibon, Fuhrmann, Levy, Simons, & Henson, 2019; Vilberg & Rugg, 2007, 2009), providing further evidence for the contribution of this region to qualitative aspects of episodic memory retrieval.

Whether the angular gyrus may also play a role in the encoding of episodic memories is less clear. In contrast to increased activity observed for successful episodic memory retrieval, the ventrolateral parietal cortex typically displays diminished encoding activity for events that are subsequently remembered (Daselaar et al., 2009; Kim, 2011; Otten & Rugg, 2001; Uncapher & Wagner, 2009). Similar to retrieval activations, the negative association between encoding activity and later memory performance has been interpreted in light of "bottom-up" attentional processing, where a shift in attentional focus toward irrelevant stimuli or internal thoughts during memory acquisition may be detrimental for the successful encoding of new information (Cabeza et al., 2012; Uncapher & Wagner, 2009). A related proposal has been motivated by the notion that the angular gyrus is a part of the brain's default-mode-network (DMN) (Buckner, Andrews-Hanna, & Schacter, 2008). The DMN typically activates during periods of rest and internally-oriented cognition, but deactivates during externally-oriented cognitive tasks (Buckner et al., 2008; Buckner & DiNicola, 2019). Reduced encoding activations in this network may therefore reflect the successful engagement of externally-directed encoding processes and the suppression of internally-oriented cognition and irrelevant thoughts (Daselaar, Prince, & Cabeza, 2004; Daselaar et al., 2009; De Chastelaine, Mattson, Wang, Donley, & Rugg, 2015). However, some evidence has also demonstrated a positive relationship between encoding activity in the angular gyrus and subsequent memory retrieval (Maillet & Rajah, 2014b; Tibon et al., 2019), as well as a link between decreased univariate activity and greater specificity of patterns of activity representing the to-be-encoded information (Lee, Chun, & Kuhl, 2017). Thus, the exact role of the ventrolateral parietal cortex, and the angular gyrus more specifically, in episodic memory encoding remains to be clarified.

Age-related changes in the neural substrates of episodic memory

Functional neuroimaging studies investigating the neural basis of age-related episodic memory declines have typically found evidence for age-related reductions in activity in posterior brain regions, coupled with increases in the prefrontal cortex (Cabeza et al., 2004; Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Maillet & Rajah, 2014a; Wang & Cabeza, 2016). During encoding of visual stimuli, older adults commonly exhibit diminished encoding activity in both dorsal and ventral visual regions (Maillet & Rajah, 2014a; Park, Kennedy, Rodrigue, Hebrank, & Park, 2013; Wang & Cabeza, 2016). Furthermore, perceptual regions are reactivated to a lesser degree in older age during memory retrieval (McDonough, Cervantes, Gray, & Gallo, 2014), suggesting impoverished quality of both encoding and retrieval of perceptual details of previous experiences in older age. Age-related over-recruitment of the lateral prefrontal cortex, on the other hand, has been observed during both episodic encoding and retrieval (Cabeza et al., 2004; Gutchess et al., 2005; Morcom, Good, Frackowiak, & Rugg, 2003). The increases in prefrontal activity have been suggested to reflect compensation for the decreased activity in posterior brain regions (Davis et al., 2008), however, more recent evidence favours an interpretation of a decrease in neural efficiency or selectivity leading to the age-related activity increases (Morcom & Henson, 2018). Age-related reductions in prefrontal activity have also been observed during both memory encoding and retrieval, in particular in tasks posing greater demands on strategic processing (Dulas & Duarte, 2011, 2012). Indeed, age differences in frontal activity may be affected by task demands, with age-related increases evident when demands on cognitive processing are relatively low, but decreases observed for cognitively more challenging tasks (Reuter-Lorenz & Cappell, 2008).

Additionally, hippocampal encoding and retrieval activity has been observed to exhibit age-related declines (Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Dennis, Daselaar, & Cabeza, 2007; Dennis, Kim, & Cabeza, 2008). However, findings regarding age-related changes in this region have not been ubiquitous, and lack of age differences in activity associated with successful memory encoding and retrieval have also been reported (De Chastelaine et al., 2015; Vidal-Piñeiro et al., 2018; Wang, Johnson, De Chastelaine, Donley, & Rugg, 2016). This inconsistency in age-related functional changes in the hippocampus may be due to differences in the participant groups across studies. Emerging evidence from longitudinal studies suggests that a decline in

hippocampal recruitment may be characteristic of older individuals exhibiting memory decline (Persson et al., 2012), while individuals maintaining their memory abilities may display hippocampal activation levels comparable to those of the younger adults (Pudas et al., 2013). Thus, changes in memory-related activity in the hippocampus in older age may be sensitive to the cognitive status of the individual.

Although, the ventrolateral parietal cortex has received less attention in the aging literature in comparison to the medial temporal and prefrontal regions, age-related decreases in activity associated with successful memory retrieval are commonly observed in this region also (Angel et al., 2013; Daselaar et al., 2006; Duarte, Graham, & Henson, 2010; Duarte, Henson, & Graham, 2008). Parietal reductions appear to be particularly evident on tasks requiring retrieval of associative information in contrast to tasks relying on item memory (reviewed in Wang & Cabeza, 2016). Furthermore, while in younger adults greater deactivation of the ventrolateral parietal cortex typically predicts later successful remembering (Daselaar et al., 2009; Kim, 2011; Uncapher & Wagner, 2009), these negative subsequent memory effects are often reduced in older age (De Chastelaine et al., 2015; Maillet & Rajah, 2014a; Park et al., 2013), indicating age-related alterations in lateral parietal recruitment during both episodic memory encoding and retrieval.

The structural integrity of brain regions underpinning episodic memory has also been demonstrated to decline with advancing age (Fjell & Walhovd, 2010; Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012). The grey matter volume of the brain decreases with older age, affecting most notably the association cortices, in particular the prefrontal cortex (e.g., McGinnis, Brickhouse, Pascual, & Dickerson, 2011; Raz et al., 1997; Resnick, Pham, Kraut, Zonderman, & Davatzikos, 2003), whereas the primary sensory and motor areas are typically considered less vulnerable to age-related declines (e.g., Allen, Bruss, Brown, & Damasio, 2005; Raz et al., 2005). In the hippocampus, little grey matter loss may be observed until midlife, after which an accelerated decline appears to be evident (Coupé, Catheline, Lanuza, & Manjón, 2017; Nobis et al., 2019; Walhovd et al., 2005; Ziegler et al., 2012). In addition to age-related grey matter changes, the integrity of both intra- and inter-regional white matter tracts declines in older age (Bennett & Madden, 2014; Fjell & Walhovd, 2010). As for grey matter, the particular vulnerability of prefrontal white matter to age-related decline has been noted (Head et al., 2004; Salat, Tuch, Greve, et al., 2005; Salat, Tuch, Hevelone, et al., 2005), but

decreases are evident widespread across the brain (Barrick, Charlton, Clark, & Markus, 2010; Giorgio et al., 2010).

Alterations in the structural integrity of the brain have been shown to partly mediate age-related differences in brain function and cognition. Loss of regional grey matter volume has been demonstrated to partly explain age-related under-recruitment of occipital regions during episodic memory encoding, as well as age-related increases in lateral prefrontal and parietal activity observed during retrieval (Kalpouzos, Persson, & Nyberg, 2012). Variation in both grey and white matter integrity of the brain, most frequently in the hippocampal and prefrontal regions, has further been linked to behavioural differences in episodic memory performance across older individuals (e.g., Becker et al., 2015; Head, Rodrigue, Kennedy, & Raz, 2008; Hedden et al., 2016; Henson et al., 2016; Persson et al., 2012). Studies examining the neuroanatomical substrates of individual differences in episodic memory performance in older age will be discussed in more detail in Chapter 5.

Patterns of age-related episodic memory decline

On the behavioural level, age-related declines in episodic memory have often been attributed to a particular deficit in recollection-based retrieval (Howard, Bessette-Symons, Zhang, & Hoyer, 2006; Koen & Yonelinas, 2014, 2016; Prull, Dawes, Martin, Rosenberg, & Light, 2006). Recollection refers to the explicit retrieval of previous events and their associated qualitative details, such as the spatial or temporal context as well as perceptual details of a previous event, and is typically contrasted to familiarity; a sense of knowing that an item was previously encountered without the explicit retrieval of any associated qualitative details (Yonelinas, 2002; Yonelinas, Aly, Wang, & Koen, 2010). In prior studies, age-related decreases in recollection have been evident for both objective and subjective measures (e.g., Koen & Yonelinas, 2016; Prull et al., 2006). For instance, in source memory tasks where participants are asked to retrieve qualitative information about the context in which an item was studied, older adults typically display poorer memory for different source attributes, such as spatial location (Cansino et al., 2018; Chalfonte & Johnson, 1996; Kukolja, Thiel, Wilms, Mirzazade, & Fink, 2009), temporal order (Dumas & Hartman, 2003; Parkin, Hunkin, & Walter, 1995), speaker identity (Simons, Dodson, Bell, & Schacter, 2004), and the encoding task engaged with at study

(Morcom, Li, & Rugg, 2007). Furthermore, older adults typically report their memory retrieval to be less frequently accompanied by a subjective experience of recollection (Bastin & Van der Linden, 2003; Koen & Yonelinas, 2016; Perfect, Williams, & Anderton-Brown, 1995; Prull et al., 2006). Additionally, comparisons of retrieval performance for different test formats and the types of information to-be-remembered have demonstrated that age differences in episodic memory retrieval are greater for recall in contrast to recognition tasks (Craik & McDowd, 1987; Danckert & Craik, 2013; Rhodes, Greene, & Naveh-Benjamin, 2019), as well as for retrieval of associative relative to item information (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). While familiarity is considered sufficient to support the recognition of individual items as previously encountered, recollection is thought to be required for the retrieval of associative information as well as for cued and free recall (Yonelinas, 1997, 2002). The relative vulnerability of recall and associative retrieval to age-related declines is therefore consistent with a particular deficit in recollection-based retrieval in older age.

Whereas familiarity is thought to be underpinned by a continuous memory strength signal, episodic recollection is generally thought to operate in a thresholded manner (Yonelinas, 1994, 1999; but see Squire, Wixted, & Clark, 2007; Wixted, 2007). In particular, recollection has been proposed to reflect a 'some-or-none' threshold (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Onyper, Zhang, & Howard, 2010), where memory retrieval can sometimes categorically fail, leading to no relevant information being accessed from memory, but when it succeeds, the information retrieved from memory can vary both in terms of the amount and quality of details recollected (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Vilberg & Rugg, 2007, 2009). For instance, you may only have a vague memory of parking your bicycle somewhere outside of the shopping centre before heading in or precisely remember locking it onto a lamp post on the right hand side of the main entrance. In studies examining age-related changes in episodic recollection, the focus has typically been on examining the effects of ageing on the probability of successful recollection, whereas less is known about whether ageing may also have more subtle effects on the quality of information successfully recollected from memory.

Memory quality in ageing

Evidence from studies examining the effects of ageing on autobiographical memory; the memory for personally experienced past events, suggests that older adults' recollections of previous events may be diminished in the richness of specific details associated with a given memory (Addis et al., 2008; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; St. Jacques & Levine, 2007). In particular, older adults typically recall fewer *internal* details about a past event, along with an increase in *external* event details (Addis et al., 2008; Levine et al., 2002; St. Jacques & Levine, 2007). While internal details refer to episodic aspects of a previously experienced event, such as the place or time it occurred as well as the perceptual and emotional details associated with it, external details refer to semantic information not bound to the specific past event (Levine et al., 2002). Importantly, the age-related decreases in autobiographical memory detail cannot be fully accounted for by age-related changes in descriptive style (Gaesser, Sacchetti, Addis, & Schacter, 2011), suggesting a memory basis for this decline.

In addition to reductions in the amount of information correctly retrieved, older adults typically also display an increased tendency to falsely recognize novel items as previously studied (reviewed in Devitt & Schacter, 2016). These increases are particularly evident in tasks requiring the discrimination of studied items from related material, such as novel pictures from the same category as studied stimuli (e.g., Koutstaal & Schacter, 1997) or words semantically associated with a studied word list (e.g., Kensinger & Schacter, 1999; Norman & Schacter, 1997). This age-related increase in susceptibility to false recognition has been proposed to reflect an increased reliance on gist-like representations of previous events, while the specific details disambiguating similar events from each other may be encoded and/or retrieved to a lesser degree in older age (Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997). These results suggest that the quality of event-specific memory traces may be impoverished in older age, leading to increases in false recognition of novel items that share similar features with previously studied items.

Age-related decreases in memory specificity are also implied by age-related increases in false recognition observed in mnemonic discrimination paradigms (Reagh et al., 2014; Stark, Yassa, Lacy, & Stark, 2013; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Trelle et al., 2017; Yassa et al., 2011). In these paradigms, participants are asked to make fine-

grained distinctions between studied material and perceptually similar lure items, such as two similar objects or spatial locations (Reagh et al., 2014; Stark, Yassa, & Stark, 2010; Stark et al., 2013). While older adults are often able to correctly recognize studied items as 'old', and to identify unrelated novel items as 'new', they typically exhibit impairments in discriminating between studied and similar lure items (Stark et al., 2013; Toner et al., 2009; Trelle et al., 2017; Yassa et al., 2011). Indeed, greater dissimilarity of the perceptual input appears to be required for older adults to be able to successfully distinguish between studied and novel material, consistent with the notion that an age-related deficit in pattern separation might underlie these reductions (Yassa et al., 2011; Yassa & Stark, 2011). The age-related mnemonic discrimination deficits have been observed for a variety of materials, including everyday objects (Stark et al., 2013; Toner et al., 2009; Yassa et al., 2011), scenes (Stark & Stark, 2017), and object locations (Reagh et al., 2016, 2014), but importantly also for stimuli not sharing any conceptual overlap, such as novel abstract objects (Pidgeon & Morcom, 2014) and phonologically related words (Ly, Murray, & Yassa, 2013). The age-related increases in false recognition thus do not appear to be solely driven by the semantic relatedness of the studied and lure items but can also be induced by perceptual overlap. Indeed, mnemonic discrimination deficits in older age have been linked to perceptual discrimination ability for abstract object stimuli (Trelle et al., 2017), suggesting that these declines may partly arise from age-related deficits in the quality of perceptual representations.

In addition to the changes observed on the behavioural level, computational accounts of cognitive ageing have proposed reduced specificity, or differentiation, of neural representations to underlie age-related cognitive decline (Li, Lindenberger, & Sikström, 2001; Li, Lindenberger, & Frensch, 2000; Li & Sikström, 2002). Age-related decreases in catecholaminergic, in particular dopaminergic, neuromodulation have been proposed to decrease the signal-to-noise ratio of neural signalling, resulting in less distinctive neural representations in older age (Li et al., 2001; Li & Rieckmann, 2014). This model has further been demonstrated to account for several cognitive changes typically associated with older age, including deficits in associative memory, susceptibility to interference, and increases in both intra- and inter-individual behavioural variability (Li et al., 2001; Li et al., 2000; Li, Naveh-Benjamin, & Lindenberger, 2005).

Findings supporting age-related dedifferentiation, or loss of specificity, of neural activity have been observed in several functional neuroimaging studies. For instance, on a

process-level, the brain activity underlying autobiographical versus episodic memory retrieval (St-Laurent, Abdi, Burianová, & Grady, 2011), as well as implicit versus explicit memory (Dennis & Cabeza, 2011), has been observed to exhibit greater overlap in older in comparison to younger adults. Furthermore, the selectivity of neural responses to different categories of visual stimuli (e.g., faces vs. houses) and to individual exemplars from the same category (e.g., two different faces) has been demonstrated to decrease in older age during both mnemonic and perceptual processing (Carp, Park, Polk, & Park, 2011; Goh, Suzuki, & Park, 2010; Park et al., 2004; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014; Trelle, Henson, & Simons, 2019; Zheng et al., 2018). At perception, neural responses in visual regions display reduced category- and item-specificity (Carp et al., 2011; Goh et al., 2010; Park et al., 2004; Park, Carp, Hebrank, Park, & Polk, 2010), with the degree of this neural dedifferentiation correlating with individual differences in cognitive performance across older adults (Park et al., 2010). Similarly, age-related decreases in the specificity of both category- and item-specific neural representations have been observed during encoding and retrieval of episodic memories (Abdulrahman, Fletcher, Bullmore, & Morcom, 2017; Bowman, Chamberlain, & Dennis, 2019; St-Laurent et al., 2014; Trelle et al., 2019; Zheng et al., 2018, but see Wang et al., 2016). During memory encoding, the quality of item-specific neural representations in ventral visual regions has been shown to exhibit age-related decline (Trelle et al., 2019; Zheng et al., 2018) and to correlate with recognition performance across older adults (Zheng et al., 2018). On the category level, the specificity of neural representations corresponding to different visual stimulus categories has been observed to decline across cortical regions and to account for age differences in the specificity of neural reinstatement during retrieval (Johnson, Kuhl, Mitchell, Ankudowich, & Durbin, 2015). Others have observed more pronounced effects of age on neural differentiation during memory retrieval. For instance, Abdulrahman et al. (2017) observed no age differences in the quality of neural representations corresponding to two different encoding tasks during memory formation, but rather a reduced specificity of reinstatement of this information during retrieval in older age. Similarly, St-Laurent and colleagues (2014) observed reduced specificity of neural reinstatement of encoding activity patterns corresponding to individual video clips that could not be explained by age differences in neural specificity at encoding. The specificity of neural reinstatement was further observed to correlate with memory performance in both young and older adults in this study. Thus, although the evidence is not entirely consistent, the quality of

neural representations during both memory encoding and retrieval appears to exhibit age-related declines and to be associated with individual differences in memory performance in older age.

Distinguishing the success and precision of episodic memory retrieval

The evidence described above highlights the possibility that age-related memory reductions may at least in part result from declines in the quality and specificity of information retained in memory. However, thus far studies have predominantly relied on categorical measures of memory performance or participants' subjective reports to investigate age-related changes in memory quality. Typically, these paradigms are unable to separate memory quality from other aspects of memory retrieval. To obtain a more direct behavioural measure of memory fidelity, more recent studies in younger adults have begun to employ continuous measures of memory performance, in which participants recreate attributes of studied items, such as their location or colour, using a continuous response scale (e.g., Brady, Konkle, Gill, Oliva, & Alvarez, 2013; Harlow & Donaldson, 2013; Richter, Cooper, Bays, & Simons, 2016). This approach enables more fine-grained assessment of retrieval performance, as well as the segregation of different types of memory errors by modelling the distribution of participants' retrieval errors across trials (e.g., Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008). Most commonly, data from these types of continuous report tasks has been analysed with a two-component mixture model consisting of a von Mises distribution (i.e., the circular equivalent of a Gaussian distribution) and a circular uniform distribution (e.g., Brady et al., 2013; Richter, Cooper et al., 2016). This model assumes that on a proportion of trials the participant successfully retrieves some information about the cued item attribute. Retrieval from memory is assumed to be noisy, leading to a Gaussian distribution of recall errors centred at a mean error of zero degrees from the target feature value. In contrast, on some trials, memory retrieval is assumed to fail to bring any diagnostic information about the target to mind, leading to the participant selecting a random location on the response wheel. Such guess responses are assumed to be uniformly distributed around the circular space, captured by the second mixture component. By fitting this mixture model to participants' retrieval errors, two parameters capturing two theoretically distinct sources of memory error can be estimated: the probability of

successful memory retrieval (i.e., the proportion of responses stemming from the target von Mises distribution) and the precision of memory retrieval (i.e., the concentration, or "peakedness", of the von Mises distribution).

While this model was originally developed for analysis of continuous report data in working memory (Zhang & Luck, 2008), more recent studies employing similar paradigms in long-term memory have demonstrated that retrieval from long-term memory can also be characterized by a combination of memory failures leading to random guessing and variability in the fidelity with which memories are successfully retrieved (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Richter, Cooper et al., 2016). Although the probability of successful retrieval and memory precision have been observed to correlate across participants, the majority of variance in each measure is nevertheless unaccounted for by the other, suggesting that they may capture at least partially separable aspects of memory performance (Richter, Cooper et al., 2016). These two aspects of memory retrieval have also been shown to be associated with different metacognitive judgements; with participants being able rate their confidence separately for the success and the precision of their memory retrieval (Harlow & Yonelinas, 2016). Thus, in addition to being objectively dissociable (e.g., Harlow & Donaldson, 2013; Richter, Cooper et al., 2016), the success and precision of memory retrieval appear to be associated with distinct phenomenological characteristics (Harlow & Yonelinas, 2016).

Further evidence supporting the dissociability of the success and precision of episodic memory retrieval has been provided by studies demonstrating that experimental manipulations can selectively affect each of these aspects of memory retrieval. For instance, while engaging in retrieval practice has been demonstrated to enhance the later probability of successfully retrieving a memory, the precision with which the memory is recalled appears to be unaffected (Sutterer & Awh, 2016). In contrast, negative emotional stimuli have been observed to enhance the precision, but not the success, of later memory retrieval (Xie & Zhang, 2017). The reinstatement of positive and negative encoding contexts has also been demonstrated to have opposing effects on the success and precision of episodic memory retrieval (Xie & Zhang, 2018). While the reinstatement of a positive encoding context has been shown to lead to increases in the probability of successful memory retrieval, reinstatement of a negative context increases the precision of retrieved memories (Xie & Zhang, 2018). Over shorter term, the degree of perceptual overlap between studied items and subsequently presented interfering stimuli has further

been observed to differentially affect the probability of successful memory retrieval and memory precision (Sun et al., 2017). Thus, the probability of successful memory retrieval and memory fidelity appear to be differentially sensitive to experimental manipulations affecting encoding (Xie & Zhang, 2017), post-encoding (Sun et al., 2017), and retrieval (Xie & Zhang, 2018) processes.

Moreover, impairments in episodic memory performance in different populations have been attributed to declines in distinct components of memory retrieval. In a recent study, high-functioning individuals with autism spectrum disorder were observed to exhibit decreases in successful memory retrieval, while no evidence for comparable declines in memory precision was observed (Cooper et al., 2017). In contrast, individuals with medial temporal lobe resection have been observed to display reductions in memory precision, along with intact probability of successful memory retrieval (Nilakantan, Bridge, VanHaerents, & Voss, 2018). Thus, the success and precision of memory retrieval appear to be differentially affected not only by experimental manipulations, but also by neurological condition.

In addition to being separable on the behavioural level, the success and precision of episodic memory retrieval have been demonstrated to rely on distinct neural substrates (Richter, Cooper et al., 2016). In a recent fMRI study, Richter, Cooper and colleagues (2016) observed hippocampal retrieval activity to predict the binary success of memory retrieval on a trial-wise basis, while activity in the angular gyrus predicted trial-by-trial estimates of the graded precision of memory retrieval. In line with these findings, transcranial magnetic simulation of the lateral parietal cortex has been observed to increase the precision of object location retrieval, while not affecting the probability of successful memory retrieval (Nilakantan, Bridge, Gagnon, VanHaerents, & Voss, 2017). However, it should be noted that this finding was suggested to reflect modulation of the wider hippocampal-posterior medial memory network, rather than the lateral parietal cortex specifically (Nilakantan et al., 2017). Indeed, the connectivity between the angular gyrus and regions of both the posterior-medial and anterior-temporal memory networks has been observed to increase with greater precision of memory retrieval (Cooper & Ritchey, 2019), highlighting the contribution of a more distributed network of brain regions to memory precision.

In addition to the lateral parietal cortex, others have emphasized a critical role for the medial temporal lobes in the retrieval of precise memories (Montchal, Reagh, & Yassa, 2019; Nilakantan et al., 2018; Stevenson et al., 2018; Yonelinas, 2013). For instance, gamma power in the hippocampal CA1 subfield has been shown to correlate with the precision of memory retrieval, but also to predict retrieval success (Stevenson et al., 2018). Furthermore, Montchal and colleagues (2019) recently observed that activity in the lateral entorhinal cortex, perirhinal cortex and the hippocampus increased with greater precision of temporal memory retrieval. However, similar effects were also reported in regions beyond the medial temporal lobes, specifically the medial prefrontal cortex, angular gyrus and precuneus (Montchal et al., 2019). Furthermore, Montchal and colleagues (2019) only investigated activity associated with a categorical distinction between memories retrieved with low versus high precision and did not compare these effects to the difference in activity for successful versus unsuccessful retrieval. It is therefore unclear whether activity in all of the regions above predicts the precision of memory retrieval on a continuous scale (as demonstrated for angular gyrus in Richter, Cooper et al., 2016) or whether it is sensitive to a more coarse distinction between high and low fidelity memory retrieval and whether these effects are distinct from those observed for successful versus unsuccessful retrieval.

Thus, emerging evidence suggests that the mixture modelling approach may be useful for more detailed characterization of episodic memory on both the cognitive and neural level. However, it should be noted that the degree to which the two parameters of memory performance obtained from this model reflect distinct psychological constructs has been questioned (Schurgin, Wixted, & Brady, 2018). Recently, Schurgin et al. (2018) provided evidence to suggest that a simpler one-parameter model may better account for the distribution of retrieval errors in both working and long-term memory. In particular, Schurgin et al. (2018) argued that after taking into account the non-linear relationship between physical and psychological stimulus spaces, performance in a continuous report task can be described by a signal detection process, with one parameter capturing memory strength. Similarly, in WM, neural-level models have proposed changes in the gain of neuronal populations encoding stimulus features to account for recall errors resembling both memory imprecision and guessing (Bays, 2014, 2015; Taylor & Bays, 2019).

While in WM increasing numbers of studies have sought to evaluate mathematical models accounting for the distribution of recall errors in continuous report tasks (e.g., Bays et al., 2009; Fougnie, Suchow, & Alvarez, 2012; van den Berg, Shin, Chou, George, & Ma, 2012; Zhang & Luck, 2008), to date the existing literature on long-term memory has predominantly relied on the von Mises and uniform mixture model described previously (e.g., Brady et al., 2013; Cooper & Ritchey, 2019; Richter et al., 2016; Stevenson et al., 2018; Xie & Zhang, 2017). Although debate regarding the theoretical interpretation of the mixture model parameters is emerging (Schurgin et al., 2018), they nevertheless provide a good descriptive account of the distribution of retrieval errors in continuous report paradigms (Bays & Taylor, 2019). Thus, to facilitate the comparison of the current findings to existing research on LTM in younger populations (e.g., Brady et al., 2013; Richter, Cooper et al., 2016), as well as to findings from short-term memory in older age (Noack, Lövdén, & Lindenberger, 2012; Peich, Husain, & Bays, 2013), this two-component mixture model will also be employed for data analysis in the experiments presented in the current thesis. In Chapters 2-3, I will further compare this model to a more complex model assuming a further component of retrieval error: non-target reports resulting from misbinding of object features (Bays et al., 2009; Peich et al., 2013).

Thesis overview

The research presented in the current thesis aims to provide more detailed insight into the specific nature of age-related memory impairments; specifically whether they may result from a decreased probability of successfully retrieving information from memory or from reductions in the quality, or precision, of the retrieved information. Across four experimental chapters, I use continuous measures of memory retrieval, which have been successfully employed to dissociate the success and precision of memory retrieval in younger adults (e.g., Brady et al., 2013; Harlow & Donaldson, 2013; Richter, Cooper et al., 2016), to examine the effects of healthy ageing on these two components of episodic memory retrieval and their cognitive and neural underpinnings.

The two behavioural experiments described in Chapter 2 aimed to examine the effects of healthy ageing on the success and precision of memory retrieval for different features of episodic memories. In these experiments, young and older adults encoded visual object displays, and at retrieval reconstructed different features (object location, colour and

orientation) of the encoded displays using a continuous response dial. Findings across the two experiments provided consistent evidence for an age-related decline in memory precision across retrieval of different object features, whereas significant age-related reductions in the probability of successful memory retrieval were observed in the object orientation condition only. The age-related declines in memory precision for object locations were further disproportionate to any age differences in the probability of successful memory retrieval in both Experiment 1 and 2, suggesting that this aspect of memory retrieval may be more sensitive to age-related decline.

The behavioural experiment described in Chapter 3 sought to assess whether the age-related reductions in mnemonic precision are specific to long-term memory processes or may arise from age-related decreases in the fidelity of perceptual or working memory representations. In this experiment, young and older adults completed a perceptual, working memory (WM) and long-term memory (LTM) version of the continuous report task used in Chapter 2, but this time assessing object colour only. Interestingly, results from this experiment demonstrated age-related decreases in response precision in all three tasks, suggesting that the age-related declines in representational fidelity were not limited to long-term memory retrieval. Examining the relationship between individual differences in the precision of perception, WM and LTM further indicated a significant relationship between the precision of working memory and long-term memory retrieval in older age. However, significant age-related reductions in the precision of long-term memory retrieval still persisted after controlling for variability in the fidelity of both perception and working memory. Thus decreases in the precision of WM appear to play a role in the age-related reductions in LTM memory precision, but cannot solely account for these decreases, suggesting additional age-related degradation of information retained in LTM.

The findings from Chapter 3, demonstrating that WM precision contributes but does not fully explain the age-related loss of LTM precision, highlight the possibility of both encoding and retrieval contributions to the age-related declines. In Chapter 4, I used functional magnetic resonance imaging (fMRI) in combination with the continuous report task to more directly assess the integrity of encoding and retrieval processes underlying the success and precision of episodic memory retrieval. In this experiment, both the probability of successful memory retrieval and memory precision were observed to be significantly reduced in the older group. These behavioural decreases were

accompanied by age differences in both encoding and retrieval activity associated with each memory component. During retrieval, older adults demonstrated reduced hippocampal activity associated with successful memory retrieval, and a reduced relationship between activity in the angular gyrus and the precision of memory retrieval. This is consistent with previous evidence from younger adults implicating these two regions as underlying distinct aspects of retrieval performance (Richter, Cooper et al., 2016). Furthermore, while encoding activity predicting both later memory accessibility and precision was reduced in the older group in the fusiform gyrus, age-related reductions in the prefrontal cortex were observed only for activity associated with the later success of memory retrieval. These results thus highlight distinct encoding and retrieval contributions to age-related decreases in the success and precision of memory retrieval.

In the experiments presented in Chapters 2-4, older adults displayed considerable variability in both the probability of successful memory retrieval and the precision of the retrieved information. In Chapter 5, I sought to examine the contribution of structural integrity of the brain regions underpinning episodic memory to this variability. Specifically, I used voxel-based morphometry (VBM) to examine the relationship between variation in regional grey matter volume and individual differences in the success and precision of memory retrieval in older age. Consistent with findings from Chapter 4, suggesting a role for the angular gyrus in memory precision deficits in older age, the results from this experiment demonstrated a positive relationship between grey matter volume in the angular gyrus and the precision of memory retrieval in older age. Importantly, this relationship persisted after controlling for variability in the probability of successful retrieval, indicating a contribution over and above any relationship shared with retrieval success.

Together, the findings from the four experimental chapters highlight the sensitivity of memory precision to age-related decline and provide evidence to suggest that both distinct and shared neurocognitive factors contribute to age-related decreases in the success and precision of episodic memory retrieval. In Chapter 6, I will present a discussion of these findings in relation to previous accounts of age-related memory deficits, identifying outstanding questions and providing directions for further research.

Chapter 2: Distinguishing the effects of healthy ageing on the success and precision of episodic memory retrieval

Episodic memory declines in older age, but it is unresolved whether these declines may reflect a reduced probability of successfully retrieving information from memory, or more qualitative changes in the fidelity with which memory traces can be encoded into and retrieved from memory. The two behavioural experiments presented in this chapter used continuous measures of episodic memory retrieval in combination with mixture modelling of participants' retrieval errors to distinguish between these two potential accounts of age-related memory deficits. In each experiment, young and older participants encoded stimuli displays consisting of everyday objects varying along different perceptual features (e.g., location, colour and orientation) in a circular space. At test, participants recreated the features of the studied objects using a continuous response dial. Results from the first experiment provided evidence for an age-related reduction in the precision of object-location retrieval, whereas no significant age differences in the probability of successful location retrieval were observed. In the second experiment, I examined whether age-related declines in mnemonic precision may extend to other types of information retrieved from long-term memory. Results from the second experiment displayed consistent age-related declines in memory precision across different object features (location, colour, orientation), whereas significant age differences in the probability of successful memory retrieval were evident in the orientation condition only. Together, the findings from this chapter provided evidence for age-related declines in the precision of episodic memory retrieval, and suggest that healthy ageing may differentially affect distinct components of episodic memory.

Introduction

In studies investigating age-related episodic memory changes, participants' memory performance is typically measured using categorical response options, for example by asking a participant to judge whether a test stimulus has been previously encountered ("old") or not ("new"). While affording categorical distinctions between successful and unsuccessful memory retrieval, these types of measures are unable to fully capture the multifaceted nature of episodic recollection. Indeed, increasing evidence suggests that instead of an "all-or-none" process, varying only in the dichotomy between successful

and unsuccessful retrieval, episodic recollection likely operates in a "some-or-none" manner, where the quality, or precision, of the successfully retrieved information can vary on a graded scale (Harlow & Donaldson, 2013; Onyper et al., 2010; Yonelinas & Parks, 2007). To investigate these more fine-grained variations in episodic memory, recent studies have begun to utilize continuous measures of retrieval performance, where participants are asked to reconstruct aspects of the studied stimuli using a continuous, analogue scale. Studies employing these types of tasks in younger adults have demonstrated the success and precision of memory retrieval to be separable components of long-term memory (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Richter, Cooper et al., 2016), which can be selectively affected by experimental manipulations (e.g., Sutterer & Awh, 2016; Xie & Zhang, 2017), brain stimulation (Nilakantan et al., 2017), and developmental condition (Cooper et al., 2017). Furthermore, these two aspects of episodic memory have been observed to rely on dissociable brain regions during memory retrieval, with retrieval success scaling with hippocampal activity and retrieval precision with activity in the angular gyrus (Richter, Cooper et al., 2016). Given the dissociable neurocognitive profiles of these two subcomponents of episodic memory retrieval in younger adults, it is possible that the success and precision of memory retrieval may also be differentially sensitive to age-related cognitive decline.

Prior studies have typically focused on assessing age-related changes in the success of episodic memory retrieval (e.g., Cansino et al., 2018; Naveh-Benjamin, 2000; Simons et al., 2004). However, in addition to decreases in successful memory retrieval, several strands of evidence suggest that memory function in older age might at least to some extent be constrained by reductions in the quality and specificity of information retained in memory. For instance, age-related increases in false memory have been interpreted as resulting from an increased reliance on gist-like representations of previous events coupled with diminished encoding and retrieval of specific stimuli details (Dennis, Kim, & Cabeza, 2007; Dennis, Kim, et al., 2008; Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997). Previous research has also demonstrated greater age differences in episodic recollection when participants are required to retrieve more detailed information about the study event (Luo & Craik, 2009), and that older adults tend to recall less specific details of events from their personal pasts in comparison to younger adults (Addis et al., 2008; Levine et al., 2002). Furthermore, although older adults commonly display a preserved ability to recognise studied items as previously encountered, and to

identify dissimilar novel items as new, mnemonic discrimination of studied items from perceptually similar lures is typically impaired in older age (Stark et al., 2013; Toner et al., 2009; Yassa et al., 2011), implying a reduced level of detail of the retained memory representations in older age.

In addition to these behavioural findings, age-related reductions in memory fidelity would be predicted by previous accounts proposing increased neural noise (i.e., increased uncertainty of neural signalling) to lead to more variable and less precise perceptual and cognitive representations in older age (e.g., Welford, 1958, 1981). Consistent with these accounts, age-related increases in discriminal dispersion have previously been demonstrated for short-term memory retrieval (Allen, Kaufman, Smith, & Propper, 1998; Noack et al., 2012), and modelled by age-related increases in internal noise (Allen et al., 1998). More recent computational models have proposed age-related changes in neuromodulation to underlie decreased neural signal-to-noise ratio leading to less precise representations (Li, Lindenberger, & Sikström, 2001; Li & Sikström, 2002). In line with these accounts, neuroimaging studies have demonstrated age-related decreases in the quality and specificity of neural representations corresponding to different stimuli or task contexts during both encoding and retrieval of episodic memory (Abdulrahman et al., 2017; Bowman et al., 2019; St-Laurent et al., 2014; Trelle et al., 2019; Zheng et al., 2018), potentially constraining the precision with which memory representations can be formed as well as recovered in older age.

Despite proposals of reduced memory quality in ageing, the majority of previous behavioural investigations have tended to rely on categorical measures of memory performance, which are unable to discern whether age-related performance reductions are due to changes in the success or precision of memory retrieval. For instance, a failure to correctly retrieve a specific study detail in a categorical memory task could reflect a failure to access the information in question, or decreased fidelity of the retrieved information, leading to selection of an incorrect retrieval response. In working memory (WM) research, continuous report tasks, providing a more direct measure of memory fidelity, have been fruitful in elucidating the specific components of short-term memory degradation in older age, revealing age-related decreases in mnemonic precision and increases in binding errors, whereas no age differences in the success of memory retrieval were detected (Peich et al., 2013). This approach has recently been extended to investigate age-related changes in object-spatial location binding in long-term memory,

suggesting that the precision of LTM retrieval might similarly be sensitive to age-related decline (Nilakantan et al., 2018).

The experiments presented in the current chapter employed a continuous report paradigm, adapted from recent work in younger adults (Richter, Cooper et al., 2016), to better characterize the nature of age-related changes in episodic memory. Specifically, I aimed to distinguish whether age-related memory decreases may reflect a reduced probability of successfully retrieving information from memory, and/or decreased precision of the retrieved information. In two experiments, healthy younger and older participants encoded visual stimulus displays consisting of everyday objects varying along different perceptual features in a circular space. At test, participants were asked to recreate the features of the studied objects using a continuous response dial, allowing for detailed assessment of retrieval performance. Fitting a mixture model (Bays et al., 2009; Zhang & Luck, 2008) to participants' retrieval error data allowed the estimation of both the probability of successful retrieval and the precision of the retrieved information from the same data, distinguishing between these two alternative sources of memory errors in older age. In addition to these two memory components, I also examined whether binding errors (i.e., mistakenly reporting the probed feature of another, uncued, item from the same study display) may contribute to memory performance in either age group. These types of errors have been demonstrated to contribute to age differences in short-term memory (Peich et al., 2013), suggesting a possible role for misbinding of object features in the age-related long-term memory reductions also.

The first experiment presented in the current chapter examined the effects of healthy ageing on the success and precision of object location retrieval. While no significant age differences in the probability of successful memory retrieval were observed, this experiment revealed significant age-related declines in the fidelity with which object locations were retrieved from memory. In the second experiment, I sought to further assess whether these age-related deficits in memory precision were specific to the retrieval of object locations or evident across different types of information retained in long-term memory. In the second experiment, participants encoded and retrieved objects varying in three different perceptual features (location, colour and orientation) in a circular space. Age-related deficits in memory precision were consistently observed across the feature conditions, whereas significant age-related reductions in the rate of successful memory retrieval were evident in the orientation condition only. Orientation

was also the condition exhibiting the lowest retrieval success in the younger adults, suggesting a potential effect of task difficulty.

General methods

In each experiment, participants encoded object stimulus displays and later recreated the features (location, colour, or orientation) of the studied objects as precisely as they could using a 360-degree response dial. Both studied feature values and participants' responses mapped onto a circular space, enabling the distinction between the probability of successful memory retrieval (i.e., probability of retrieving some information about the correct target feature value) and the precision of retrieved information (i.e., variability in successful target retrieval) with a mixture modelling approach derived from working memory research (Bays et al., 2009; Zhang & Luck, 2008), but more recently also applied to long-term memory studies (e.g., Brady et al., 2013; Richter, Cooper et al., 2016). At the beginning of each experiment, participants completed a demographic questionnaire and the Shipley Institute of Living Vocabulary Scale (SILVS) (Zachary & Shipley, 1986) measure of crystallized intelligence. To exclude any older participants displaying signs of cognitive impairment, the older adults additionally completed the Montreal Cognitive Assessment (MoCA) (Nasreddine et al., 2005), a standardized 10-minute pen-and-paper screening tool for detection of mild cognitive impairment. Before each of the continuous report tasks, participants completed practice trials of the task.

Participants

Participants for both experiments were native English-speakers who reported normal or corrected-to-normal vision, no colour blindness, and no current or historical diagnosis of any psychiatric or neurological condition, or learning difficulty. Participants were recruited via online and community advertisements and a volunteer database at the Memory Lab of the University of Cambridge. Older participants scored in the healthy range (26 or above) on the MoCA (Nasreddine et al., 2005). Participants gave written and informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee, and were compensated for their participation at the rate of £7.50 per hour.

Data analysis

Retrieval error on each trial was calculated as the angular difference between participants' response value and the target feature value (0 ± 180 degrees). To distinguish between different sources of memory errors (i.e., reduced retrieval success vs. reduced memory precision), a probabilistic mixture model was fitted to participants' error data (Bays et al., 2009; Zhang & Luck, 2008) (code available at http://www.paulbays.com/code/JV10/index.php) (see Figure 1A). In this model two sources of error contribute to participants' performance: variability, that is, noise, in reporting the correct feature value when information about the target has been retrieved, and a proportion of trials where memory retrieval has failed and responses reflect random guessing. These two sources of error are modelled by two components: a von Mises distribution (circular equivalent of a Gaussian distribution) centred at a mean error of zero degrees from the target value, with a concentration *K*, and a circular uniform distribution with a certain probability *pU*. The concentration parameter, *K*, of the von Mises distribution captures variability in successful target retrieval (higher values reflect higher precision), and the probability of the uniform distribution, *pU*, reflects the likelihood of random guess responses, evenly distributed around the circular space. The probability of successful memory retrieval (*pT*) can be estimated as the probability of responses stemming from the target von Mises distribution ($pT = 1 - pU$). Maximum likelihood estimates of the success (*pT*, probability of responses stemming from the target von Mises distribution) and precision (*K*, concentration of the von Mises distribution) of memory retrieval were obtained for each participant and experimental condition using an Expectation-Maximization (EM) algorithm (Bays et al., 2009). A range of initial parameter values were used to ensure that the global maxima parameter estimates were obtained (Bays et al., 2009). The probability of uniform (*pU*) and target (*pT*) responses were constrained between 0 and 1. Kappa had a minimum value of 0, corresponding to a flat, or uniform, distribution, but no upper bound.

This mixture model has previously been shown to best characterize younger adults' long-term memory performance in an equivalent task (Richter, Cooper et al., 2016). To ensure that the model also provided the best fit for the older adults' data, I further compared this model to two alternative models (see Figure 1B). The first of these alternative models consisted of a target von Mises distribution alone. This model is characterized by one parameter corresponding to concentration (*K*) of the von Mises distribution and assumes

that on all trials the participant successfully retrieves some information about the target feature value, with a variable degree of noise. The second alternative model consisted of a von Mises distribution centred at the target feature value, a circular uniform distribution, as well as von Mises distributions centred at the non-target feature values from the same encoding display. In this model, participants' performance reflects variability in successful retrieval, random guessing, as well as non-target errors (i.e., mistakenly reporting a cued feature value of another item from the same study display) (Bays et al., 2009). In addition to the probability of successful memory retrieval (*pT*), the probability of guessing (*pU*), and the precision (*K*) of successful memory retrieval, this model includes an additional parameter capturing the probability of non-target reports (*pNT*). Note that this model assumes that non-target features are recalled with similar precision as the target features (Bays et al., 2009).

Consistent with previous results from younger adults (Richter, Cooper et al., 2016), a combination of the target von Mises and uniform distributions was found to fit the current data better than either of these two alternative models for both the younger and older adults, as indicated by a lower Bayesian information criterion (BIC) for this model in comparison to the two alternative models (see Tables 2 and 4). This model was therefore fitted to participants' data in each experiment. Effects of group and task condition on the mean parameter estimates were assessed by t-tests and ANOVAs. Greenhouse-Geisser correction was applied when the assumption of sphericity was not met in the ANOVAs. For statistical analyses conducted on individual participant parameter estimates, outliers were excluded with a pre-defined criterion of a retrieval success (*pT*) or precision (*K*) estimate more than three standard deviations from the group mean.

Due to the relatively small number of trials per feature condition in the second experiment, I further replicated all analyses by modelling performance across all trials and participants in each age group and task condition (minimum number of trials per condition via this method was 1920 trials). This approach is less susceptible to noise in parameter estimates in the cases of individual participants with poor performance (cf., Cooper et al., 2017). For the aggregate analyses, the statistical significance of the observed age differences on each parameter estimate were assessed via permutation tests, where participants' data was remodeled over 1000 iterations of random participant-to-group assignments. To obtain a two-tailed *p*-value, the absolute observed group

difference was compared to the distribution of permuted group differences across the iterations.

Model fits were visualized with MATLAB MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013; available at http://visionlab.github.io/MemToolbox/). Two-tailed *p*-values are reported for all analyses. For any non-significant findings observed in the main analyses, I performed complementary Bayesian analyses to assess the strength of evidence in favour of the null hypothesis. Bayes Factors were calculated with JASP version 0.10.2 (JASP team, 2019) using default priors (for t-tests a Cauchy distribution with a scale parameter (r) = .707, for ANOVAs a multivariate Cauchy distribution with r = .50, both centred at zero). A Bayes factor (BF_{01}) of > 3 in favour of the null hypothesis was interpreted as positive evidence for the null hypothesis (Jeffreys, 1961). For the model comparison analyses, a BIC difference > 2 was interpreted as positive evidence for the preferred model (Raftery, 1995).

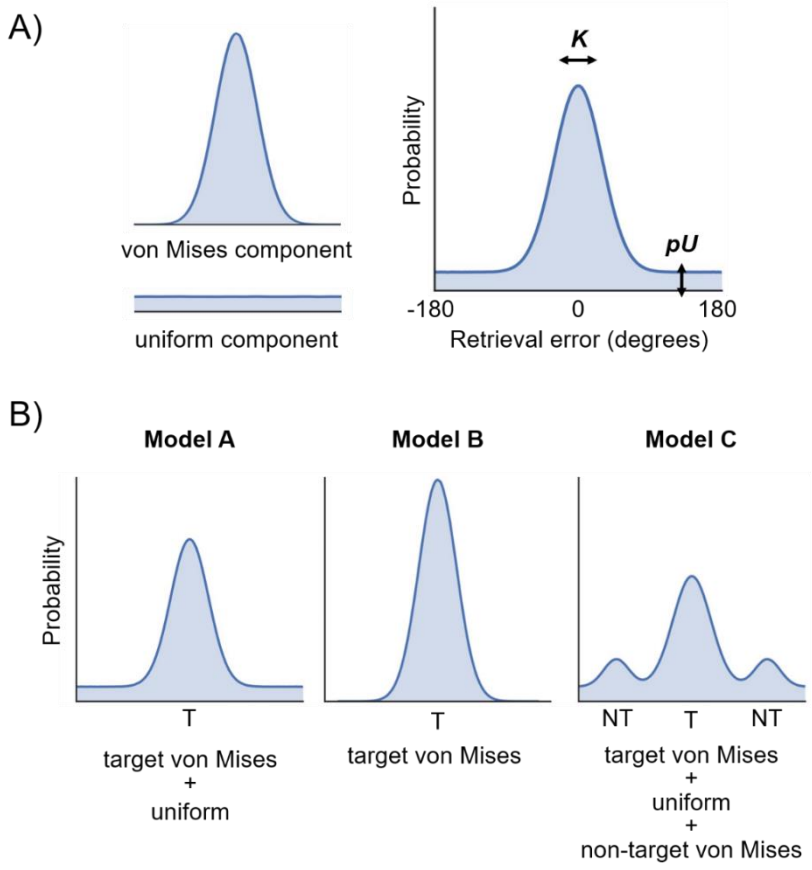

Figure 1. A) The probabilistic mixture model fitted to participants' retrieval error data consisted of a von Mises distribution (circular equivalent of a Gaussian distribution)

centred at the target feature value (with a concentration, *K*), and a circular uniform distribution (with a probability, *pU*). Success of memory retrieval was defined as the probability of responses stemming from the target von Mises distribution (*pT*), and precision as the concentration (*K*) of the von Mises distribution. B) This model (Model A) was compared to two alternative models (Models B and C) capturing participants' performance in each experiment. Model B consisted of a von Mises distribution centred at the target (T) feature value only. Model C included a target von Mises and uniform distribution, as well as von Mises distributions centred at the non-target (NT) features values from the same encoding display.

Experiment 1

The first experiment of the current chapter aimed to examine whether age-related declines in episodic memory are attributable to reduced probability of successful memory retrieval, or to reduced precision of the retrieved memories. Young and older adults completed a continuous object location report task requiring participants to encode stimulus displays consisting of three everyday objects overlaid on a scene background. The location of each object on its associated background was pseudo-randomly selected from a circular space. At retrieval, participants were asked to recreate the locations of studied objects by moving the object back to its original position as accurately as they could using a continuous response dial.

Methods

Participants

Twenty younger adults (19-23 years old), and 22 older adults (60-73 years old) participated in Experiment 1. One older adult participant with a precision estimate > 3 *SDs* from the group mean was excluded from the analyses conducted on individual participant parameter estimates, leaving 20 younger and 21 older adults contribute to the analyses (see Table 1 for participant demographics). Sensitivity analysis indicated that this sample size enabled the detection of a significant difference between the age groups of the size of $d = 0.90$ at alpha < .05 with the power of 0.80. Older adults reported a marginally higher number of years of formal education than younger adults, $t(39) = 1.86$,

p = .070, d = 0.59. Moreover, the older adults also had higher scores than the younger adults on the SILVS (Zachary & Shipley, 1986), $t(39) = 6.01$, $p < .001$, $d = 1.86$, as typically observed in studies of cognitive ageing (Verhaeghen, 2003), indicating higher crystallized intelligence in the older group.

Table 1. *Participant demographic information in Experiment 1 (means and standard deviations).*

	Younger adults	Older adults
N	20	21
Age	20.60 (0.99)	67.14 (3.61)
Gender (N)	12 M, 8 F	10 M, 11 F
Years of education	16.35 (1.04)	17.48 (2.50)
SILVS	32.15 (2.89)	36.52 (1.63)
MoCA	n/a	27.95 (1.16)

Note. M = males, F = females.

Materials

The stimuli consisted of 180 images of distinct everyday objects, and 60 images of outdoor scenes. Object and scene images were obtained from existing stimuli sets (objects: Brady, Konkle, Alvarez, & Oliva, 2008; Konkle, Brady, Alvarez, & Oliva, 2010; scenes: Richter, Cooper et al., 2016) and Google image search. Three object images were randomly allocated to each scene image, forming a total of 60 trial-unique stimulus displays (750 x 750 pixels). The objects were each overlaid on the background scene in a location pseudo-randomly selected from a 360-degree circle with a radius of 247 pixels, with a minimum distance of 62.04 degrees to ensure that the object locations did not overlap on any given study display. Stimulus displays were generated once, and all participants learned the same displays.

Design and procedure

The location memory task consisted of 120 retrieval trials, divided into 5 study-test blocks (see Figure 2). In each study phase, participants viewed 12 stimulus displays for 9s each. Participants were instructed to try and memorise the appearance of each of the

displays the best they could, paying particular attention to the identity and location of each of the objects. The study phase was followed by a 30s delay, during which participants counted backwards by threes aloud, to prevent rehearsal of the studied stimuli. In the test phase, participants were first presented with a previously studied scene image with no objects overlaid on it for 9s, during which they were instructed to think about which objects had been associated with the given scene and where they had been located. Participants were then asked to sequentially reconstruct the locations of two out of three objects that had been associated with the scene as precisely as they could (one object on the screen at a time). Each object initially appeared in a random location on the associated background, along with a response dial. Participants were able to move the object clockwise and anti-clockwise around the 360-degree response dial by pressing the left and right arrow keys on the keyboard, and confirmed their answer by pressing the space bar. Response time was not limited to avoid disadvantaging the older adults; however, participants were encouraged to try and respond within 15s. The passing of 15s was indicated by the central retrieval cue ("Location") changing colour from white to red. Participants in both groups responded within the first 15s on 98% of trials. Participants completed 24 location retrieval trials in each block. Encoding and retrieval trials were separated by a central fixation cross of 1s. The allocation of displays to task blocks and the order of display presentation at study and test was randomised across participants. Which two out of the three studied objects per display were selected for location retrieval, and their test order, were randomized but kept constant across participants.

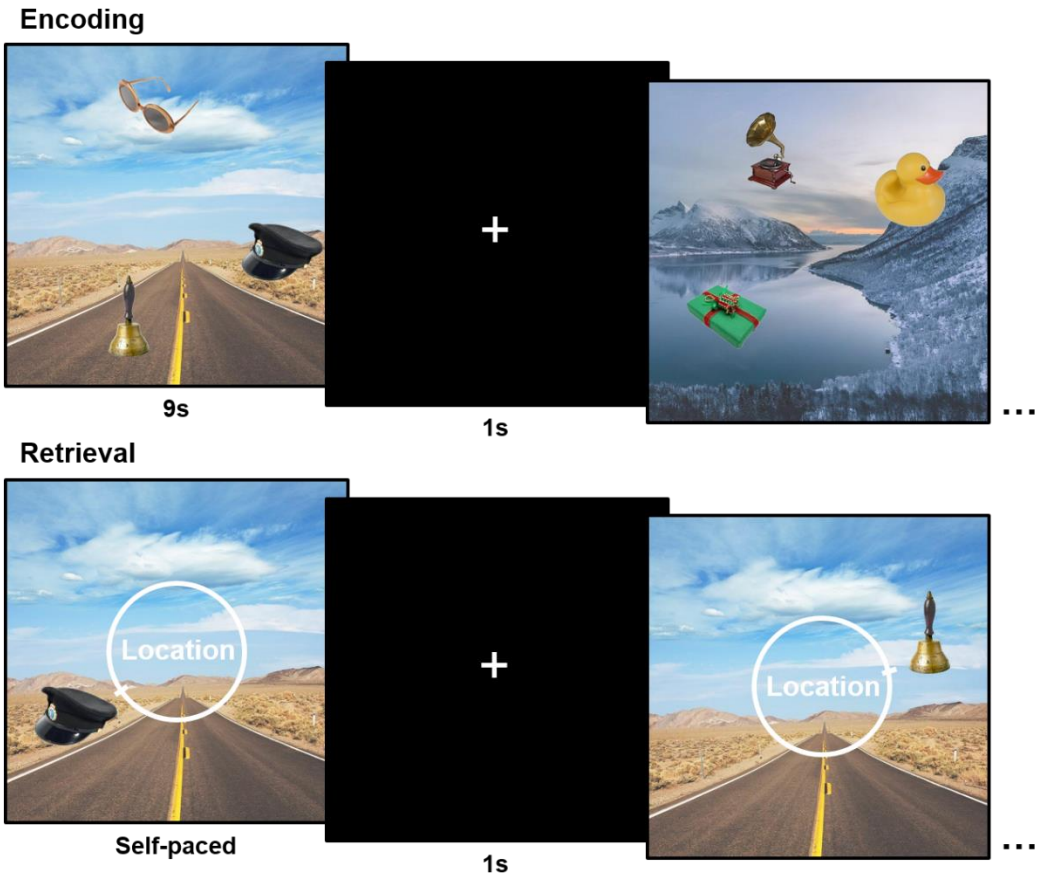

Figure 2. Example study and test trials in the location memory task in Experiment 1. Participants viewed stimulus displays (stimulus duration: 9s) consisting of three objects overlaid on a scene background, and later recreated the locations of two objects associated with each display, by moving the object around a 360-degree response dial via keypress. Retrieval error on each trial was calculated as the angular deviation between participants' response value and the target location value (0 ± 180 degrees).

Results

The distributions of participants' retrieval errors, calculated as the angular difference between the studied target feature value and the participant's response value, across the 120 retrieval trials in each age group are displayed in Figure 3. Mean absolute retrieval error across trials was significantly higher in the older (*M*: 29.61, *SD*: 11.81) in comparison to the younger adults (*M*: 21.46, *SD*: 8.75), $t(39) = 2.50$, $p = .017$, $d = 0.78$, indicating that overall task performance was lower in the older group. The older adults

also demonstrated significantly longer reaction times (*M*: 6.46s, *SD*: 1.68s) in comparison to the younger adults (*M*: 4.66s, *SD*: 1.35s), $t(39) = 3.79$, $p = .001$, $d = 1.19$.

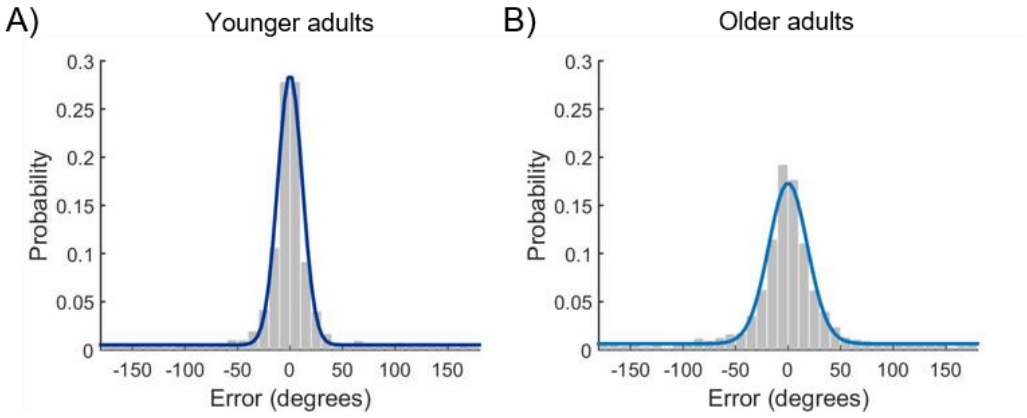

Figure 3. Distribution of retrieval errors (response feature value – target feature value) in the A) young and B) older adults. Coloured lines (dark blue: younger adults, light blue: older adults) indicate response probabilities predicted by the mixture model with target von Mises and circular uniform components (model fit to aggregate data in each group for visualization), illustrating similar retrieval success (similar height of the uniform components), but reduced memory precision in the older group (broader Gaussian component).

Comparison of the three alternative models characterizing participants' error distributions indicated that, consistent with previous findings from younger adults (Richter, Cooper et al., 2016), participants' performance in the current task was best characterized by a mixture of random guessing and variability in successful memory retrieval as indicated by a lower BIC for this model in comparison to the two alternative models (see Table 2). To quantify the success and precision of memory retrieval, the preferred mixture model consisting of the target von Mises and uniform distributions was fitted to participants' retrieval error data, yielding maximum likelihood estimates of the probability of successful memory retrieval (*pT*), and the precision of successful memory retrieval (*K*) for each participant (see Figure 4).

Examination of age differences in the model-estimated success of memory retrieval, defined as the probability of responses stemming from the von Mises distribution around

the target feature value (*pT*), indicated no significant differences in the mean probability of retrieval success between the younger (*M*: 0.81, *SD*: 0.13) and older (*M*: 0.80, *SD*: 0.13) adults, $t(39) = 0.43$, $p = .669$, $BF_{01} = 3.04$. In contrast, the precision of memory retrieval, defined as the concentration of the target von Mises distribution (*K*), was significantly reduced in the older (*M*: 10.14, *SD*: 5.25) in comparison to the younger (*M*: 31.89, *SD*: 19.37) adults, $t(39) = 4.96$, $p < .001$, $d = 1.55$, indicating increased variability, i.e., noise, in target retrieval in the older group. The findings from the analyses conducted on the individual participant parameter estimates were further confirmed by aggregate analyses where the retrieval error data was modelled across all trials and participants in each age group. Permutation tests indicated no significant age differences in the aggregate estimates of the probability of successful memory retrieval (young: 0.82, old: 0.77, $p = .407$), but a significant decline in retrieval precision in the older group (young: 24.30, old: 10.35, $p < .001$).

To examine whether the observed age-related declines in memory precision were significantly greater than any age differences in retrieval success, participants' retrieval success and precision estimates were converted to z-scores. A mixed ANOVA with the factors of memory measure (retrieval success vs. precision) and age group (young vs. old) displayed a significant interaction between memory measure and age group, $F(1, 39) = 6.00$, $p = .019$, *partial* $\eta^2 = 0.13$, indicating disproportionate age-related declines in memory precision. Age-related differences in memory performance in Experiment 1 were thus characterized by a selective deficit in the precision of episodic memory retrieval.

Table 2. *Mean BIC difference between the preferred model (Model A: target von Mises distribution + uniform distribution) and the two alternative models (Model B: target von Mises distribution; Model C: target von Mises distribution + uniform distribution + non-target von Mises distributions) in each age group.*

Younger adults		Older adults	
BIC Mod B – Mod A	BIC Mod C – Mod A	BIC Mod B – Mod A	BIC Mod C – Mod A
74.72	4.41	28.41	4.62

Note. Mod A = Model A; Mod B = Model B; Mod C = Model C.

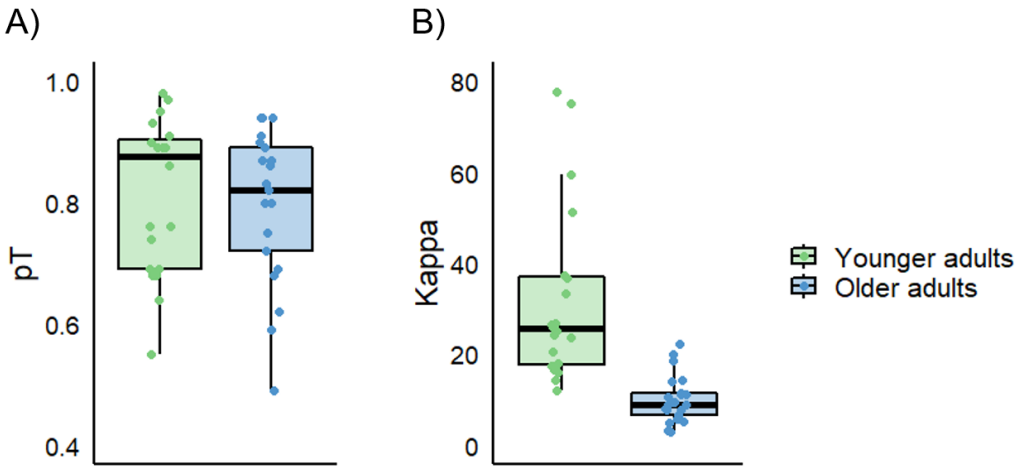

Figure 4. Distribution of model-estimated A) probability of successful memory retrieval (*pT*) and B) memory precision (*K*) in the younger and older adults. Boxplots display the median and upper and lower quartiles, and the error bars the largest/smallest value within 1.5 interquartile range from the upper/lower quartile. Jittered data points display individual participant parameter estimates.

Experiment 2

Following the finding of reduced precision of location memory retrieval in Experiment 1, I next explored whether this deficit may extend to the retrieval of different types of information from LTM. In younger adults, different object attributes have been shown to be independently remembered or forgotten from long-term memory (Brady et al., 2013; Utochkin & Brady, 2019). Similarly, the fidelity with which different event features are remembered has been found to be behaviourally unrelated and to rely on distinct neural circuits (Cooper & Ritchey, 2019). The relative memory independence for different object features in younger adults suggests scope for variability in age differences in the precision of memory retrieval across different object features. Thus, in the second experiment I aimed to assess whether the observed age-related declines in memory precision were specific to retrieval of spatial locations, or whether they may extend to different object features retained in long-term memory.

In Experiment 2, participants encoded and retrieved stimulus displays consisting of three everyday objects that varied in terms of their locations, colours and orientations in circular spaces. At test, participants recreated the appearance of each feature using the

continuous response dial. I further assessed whether age-related reductions in the objective precision of memory retrieval may be accompanied by age-related changes in the subjective quality of retrieved memories, by asking participants to rate the subjective vividness of their memory retrieval for each display on a continuous scale.

Methods

Participants

Twenty-four younger (18-28 years old) and 24 older adults (62-79 years old) participated in Experiment 2. Two younger adults and one older adult outlier (parameter estimates > 3 *SDs* from the group mean) were excluded from the analyses, leaving 22 younger adults and 23 older adults to contribute to the analyses based on individual participant parameter estimates (see Table 3 for participant demographics). Sensitivity analyses indicated that this sample size enabled the detection of a main effect of age of the size of Cohen's f = 0.33, and an interaction between age and feature condition of the size of Cohen's f = 0.21 at alpha < .05 with the power of 0.80 in the ANOVAs. Six of the older adults had also participated in Experiment 1 (no overlap in task stimuli). No significant differences in memory performance (mean absolute retrieval error across trials) were detected between these six participants and the remaining older adults, $t(21) = 1.44$, $p = .165$. The older adults reported a significantly higher number of years of formal education than younger adults, $t(43) = 2.66$, $p = .011$, $d = 0.80$, and scored on average higher on the SILVS (Zachary & Shipley, 1986), $t(42) = 4.20$, $p < .001$, $d = 1.26$.

Table 3. *Participant demographic information in Experiment 2 (means and standard deviations).*

	Younger adults	Older adults
N	22	23
Age	20.95 (2.46)	71.91 (4.65)
Gender (N)	12 M, 10 F	12 M, 11 F
Years of education	16.05 (1.43)	17.83 (2.81)
SILVS[a]	33.77 (3.66)	37.41 (1.76)
MoCA	n/a	28.22 (1.17)

Note. M = males, F = females. [a] SILVS score missing for one older adult due to experimenter error.

Materials

Stimuli for the continuous report task in Experiment 2 consisted of 120 images of distinct everyday objects and 40 images of textured backgrounds. The object images were obtained from an existing colour-rotated stimuli set (Brady et al., 2013, available at http://timbrady.org/stimuli/ColorRotationStimuli.zip), and the background images from Google Image Search (no overlap in stimuli with Experiment 1). Objects displaying rotational symmetry or associated with a particular colour were excluded from the stimuli. The stimuli were randomly allocated to form a total of 40 trial-unique study displays each consisting of three objects overlaid on a texture background. In Experiment 2, the objects on each display varied along three perceptual features: location, colour and orientation. Values for each of these features were pseudo-randomly drawn from a circular space (0-360 degrees) with the constraint of a minimum distance of 62.04 degrees between two features of the same type on each display. This minimum distance was required to create non-overlapping object locations, and was for consistency also applied to the other two feature dimensions. All participants studied the same displays.

Design and procedure

The continuous report task used in Experiment 2 consisted of 10 study-test blocks (see Figure 5). In each study phase, participants sequentially viewed four stimulus displays (stimulus duration: 12s), and were instructed to memorize each display the best they could, including both the background image and the identity and appearance (location, colour and orientation) of each of the objects. In the test phase, participants were first asked to rate the vividness of their memory for each display, and to base this vividness judgement on how vividly they could recall the appearance of all of the three objects associated with that display. Participants were presented with the background image only, along with a question "How vividly do you remember this display?" in the centre of the image. After a 2s delay, a response scale was added and participants could indicate the vividness of their memory by moving a slider on a 100-point continuous scale (0 = "not vivid", 100 = "very vivid"). After the vividness rating, participants sequentially reconstructed the features (location, colour, and orientation) of two out of the three objects on each display. For feature retrieval, the test object initially appeared in a randomly allocated location, colour and orientation on the associated background along

with the response dial. A central cue noted the feature being tested ("Location", "Colour", or "Orientation"), and after responding to one of the feature questions, participants' reconstruction of that feature's appearance remained unchanged for the following feature questions for the same object. As in Experiment 1, the test phase was self-paced, but participants were encouraged to respond within 15s. The study and test trials were separated by a fixation cross of jittered duration (400ms to 2500ms, mean: 1025ms), and the study and test phases by a 10s delay.

Participants completed 40 vividness trials, and 240 feature retrieval trials (80 per feature) in total. The allocation of study displays to task blocks and the order of display presentation at study and test was randomized across participants. Selection of two objects from each display for feature retrieval and their test order was randomized but kept constant across participants. The order of feature questions for each object was pseudo-randomised across participants with the constraint of no individual feature tested more than 4 consecutive times in the same sequential position (i.e., first, second, or third), and with each feature tested 26-28 times in each position.

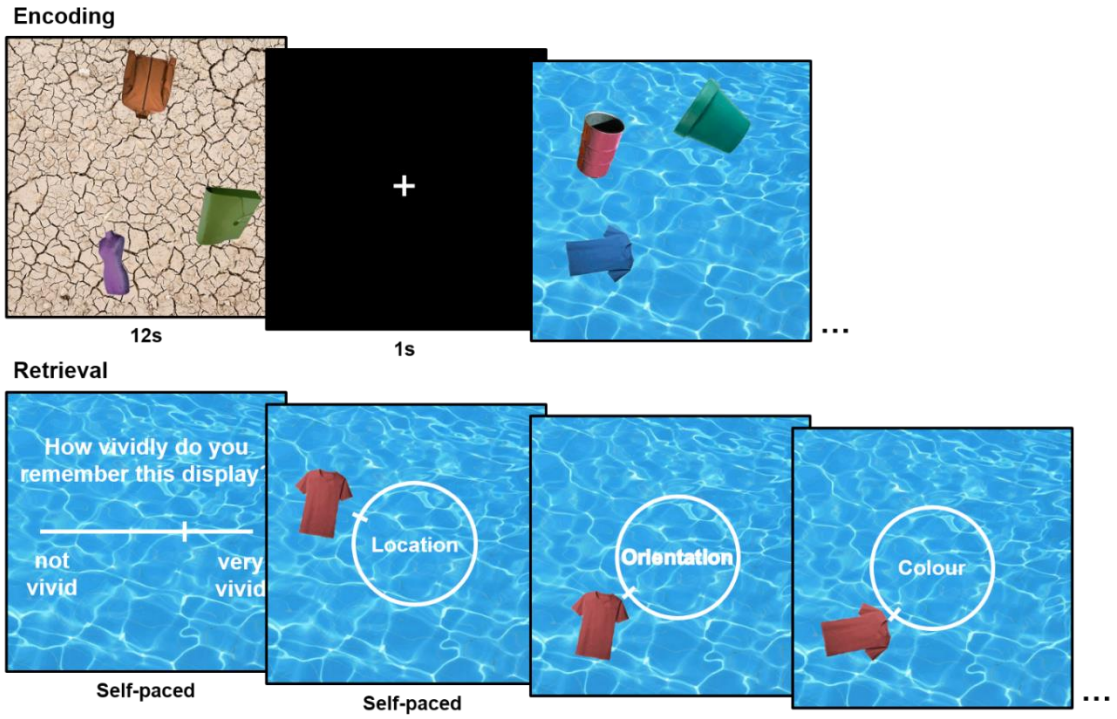

Figure 5. Participants studied stimulus displays consisting of three objects varying along three features: location, colour and orientation (stimulus duration: 12s). For each display,

participants first rated the vividness of their memory retrieval, and then recreated the features of two out of the three objects on each display, using the continuous response dial.

Results

Table 4. *Mean absolute error (degrees) and reaction time (s) in each age group and feature condition. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	Absolute error	RT	Absolute error	RT
Location	28.13 (14.22)	3.86 (0.94)	32.11 (16.16)	6.69 (1.48)
Colour	38.33 (14.80)	5.67 (1.00)	50.07 (15.17)	9.32 (2.32)
Orientation	51.36 (16.58)	4.43 (1.03)	64.86 (19.63)	7.56 (1.74)

Distributions of retrieval errors in each feature condition and age group in Experiment 2 are displayed in Figure 6. A mixed ANOVA with the factors of age group (young vs. old) and feature condition (location, colour, orientation) indicated a main effect of age, $F(1, 43) = 5.22$, $p = .027$, *partial* $\eta^2 = 0.11$, on mean absolute error in Experiment 2 (see Table 4). Furthermore, there was a marginal interaction between age group and feature condition, $F(1.68, 72.15) = 3.30$, $p = .051$, *partial* $\eta^2 = 0.07$, $BF_{01} = 0.63$ (Greenhouse-Geisser corrected). Absolute error did not significantly differ between the age groups in the location condition, $t(43) = 0.88$, $p = .386$, $BF_{01} = 2.49$. However, the older adults displayed significantly higher mean absolute error than the younger adults in the colour, $t(43) = 2.63$, $p = .012$, $d = 0.78$, and orientation, $t(43) = 2.49$, $p = .017$, $d = 0.74$, conditions.

Furthermore, a mixed ANOVA with the factors of age group (young vs. old) and feature condition (location, colour, orientation) indicated a main effect of age on reaction times, $F(1, 43) = 61.03$, $p < .001$, *partial* $\eta^2 = 0.59$ (see Table 4). Although there was a marginal interaction between age group and feature condition, $F(1.37, 58.82) = 3.25$, $p = .064$, *partial* $\eta^2 = 0.07$, $BF_{01} = 0.82$ (Greenhouse-Geisser corrected), significant age-related increases in reaction times were observed across the location, $t(43) = 7.60$, $p < .001$, $d =$

2.26, colour, $t(43) = 6.80$, $p < .001$, $d = 2.03$, and orientation, $t(43) = 7.30$, $p < .001$, $d = 2.17$, conditions.

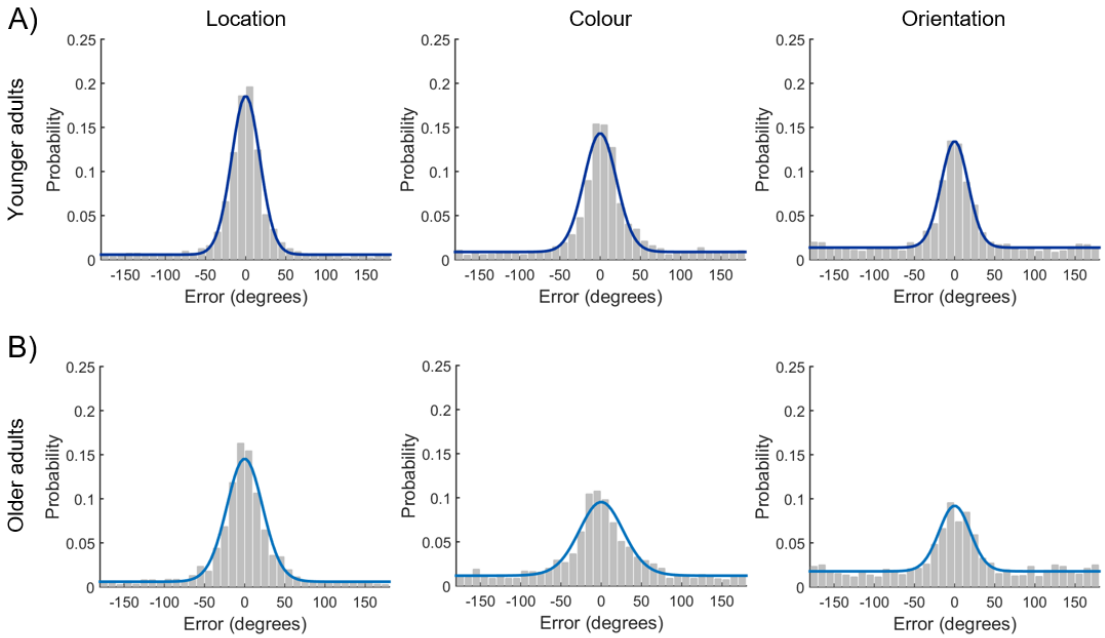

Figure 6. Distribution of retrieval errors in each feature condition in the A) younger and B) older adults. Coloured lines (dark blue: younger adults, light blue: older adults) illustrate response probabilities predicted by the mixture model (model fit to aggregate data for visualization).

Table 5. *Mean BIC difference between the preferred model (Model A: target von Mises + uniform) and the two alternative models (Model B: target von Mises; Model C: target von Mises + uniform + non-target von Mises) in each age group.*

	Younger adults		Older adults	
	BIC Mod B – Mod A	BIC Mod C – Mod A	BIC Mod B – Mod A	BIC Mod C – Mod A
Location	19.63	3.80	7.86	4.11
Colour	17.81	3.85	5.21	3.77
Orientation	26.09	4.16	11.64	3.93

Note. Mod A = Model A; Mod B = Model B; Mod C = Model C.

As in Experiment 1, model comparison analyses indicated that the combination of target von Mises and uniform distributions provided a better fit for the current data than two alternative models, as indicated by a lower BIC for this model in both age groups (see Table 5). This model was fitted to data from each individual participant and feature condition (see Figure 7). A mixed ANOVA with the factors of age group (young vs. old) and feature condition indicated no significant main effect of age group, $F(1, 43) = 2.29$, $p = .138$, $BF_{01} = 1.63$, but a significant effect of feature, $F(2, 86) = 85.26$, $p < .001$, *partial* $\eta^2 = 0.67$, on the mean model-estimated probability of successful memory retrieval. Importantly, there was a significant interaction between age group and feature, $F(2, 86) = 5.03$, $p = .009$, *partial* $\eta^2 = 0.11$, indicating that age differences in retrieval success varied across the three feature conditions (see Table 6). No significant age differences in the probability of successful retrieval were observed in the location, $t(43) = 0.13$, $p = .901$, $BF_{01} = 3.37$, or colour, $t(43) = 1.34$, $p = .186$, $BF_{01} = 1.64$, conditions. However, the older adults exhibited significantly lower probability of successful memory retrieval than younger adults in the orientation condition, $t(43) = 2.45$, $p = .018$, $d = 0.73$. The orientation condition also had the lowest retrieval success out of the three feature conditions in the younger group (lower retrieval success than colour, $t(21) = 4.17$, $p < .001$, $d = 0.89$, and location, $t(21) = 8.01$, $p < .001$, $d = 1.71$), indicating that the only significant age differences in retrieval success were observed for the condition that also resulted in the lowest probability of successful memory retrieval in the younger group.

In contrast, for retrieval precision, a mixed ANOVA with the factors of age group (young vs. old) and feature condition (location, colour, orientation) displayed a significant main effect of age group, $F(1, 43) = 11.54$, $p = .001$, *partial* $\eta^2 = 0.21$, indicating reduced precision of memory retrieval in the older group (see Table 6). Age differences in retrieval precision did not significantly vary across the feature conditions, $F(2, 86) = 0.14$, $p = .872$, $BF_{01} = 7.28$, suggesting a comparable degree of loss of mnemonic precision across different object features retained in LTM.

Table 6. *Mean model-estimated probability of successful memory retrieval (pT) and memory precision (K) in each age group and feature condition. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	pT	Kappa	pT	Kappa
Location	0.81 (0.18)	11.44 (4.94)	0.82 (0.20)	7.35 (3.66)
Colour	0.70 (0.19)	9.30 (5.11)	0.62 (0.22)	6.23 (5.15)
Orientation	0.54 (0.21)	12.72 (7.31)	0.37 (0.25)	9.61 (5.97)

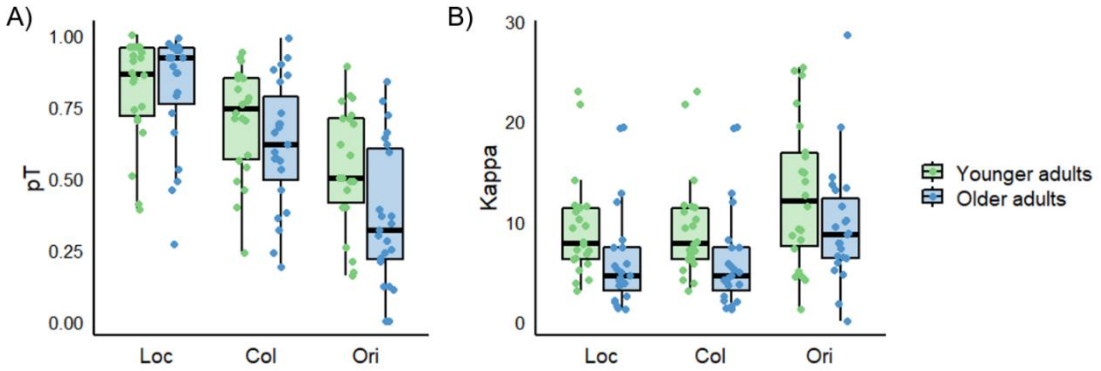

Figure 7. Distribution of model-estimated A) probability of successful memory retrieval (*pT*) and B) memory precision (*K*) in each age group and feature condition (Loc = location, Col = colour, Ori = orientation). Boxplots display the median and upper and lower quartiles, and error bars the largest/smallest value within 1.5 interquartile range from the upper/lower quartile. Jittered data points display individual participant parameter estimates.

Of note, two older participants had a retrieval success estimate close to zero in the orientation condition, suggesting that responses in the orientation condition for these two participants reflected mainly guessing. Exclusion of these two participants from the memory precision analysis similarly resulted in a significant main effect of age on memory precision, $F(1, 41) = 9.39$, $p = .004$, *partial* $\eta^2 = 0.19$, and no interaction between age group and feature condition, $F(2, 82) = 0.26$, $p = .776$, $BF_{01} = 6.43$, as the main analysis described above. A significant interaction between age group and feature

condition was also observed for the probability of successful memory retrieval after the exclusion of these two participants, $F(1.73, 70.78) = 5.21$, $p = .011$, *partial* $\eta^2 = 0.11$. However, note that the age difference in retrieval success in the orientation condition was marginal after the exclusion of these two participants, $t(41) = 1.99$, $p = .054$, $d = 0.60$, $BF_{01} = 0.71$. No significant age differences in the probability of successful memory retrieval were detected in the location, $t(41) = 1.00$, $p = .322$, $BF_{01} = 2.22$, or colour, $t(41) = 0.91$, $p = .367$, $BF_{01} = 2.39$, condition in this analysis either.

Results obtained from the analysis of individual participant parameter estimates were further supported by results from permutation tests conducted on the aggregate estimates of the probability of successful memory retrieval (*pT*) and memory precision (*K*). The aggregate estimates were computed by modelling data across all participants for each age group and feature condition separately. Consistent with the results of the analysis conducted on individual participant parameter estimates, results from the aggregate analyses indicated no significant age differences in the probability of successful memory retrieval in the location (young: 0.78, old: 0.79, $p = .890$), and colour conditions (young: 0.67, old: 0.59, $p = .145$), however the older adults exhibited significantly lower success of memory retrieval than the younger adults in the orientation condition (young: 0.51, old: 0.36, $p = .036$). Retrieval precision, on the other hand, was significantly reduced in the older group in the location (young: 11.12, old: 6.46, $p = .002$), colour (young: 8.72, old: 4.26, $p < .001$) and orientation (young: 12.54, old: 8.84, $p = .032$) conditions in the aggregate analyses also.

Comparing the magnitude of age differences in the success and precision of memory retrieval for each feature condition with separate mixed ANOVAs with the factors of memory measure (retrieval success vs. precision) and age group (young vs. old) provided evidence for a significantly disproportionate deficit in retrieval precision in the location condition, $F(1, 43) = 5.52$, $p = .023$, *partial* $\eta^2 = 0.11$, but not in the colour, $F(1, 43) = 0.17$, $p = .679$, $BF_{01} = 3.51$, or orientation, $F(1, 43) = 0.33$, $p = .570$, $BF_{01} = 2.91$, conditions (estimates of retrieval success and precision z-scored).

Despite reductions in objective precision of memory retrieval, the mean subjective ratings of memory vividness did not significantly differ between the age groups, $t(43) = 0.71$, $p = .485$, $BF_{01} = 2.77$, with both age groups rating their memory retrieval as moderately vivid (younger: *M*: 45.09, *SD*: 13.12, older: *M*: 49.65, *SD*: 27.42, on a scale

0-100). Mean memory vividness did not significantly correlate with the success (younger: $r = .23$, $p = .313$, $BF_{01} = 2.35$; older: $r = -.06$, $p = .791$, $BF_{01} = 3.74$) or precision (younger: $r = .15$, $p = .507$, $BF_{01} = 3.08$; older: $r = .07$, $p = .748$, $BF_{01} = 3.69$) of memory retrieval, collapsed across the feature conditions in either age group.

Discussion

In Experiment 2, I assessed the fidelity of participants' long-term memory retrieval for three different object features. Consistent with results from Experiment 1, I here observed significant age-related declines in the precision of episodic memory retrieval across the features tested, indicating consistent age-related declines of memory fidelity across different types of information retained in LTM. In the present experiment, significant age-related reductions in the probability of successful memory retrieval were also observed in the orientation condition. This was also the condition resulting in the lowest retrieval success out of the three feature conditions in the younger adults (see Cooper et al., 2017 for similar results), potentially suggesting an influence of task difficulty. However, it should be noted that while the complementary Bayesian analyses provided positive evidence for age-invariant probability of successful memory retrieval in the location condition, considerable support for this null hypothesis was not observed in the colour condition. Furthermore, despite reductions in objective measures of performance, the older adults did not display decreases in the subjective vividness of their memory retrieval, consistent with previous reports of lack of age-related decline in memory vividness (Johnson et al., 2015; St-Laurent et al., 2014).

General Discussion

Declines in episodic memory retrieval are consistently observed with healthy ageing (Grady, 2012; Hedden & Gabrieli, 2004; Nyberg et al., 2012). While a wealth of studies has investigated the effects of ageing on the success of episodic memory retrieval (e.g., Cansino et al., 2018; Naveh-Benjamin, 2000; Simons et al., 2004), less is known about whether ageing may also affect the fidelity of retrieved memories (Nilakantan et al., 2018). In the current chapter, I sought to better characterize the nature of age-related declines in episodic memory retrieval by distinguishing whether age-related changes may

reflect reduced probability of successfully retrieving information from memory, and/or decreased precision of the retrieved memory representations. In two experiments, I consistently observed age-related reductions in the precision of episodic memory retrieval. These declines in mnemonic precision were evident across different types of information retrieved from long-term memory (object location, colour and orientation). In contrast to memory precision, significant age-related decreases in the probability of successful memory retrieval were observed only in the orientation condition in Experiment 2. This was also the condition resulting in the lowest retrieval success in the younger adults, suggesting an effect of task difficulty. Together, these results highlight the contribution of reduced memory fidelity to age-related episodic memory impairments, and suggest that the success and precision of episodic memory retrieval might be differentially sensitive to age-related decline.

The current findings of decreased memory precision in older age are consistent with previous proposals of age-related reductions in the quality, and specificity, of memory representations (Burke et al., 2018; Goh, 2011; Li et al., 2001; Trelle et al., 2017, 2019). However, while previous behavioural investigations have often relied on subjective judgements or categorical measures of memory success to draw inferences about age-related changes in memory quality, the current paradigm provided a more direct behavioural measure of memory fidelity, unconfounded by age-related changes in the success of memory retrieval. A similar paradigm has recently been used by Nilakantan et al. (2018), who also demonstrated intact probability of successful object-location retrieval but reduced memory precision in older age, consistent with the current findings from Experiment 1. However, in addition to object location retrieval, the findings from Experiment 2 demonstrated that the age-related declines in memory precision extend to different object features (colour and orientation) stored in long-term memory. These results suggest that decreases in memory precision may be a consistent feature of age-related memory decline, and not specific to the type of material tested. Indeed, such material-independent declines would be predicted by previous accounts proposing increases in neural noise to limit the fidelity of memory representations in older age (Welford, 1958, 1981; Li et al., 2001).

In contrast to memory precision, significant age-related decreases in the probability of successful memory retrieval were detected in the current experiments only in the orientation condition of Experiment 2. This relative sparing of retrieval success in older

age is consistent with the idea that while memory for the gist of an event, or stimulus, might be preserved in ageing, the more fine-grained details tend to be lost (Dennis, Kim, et al., 2007, 2008; Kensinger & Schacter, 1999; Nilakantan et al., 2018). Other previous studies have, however, demonstrated robust age-related declines in the success of episodic recollection (e.g., Cansino et al., 2018; Simons et al., 2004). This apparent discrepancy between the current results and previous findings may be partially explained by age-related decreases on categorical measures of memory success in previous studies being at least to some extent attributable to reduced fidelity of the underlying memory representations, rather than a failure to retrieve the representations per se (Nilakantan et al., 2018). For instance, a failure to discriminate between two similar sources of memories, such as between two female or two male voices (Simons et al., 2004), could result from a noisier memory representation of the source, leading to the selection of an incorrect retrieval response, and thereby reduced retrieval success.

However, it should be noted that the Bayes factor analyses only provided positive evidence in favour of age-invariant probability of successful memory retrieval in the location conditions of Experiment 1 and 2. Although no significant differences in the probability of successful memory retrieval were detected in the colour condition of Experiment 2, numerically the success of memory retrieval was lower in the older relative to the younger group in this condition. It therefore remains to be clarified how selective the memory precision deficits in older age are. However, the finding that age-related declines in memory precision were observed even when retrieval success was matched between the age groups, and that these declines were disproportionate to any age differences in retrieval success in the locations conditions of Experiment 1 and 2, suggests that memory precision may be more sensitive to age-related cognitive decline.

Age-related changes in retrieval success were observed in in the current experiments only in the orientation condition, which may reflect the relatively high task difficulty of this condition (as indicated by lower retrieval success in this condition in comparison to the location and colour conditions in younger adults), rather than an impairment specific to the retrieval of object orientations. Indeed, previous evidence from younger adults using a similar paradigm has demonstrated that the orientation condition tends to be more difficult than the location or colour conditions. (Cooper et al., 2017). Emergence of age-related decreases in the probability of successful memory retrieval with increased task difficulty is consistent with the notion of exaggerated age differences in cognitive

performance with increased task demands (Reuter-Lorenz & Cappell, 2008). These findings suggest that while the success of memory retrieval may remain at a level similar to the young in the older group when task demands are relatively low, multiple aspects of memory retrieval might begin to break down when task demands are increased. However, given that task difficulty was confounded with feature condition in the current experiment, future research using different load manipulations on the same feature condition is required to distinguish between feature-based and task difficulty-based interpretations.

Interestingly, previous research has demonstrated older age to be associated with increases in false memory, including associative and misattribution errors (reviewed in Devitt & Schacter, 2016). In addition to assessing age-related changes in the success and precision of memory retrieval, I also assessed whether increases in binding errors may contribute memory performance using a model comparison approach. Specifically, I compared the model consisting of target von Mises and uniform distributions to a model additionally incorporating von Mises distributions around the non-target feature values from the same encoding display. In this alternative model, participants are assumed to also make binding errors, where they report a cued feature or a non-target item from the same study display (e.g., reporting the location of another object from the same study display as the object tested) (Bays et al., 2009). However, the model comparison indicated that the combination of target von Mises and uniform distributions provided a better fit for the current data than this alternative model in both age groups, thus providing little evidence for binding errors in either young or older adults. In the current experiments, a minimum distance of 60 degrees was enforced between any two features of the same kind on any given encoding display (to ensure non-overlapping object locations). It may be that this minimum distance was sufficient to make the object features more distinguishable in memory, thereby reducing the likelihood of mistakenly reporting a cued feature of a non-target item. It is also possible that rather than making binding errors between the objects from the same study display, participants may have made binding errors *across* study displays, potentially driven by semantic or perceptual similarity of the items themselves rather than the shared context (i.e., background pictures). Future experiments could distinguish these hypotheses by manipulating the semantic and perceptual relatedness of stimuli both within and across study displays.

The current findings of differential effects of ageing on the success and precision of episodic memory retrieval may suggest distinct neurocognitive factors contributing to age-related changes on each component. At the neural level, previous results by Richter, Cooper and colleagues (2016) in younger adults have demonstrated the success and precision of episodic memory retrieval to rely on dissociable brain regions of the core recollection network, with retrieval success associated with activity in the hippocampus, and retrieval precision scaling with activity in the angular gyrus. Given the putative roles of the hippocampus and angular gyrus in the success and precision of episodic memory retrieval, respectively, it might be that the behavioural results observed in the current chapter are reflected in distinct age-related functional and structural alterations in these two brain regions. This question will be examined in Chapter 4 and 5.

In conclusion, the current chapter provided evidence for age-related declines in the precision of episodic memory retrieval. Age-related decreases in memory fidelity were evident even in the absence of age differences in the probability of successful retrieval, suggesting that this aspect of episodic retrieval may be more sensitive to age-related degradation in the healthy population. Interestingly, previous studies have shown the precision of working memory retrieval to also decline in older age (Noack et al., 2012; Peich et al., 2013; Pertzov, Heider, Liang, & Husain, 2015). In the next chapter, I will explore the potential contribution of decreased fidelity of perception and/or working memory to the age-related deficits in the precision of episodic memory retrieval.

Chapter 3: Precision of perception, working memory and long-term memory in older age

Results from the two experiments presented in Chapter 2 demonstrated consistent age-related declines in memory precision across different object features retained in long-term memory. A question arising from these findings is whether the age-related declines in mnemonic precision are specific to long-term memory retrieval, or whether they may, at least to some extent, be explained by age-related declines in the fidelity of perceptual and/or working memory representations. In the present chapter, healthy young and older adults completed a perceptual, WM and LTM version of the continuous report task for object colour, enabling the examination of age-related changes in the fidelity of all three cognitive processes. In addition to the declines in LTM precision previously observed in Chapter 2, results from the current chapter demonstrated additional evidence for age-related declines in the precision of object colour reports in perception and WM. Moreover, the precision of WM predicted individual differences in the precision of LTM in the older group. Critically, however, significant age-related decreases in LTM precision persisted after controlling for variability in the fidelity of both perception and working memory, suggesting additional age-related degradation of information retained in LTM.

Introduction

In addition to changes in higher cognition, decreases in sensory function become evident in older age (Faubert, 2002; Liu & Yan, 2007; Owsley, 2011). The fidelity of visual perception for different stimulus attributes such as spatial contrast (Derefeldt, Lennenstrand & Lundh, 1979; Elliott, Whitaker, & MacVeigh, 1990; Owsley, Sekuler, & Siemsen, 1983) and motion (Bennett, Sekuler, & Sekuler, 2007; Snowden & Kavanagh, 2006; Trick & Silverman, 1991), as well as the quality of more complex perceptual representations comprising conjunctions of multiple stimulus features (Ryan et al., 2012), has been demonstrated to degrade in older age. Additionally, age-related decreases in the fidelity of perceptual processing have been implied by functional neuroimaging studies demonstrating age-related reductions in the activity of visual regions across a range of cognitive tasks (Cabeza et al., 2004; Davis et al., 2008; Li et al., 2015; Spreng, Wojtowicz, & Grady, 2010). In addition to the age-related decreases

in task-related brain activity, the selectivity of neural responses in visual regions during perception of different stimulus categories (Carp et al., 2011; Park et al., 2004; Park et al., 2010) as well as exemplars from the same category (Goh et al., 2010) declines in older age. Reductions in representational specificity in visual regions have been found to correlate with individual differences in an independent set of tasks of fluid cognitive processing in older age (Park et al., 2010), suggesting a contribution of reduced fidelity of visual processing to declines in higher order cognition in older age.

A relationship between sensory and cognitive declines in older age has been highlighted in several studies, with measures of sensory acuity accounting for a substantial proportion of age-related variance in higher order cognitive tasks (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994). While some have attributed this relationship to reflect a common cause, such as neural degeneration, leading to declines in both the sensory and cognitive domain (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994), others have proposed a more direct influence of sensory decreases on cognitive performance (Monge & Madden, 2016; Schneider & Pichora-Fuller, 2000). According to the information degradation hypothesis, deterioration of sensory inputs leads to impoverished perceptual representations of external stimuli, which in turn may have cascading effects on the integrity of higher-order cognitive processes, such as memory (Monge & Madden, 2016). Consistent with this hypothesis, experimental manipulations affecting the fidelity of sensory inputs at encoding have been demonstrated to lead to reductions in memory performance in younger adults (Murphy, Craik, Li, & Schneider, 2000; Pichora-Fuller, Schneider, & Daneman, 1995). As the fidelity of memory representations is essentially constrained by the fidelity of sensory inputs at encoding (Ma, Husain, & Bays, 2014), it is possible that age-related declines in the precision of visual perception may partially contribute to the age-related deficits observed in the precision of LTM retrieval.

Additionally, the ability to retain and manipulate information in working memory declines with older age (Brockmole & Logie, 2013; Dobbs & Rule, 1989; Oberauer, 2005; Salthouse & Babcock, 1991). While a distinction between short-term, or working, memory and long-term memory as separate systems has traditionally been emphasized (e.g., Atkinson & Shiffrin, 1968; Baddeley, & Hitch, 1974), increasing evidence suggest that WM and LTM may at least to some degree share similar operating mechanisms and neural substrates (Brady, Konkle, Alvarez, & Oliva, 2013; McElree, 2006; Nairne, 2002;

Ranganath & Blumenfeld, 2005; Yonelinas, 2013). Several studies have highlighted a particular role of WM in the successful formation of long-term memories (Blumenfeld & Ranganath, 2006; Davachi, Maril, & Wagner, 2001; Greene, 1987; Hartshorne & Makovski, 2019; Ranganath, Cohen, & Brozinsky, 2005). The influence of WM on successful LTM encoding appears to be particularly prominent in the early stages of WM maintenance (Naveh-Benjamin & Jonides, 1984; Ranganath et al., 2005), perhaps reflecting a stage where the memory trace is still in a labile state (McGaugh, 2000).

A relationship between WM and LTM has also been evident in studies of cognitive ageing, where reductions in WM often partially account for age-related deficits in episodic memory tasks (Bender & Raz, 2012; Hertzog, Dixon, Hultsch, & MacDonald, 2003; Hultsch, Hertzog, & Dixon, 1990; Memel, Woolverton, Bourassa, & Glisky, 2018; Park et al., 2002, 1996). This link has often been interpreted in light of reduced processing resources (e.g., Bender & Raz, 2012; Hertzog et al., 2003; Park et al., 2002), or more specific components of WM, such as binding deficits (Bartsch, Loaiza, & Oberauer, 2019; Chen & Naveh-Benjamin, 2012). However, in addition to decreases in WM capacity and binding highlighted in previous studies (e.g., Brockmole & Logie, 2013; Oberauer, 2005), more recent research has shown that impoverished precision of working memory representations contributes to age-related short-term memory deficits (Noack et al., 2012; Peich et al., 2013; Pertzov et al., 2015). Moreover, findings from younger adults have led to the proposal that WM and LTM may exhibit similar constraints on representational fidelity (Brady et al., 2013, but see Biderman, Luria, Teodorescu, Hajaj, & Goshen-Gottstein, 2019), suggesting a potential link between WM and LTM precision declines in older age. Indeed, the precision of short- and long-term retrieval has been demonstrated to correlate in the domain of auditory memory in younger adults (Van Hedger, Heald, & Nusbaum, 2018), however to date no such relationship between individual differences in the precision of WM and LTM for visual information has been reported.

The aim of the present experiment was to examine whether age-related declines in the precision of episodic memory retrieval may partially be explained by age-related declines in the fidelity of perception and/or working memory. Healthy younger and older participants completed a perceptual, WM and LTM version of the continuous report task for object colour. Colour was chosen as the test feature as previous research in younger adults employing a similar task has found colour to be a sufficiently sensitive feature for

investigating the fidelity of perception, WM and LTM (Brady et al., 2013). Given that the precision of memory representations is constrained by the fidelity of sensory inputs (Ma, Husain, & Bays, 2014), age-related reductions in the fidelity of perceptual processing may partially account for the loss of episodic memory precision. Furthermore, given the evidence for age-related decreases in WM precision (Peich et al., 2013; Pertzov et al., 2015), decreased fidelity of WM may alternatively, or additionally, contribute to reduced precision of LTM in older age. However, measures of WM often do not fully account for the age-related deficits in LTM (e.g., Bartsch et al., 2019; Stine & Wingfield, 1987), suggesting that there may be additional loss of fidelity as information is retained in memory over longer time scales. A relationship between perceptual, working memory and long-term memory precision would be in line with accounts proposing that common neural representations may serve different cognitive functions, including perception, short-term and long-term memory (Bussey & Saksida, 2007; Cowell, Bussey, & Saksida, 2010; Nadel & Peterson, 2013).

Methods

Participants

Twenty-six younger (18-30 years old), and 24 older adults (60-82 years old) took part in the current experiment. Two younger adults were excluded from the experiment prior to data analysis, one due to a counterbalancing, and one due to a failure to attend the second study session. Furthermore, two younger and two older adult outliers (retrieval success or precision estimate > 3 *SDs* from the group mean) were excluded from the analyses based on individual participant parameter estimates, leaving 22 younger and 22 older adults to contribute to the analyses (see Table 1 for participant demographics). Sensitivity analyses indicated that this sample size enabled the detection of a significant relationship between a predictor and an outcome variable in the within-group linear regression analyses of the size of Cohen's $f^2 = 0.39$ at alpha < .05 with the power of 0.80. Furthermore, a mean difference between the age groups of the size of Cohen's $d = 0.86$ could be detected at alpha < .05 with the power of 0.80.

Participants were all native English-speakers, reported normal or corrected-to-normal visual acuity, normal colour vision, and no current or historical diagnosis of any psychiatric or neurological condition, or learning impairment. Participants were recruited

via online and community advertisements and volunteer databases at the Memory Lab of the University of Cambridge. None of the participants had taken part in the previous behavioural experiments described in Chapter 2. Older adults reported a significantly higher number of years of formal education than younger adults, $t(42) = 2.70$, $p = .010$, $d = 0.82$, and scored significantly higher on the SILVS (Zachary & Shipley, 1986), $t(42) = 6.91$, $p < .001$, $d = 2.08$.

Table 1. *Participant demographic and neuropsychological test data (means and standard deviations).*

	Younger adults	Older adults	*p*-value
N	22	22	-
Age (years)	22.55 (3.54)	69.09 (6.12)	-
Gender (N)	6 M, 16 F	4 M, 18 F	-
Education (years)	16.36 (2.65)	19.07 (3.87)	.010
SILVS	32.55 (3.73)	38.41 (1.40)	< .001
MoCA	n/a	28.14 (1.25)	-
Trails A (sec)	36.68 (28.30)	50.41 (20.41)	.072
Trails B (sec)[a]	68.35 (37.72)	79.52 (25.80)	.231
ROCF Copy	34.86 (1.32)	34.80 (1.47)	.872
ROCF Immediate	24.82 (5.53)	19.20 (7.59)	.008
ROCF Delayed	24.66 (6.33)	19.27 (7.40)	.013
Verbal Paired Associates Immediate	27.91 (4.37)	23.00 (6.91)	.007
Verbal Paired Associates Delayed	7.91 (0.43)	7.23 (1.23)	.018
Letter fluency	49.86 (10.29)	55.18 (10.21)	.093
Digit span forward	12.23 (2.31)	11.05 (2.84)	.137
Digit span backward	8.59 (2.58)	8.00 (2.18)	.416

Note. *P*-values for independent samples t-tests comparing younger and older adults. M = males; F = females; ROCF = Rey-Osterrieth Complex Figure. [a] Scores on the Trail making B task excluded from two younger, and one older participant due to experimenter error.

Materials

Stimuli for all the colour report tasks consisted of 540 images of distinct everyday objects obtained from existing colour-rotated and standard object stimuli sets (Brady et al., 2008; Brady et al., 2013). Objects that had a strong association with a particular colour were excluded from the stimuli. The object images that were in their original colours were first

transformed to the same hue of red as the colour-rotated object stimuli (Brady et al., 2013) in the Commission Internationale de l'Éclairage (CIE) L*a*b* colour space (MATLAB scripts available at https://bradylab.ucsd.edu/stimuli.html). The object images were then randomly allocated to each task type, with 120 objects allocated to the LTM task, 360 objects to the WM task, and 60 objects to the perceptual task. For the LTM and WM tasks, 3 objects were randomly allocated for each study display, creating a total of 40 trial-unique stimulus displays for the LTM task, and 120 trial-unique stimulus displays for the WM task. The objects were overlaid on a grey background, in a colour and location pseudo-randomly chosen from circular parameter spaces with a minimum constraint of 62.04 degrees between two feature values of the same type on any given study display. This minimum distance was required to create non-overlapping object locations, but was for consistency with the experiments presented in Chapter 2 also applied in the colour domain.

To ensure that the amount of visual input was consistent across tasks, stimulus displays in the perception task also comprised three objects overlaid on a grey background. However, as this task involved no demands on memory, three versions of the same object presented in different colours were used (see Figure 1). A total of 60 stimulus displays were created for the perception task. As in the memory tasks, the colour and location of the objects on each display were pseudo-randomly chosen from circular parameter spaces with a minimum constraint of 62.04 degrees. All participants viewed the same displays.

Design and procedure

Participants attended two testing sessions, with a minimum one week delay between the sessions (delay for younger adults *M:* 11.45 days, *SD:* 6.57, older adults *M:* 10.82 days, *SD:* 7.05, no significant difference between the groups, $t(42) = 0.31$, $p = .758$). In addition to the three colour report tasks, participants completed a battery of standard neuropsychological tests including measures of verbal (Verbal Paired Associates, WMS-III) (Wechsler, 1997b) and non-verbal memory (Rey-Osterrieth Complex Figure test) (Osterrieth, 1944), executive function (Verbal fluency, Trails A & B) (Delis, Kaplan, & Kramer, 2001), and working memory (Digit span forward and backward, WAIS-III) (Wechsler, 1997a). Participants' performance on the neuropsychological tasks is presented in Table 1. The assignment of the colour report tasks and the

neuropsychological tests to each testing session was counterbalanced across participants, with the WM and LTM colour report tasks completed in separate sessions to minimize fatigue effects.

The LTM task consisted of 120 colour retrieval trials, divided into 8 study-test blocks (see Figure 1). In each study phase, participants sequentially viewed five stimulus displays (stimulus duration: 9s), separated by a 1s central fixation cross. Participants were instructed to try and memorize the colour and identity of each object the best they could. The study phase was followed by a 30s delay filled with counting backwards by threes aloud, to prevent rehearsal of the studied stimuli. In the test phase, participants recreated the colours of all the three objects of each display studied in the preceding block (15 retrieval trials per block). The test object initially appeared in a randomly allocated colour, but in its studied location as location was not tested in the current experiment. Participants were able to change the colour of the object by moving a slider around the 360-degree response dial with the left and right arrow keys on a keyboard, and pressed the space bar to confirm their answer. Similar to the tasks described in Chapter 2, response time in the test phase was not limited, but participants were encouraged to respond within 15s. After 15s had passed the feature label ("Colour") in the centre of the screen changed colour from white to red. The retrieval trials were separated by a 1s central fixation cross. The allocation of study displays to each task block, the order of study and test trials within each block, and the order of objects to test per display was randomised across participants. The initial colour the object appeared in at test was randomised, but kept constant across participants.

The WM task also consisted of 120 colour retrieval trials, divided into 8 blocks of 15 trials each (see Figure 1). In contrast to the LTM task, here participants studied only one stimulus display at a time (stimulus duration: 3s). A shorter encoding duration was used in the WM task, in comparison to the LTM task, to avoid ceiling-level performance in the young group. To prevent reliance on sensory memory, each study display was followed by presentation of a coloured mask image for 100ms, after which a central fixation cross was presented for 900ms. After the total delay of 1s, participants reconstructed the colour of one of the three objects from the preceding display using the continuous response dial. Participants were only tested on one object per display to ensure a consistent study-test delay. As in the LTM task, the test object appeared in its original location but in a randomly allocated colour. The selection of the object to test

per display and its initial colour at test were randomised, but again kept constant across participants. The order of trials was randomized across participants. Response time in the test phase was not limited, but participants were encouraged to respond within 15s. Each test trial was separated by a 1s central fixation cross.

The perceptual task included 60 trials, divided into two blocks of 30 trials each (see Figure 1). On each trial, participants saw two displays side-by-side on the screen. One of the displays had three versions of the same object presented in different colours. The other display had one test object, the colour of which participants were able to adjust with the response dial. The side of presentation of the display and test object on each trial (left vs. right) was randomised across participants. The participants' task was to match the colour of the test object to the colour of the object in the same relative location on the other display, surrounded by a white square. Similar to the memory tasks, the test object initially appeared in a randomly allocated colour. The selection of the object to test per display was randomized but kept constant across participants, and the order of trials randomized across participants. Response time in the test phase was not limited, but participants were encouraged to respond within 15s. Each test trial was followed by a 1s central fixation cross.

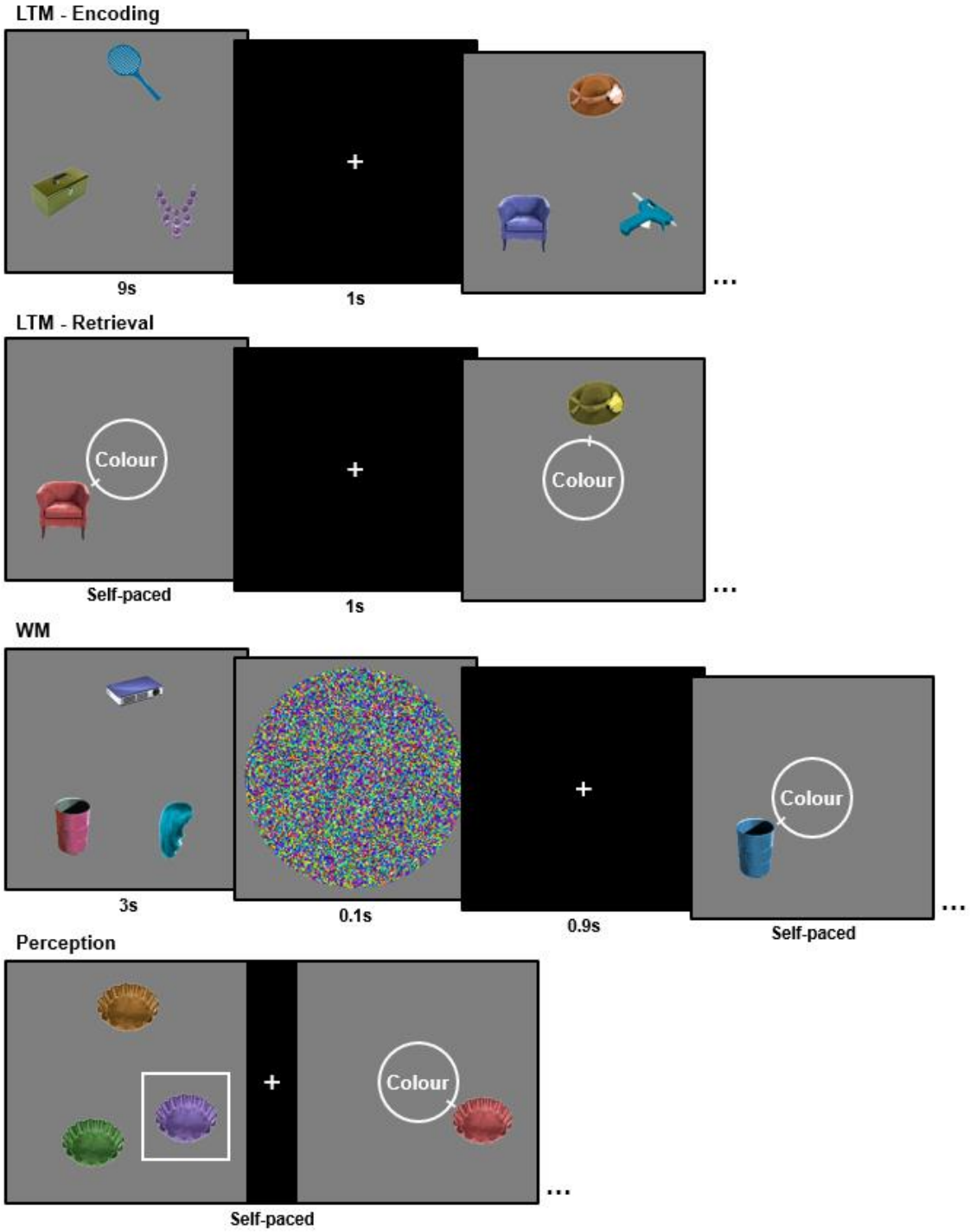

Figure 1. Example trials in each of the three colour report tasks. In the LTM task participants studied five stimulus displays in a row (9s each), before retrieving the colours of all objects after a 30s delay. In the WM task, participants studied one stimulus display at a time (3s each), and retrieved the colour of one object after 1s delay. In the perception task, participants matched the colour of one object per display while the stimulus display was simultaneously in view.

Data analysis

For each task, error on each trial was calculated as the angular deviation between participants' response value and the target colour value (0±180 degrees). As in Chapter 2, I first compared three possible models capturing participants performance in each of the tasks: 1) a model consisting of a target von Mises distribution only where participants' responses were assumed to reflect variability in target reports only, 2) a model comprising a combination of a target von Mises and uniform distribution where participants' responses reflect variability in target reports and random guessing, and 3) a model including a target von Mises distribution, a uniform distribution and von Mises distributions centred at the non-target feature values from the same encoding display where participants' responses reflect variability in target reports, random guessing, and non-target reports. Although findings from Chapter 2 indicated that the model with target von Mises and uniform components best characterized long-term memory data in both age groups, previous research has displayed age-related increases in binding errors in working memory (Peich et al., 2013), suggesting that incorporating a further non-target component may better account for the older adults' working memory data. However, consistent with Chapter 2, the model consisting of a target von Mises and uniform distributions was observed to provide the best fit in each age group and task version (see Table 3). Accordingly, the model consisting of a target von Mises and a uniform distribution was fitted to error data in each task. The model was fitted separately to data from each individual, yielding estimates of the success (*pT*; probability of the responses stemming from the target von Mises distribution) and precision (*K*; concentration of the von Mises distribution) of target reports.

Outliers with parameter estimates > 3 *SD*s from the group mean were excluded from the analyses based on individual participant parameter estimates. As in Chapter 2, results from the individual participant analyses were validated by modelling data across all participants in each age group. For these aggregate analyses, the statistical significance of the observed age differences was assessed via permutation tests, where the participants' data was remodelled over 1000 iterations of random participant-to-group assignment, and the absolute observed group difference was compared to the distribution of permuted group differences across the iterations. Two-tailed *p*-values are reported for all analyses. Where a non-significant result was observed in the main analyses, I further performed complementary Bayesian analyses to assess the strength of evidence in favour

of the null hypothesis. Bayes Factors were calculated with JASP version 0.10.2 (JASP team, 2019) using default priors (for t-tests a Cauchy distribution with r = .707, for ANOVAs a multivariate Cauchy distribution with r = .50, for linear regression a multivariate Cauchy distribution with r = .354, all centred at zero). A Bayes factor > 3 was interpreted as positive evidence for the null hypothesis (Jeffreys, 1961). For the model comparison analyses, a BIC difference > 2 was interpreted as positive evidence for the given model (Raftery, 1995).

Results

Distributions of errors (0±180 degrees) across all trials in each task and age group are displayed in Figure 2, and the mean absolute error and reaction time in each task and age group displayed in Table 2. The older adults exhibited significantly higher mean absolute error in the WM, $t(42) = 2.69$, $p = .010$, $d = 0.81$, and perception task, $t(42) = 3.34$, $p = .002$, $d = 1.01$. In the LTM task, age differences in absolute error were marginal, $t(42) = 1.84$, $p = .074$, $d = 0.55$, $BF_{01} = 0.89$. Reaction times were also higher in the older group in the LTM, $t(42) = 2.47$, $p = .018$, $d = 0.74$, WM, $t(42) = 4.53$, $p < .001$, $d = 1.37$, and perception task, $t(42) = 6.22$, $p < .001$, $d = 1.87$.

Table 2. *Mean absolute error (degrees) and reaction time (s) in each age group and task version. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	Absolute error	RT	Absolute error	RT
LTM	26.68 (10.90)	6.05 (1.87)	32.87 (11.49)	7.46 (1.91)
WM	18.36 (5.42)	4.88 (1.59)	22.74 (5.38)	7.31 (1.96)
Perception	5.16 (1.26)	6.95 (1.57)	6.89 (2.06)	10.76 (2.41)

Comparison of the three alternative models characterizing participants' performance indicated that the mixture of a target von Mises and uniform distributions best captured participants' performance in each memory task and age group (see Table 3). Note that although the probability of guessing was close to zero in the perceptual task across participants, examination of individual participant error plots revealed that a proportion

of guessing responses were evident for some participants. Modelling the perceptual data with a mixture of von Mises and uniform distributions ensured that these responses were accounted for without deflating the estimates of precision (as would be the case if guessing was present, and a model consisting of a target von Mises distribution only was fitted to the data). Note that this model also best characterized perceptual data across participants in each age group (see Table 3). For participants exhibiting no guessing responses, the probability of the uniform distribution would still be estimated as zero by this model, therefore not biasing the estimation of the probability of target reports.

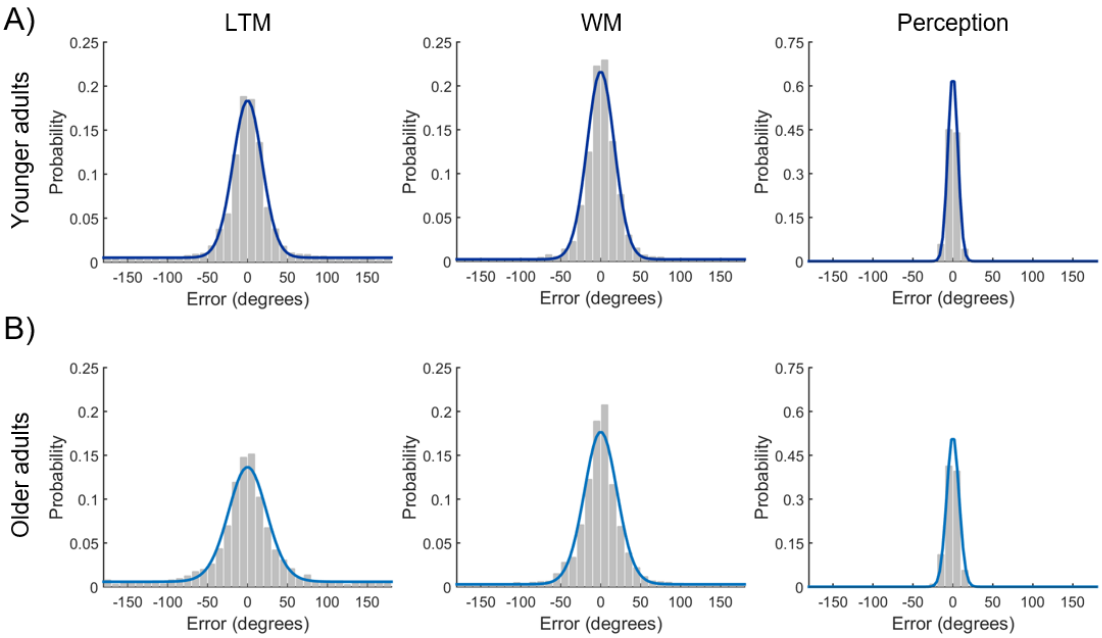

Figure 2. Distribution of errors in the LTM, WM and perception colour report tasks in the A) younger and B) older adults. Coloured lines (dark blue: younger adults, light blue: older adults) illustrate response probabilities predicted by the mixture model (model fitted to aggregate data for visualization). Note the different scaling of the y-axes for the perception task.

Table 3. *Mean BIC difference between the preferred model (Model A: target von Mises + uniform) and the two alternative models (Model B: target von Mises, Model C: target von Mises + uniform + non-target von Mises) in each age group.*

	Younger adults		Older adults	
	BIC Mod B – Mod A	BIC Mod C – Mod A	BIC Mod B – Mod A	BIC Mod C – Mod A
LTM	26.96	4.31	14.66	4.49
WM	19.78	4.31	17.71	4.02
Perception	7.66	3.32	13.09	3.15

Note. Mod A = Model 2; Mod B = Model B; Mod C = Model C.

Comparison of mean parameter estimates in the LTM task indicated no significant differences in the probability of successful long-term memory retrieval between the age groups, $t(42) = 0.76$, $p = .454$, $BF_{01} = 2.67$, but a significant decline in memory precision in the older group, $t(42) = 4.12$, $p < .001$, $d = 1.24$ (see Figure 3 and Table 4). This result was supported by the aggregate analyses indicating no significant age differences in retrieval success (young: 0.82, old: 0.77, $p = .272$), but an age-related decline in memory precision (young: 10.00 old: 5.68, $p < .001$). The deficit in LTM precision was observed to be disproportionate to any age differences in the probability of successful LTM retrieval as indicated by a significant interaction between the factors of memory measure (retrieval success vs. precision) and age group (young vs. old) in a mixed ANOVA, $F(1, 42) = 4.26$, $p = .045$, *partial* $\eta^2 = 0.09$ (retrieval success and precision estimates z-scored).

Similarly, in WM, no significant age differences in the probability of successful memory retrieval were observed, $t(42) = 0.80$, $p = .428$, $BF_{01} = 2.60$, but the older group displayed a significant reduction in memory precision, $t(42) = 3.12$, $p = .003$, $d = 0.94$, relative to the younger adults (see Figure 3 and Table 4). The aggregate analysis of WM retrieval error data similarly indicated no significant differences in the probability of successful retrieval (young: 0.91, old: 0.90, $p = .667$), but a significant decline in memory precision in the older group (young: 11.73, old: 5.68, $p < .001$). However, no evidence for a significantly disproportionate deficit in memory precision in the WM task was observed, $F(1, 42) = 2.15$, $p = .150$, $BF_{01} = 1.13$ (estimates z-scored).

Lastly, the age groups did not differ significantly in terms of the probability of reporting the correct target colour in the perception task, $t(42) = 1.70$, $p = .097$, $BF_{01} = 1.07$ (see Figure 3 and Table 4). However, even in the perceptual task, the older adults were significantly less precise at matching the colour of the objects than the younger adults, $t(42) = 3.40$, $p = .001$, $d = 1.03$ (see Figure 3 and Table 4), despite the stimulus display being simultaneously in view as participants selected their response. Similarly, in the aggregate analysis no significant differences in the probability of reporting the correct target colour were detected between the age groups (young: 0.99, old: 0.98, $p = .103$), however the older adults were significantly less precise (young: 88.45, old: 52.60, $p < .001$). No evidence for a significantly disproportionate deficit in precision in the perceptual task was observed, $F(1, 42) = 1.33$, $p = .256$, $BF_{01} = 1.82$ (estimates z-scored).

Table 4. *Mean model-estimated probability of target reports (pT) and precision (K) in each age group and task version. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	pT	Kappa	pT	Kappa
LTM	0.83 (0.15)	11.10 (5.03)	0.80 (0.14)	6.30 (2.17)
WM	0.92 (0.07)	12.57 (5.27)	0.91 (0.07)	8.44 (3.28)
Perception	1.00 (0.01)	98.63 (41.31)	0.99 (0.01)	64.51 (22.44)

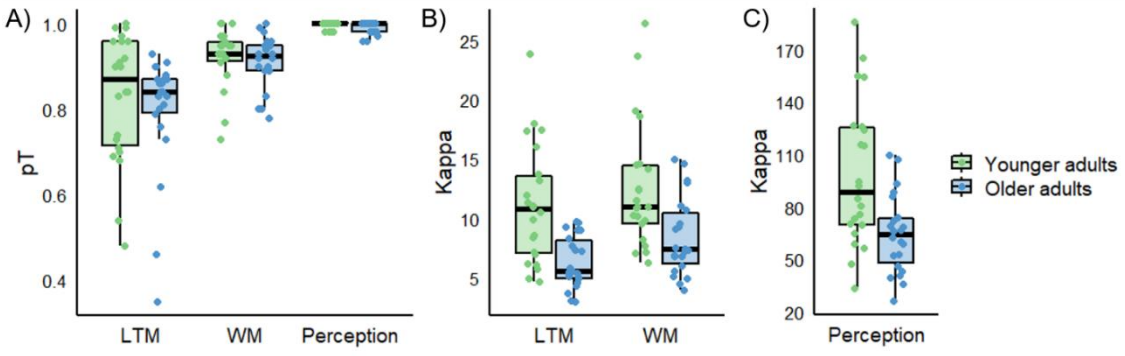

Figure 3. Distribution of the model-estimated A) probability of target reports (*pT*) and B) precision (*K*) in the LTM, WM and perceptual task in each age group. Boxplots display the median and upper and lower quartiles, and error bars the largest/smallest

value within 1.5 interquartile range from the upper/lower quartile. Jittered data points display individual participant parameter estimates.

In each age group separately, I examined the effects of perceptual precision and WM precision alone, as well as the combination of these two variables, on the precision of LTM retrieval using linear regression (see Figure 4). In younger adults, a model including both perceptual and WM precision as predictor variables did not significantly predict the precision of LTM retrieval, R^2 = .12, $F(2, 19) = 1.24$, p = .311, BF_{01} = 2.22, nor did either of these two variables alone (perception: R^2 = .11, $F(1, 20) = 2.54$, p = .126, BF_{01} = 1.07; WM: R^2 = .01, $F(1, 20) = 0.14$, p = .717, BF_{01} = 2.48). In contrast, in the older group, a model including both perceptual and WM precision was a significant predictor of LTM precision, R^2 = .36, $F(2, 19) = 5.45$, p = .014. This result was driven by a significant effect of WM precision on LTM precision, R^2 = .35, $F(1, 20) = 10.67$, p = .004, whereas perceptual precision alone did not significantly predict LTM precision in the older group, R^2 = .12, $F(1, 20) = 2.68$, p = .117, BF_{01} = 1.03. In order to examine whether the relationship between WM precision and LTM precision significantly differed between the younger and older adults, I further computed a cross-group regression analysis of LTM precision with the predictors of age group and WM precision. The interaction term between age group and WM precision was not significant in this model however, $t(40) = 1.03$, p = .307, BF_{01} = 1.65, therefore not providing evidence for a significantly different relationship between WM and LTM precision between the age groups.

Additionally, linear regression analyses indicated a trend for perceptual precision to predict WM precision in both the younger, R^2 = .15, $F(1, 20) = 3.60$, p = .072, and older adults, R^2 = .15, $F(1, 20) = 3.41$, p = .080. A trend for a relationship between the success of WM and LTM retrieval was also evident in the young, R^2 = .16, $F(1, 20) = 3.68$, p = .069, but not in the older group, R^2 = .00, $F(1, 20) = 0.05$, p = .825, BF_{01} = 2.56. The success of WM retrieval was not significantly related to LTM precision (young: R^2 = .01, $F(1, 20) = 0.15$, p = .705, BF_{01} = 2.47; old: R^2 = .01, $F(1, 20) = 0.16$, p = .698, BF_{01} = 2.46) in either age group. Note that the relationship between the probability of successful target reports in the perceptual task and other performance measures was not examined due to lack of variability on this measure in both age groups (younger adults *M*: 1.00, *SD*: 0.01, older adults *M*: 0.99, *SD*: 0.01).

Given that WM precision accounted for 35% of variance in the precision of LTM retrieval in the older group, I next examined whether the age-related deficits in LTM precision persisted after controlling for the age-related reductions in the precision of WM retrieval. Critically, significant age-related declines in the precision of LTM retrieval were still observed in an ANCOVA after controlling for variability in WM precision, $F(1, 41) = 10.23$, $p = .003$, *partial* $\eta^2 = .20$, and after controlling for variability in both WM and perceptual precision, $F(1, 40) = 6.41$, $p = .015$, *partial* $\eta^2 = .14$.

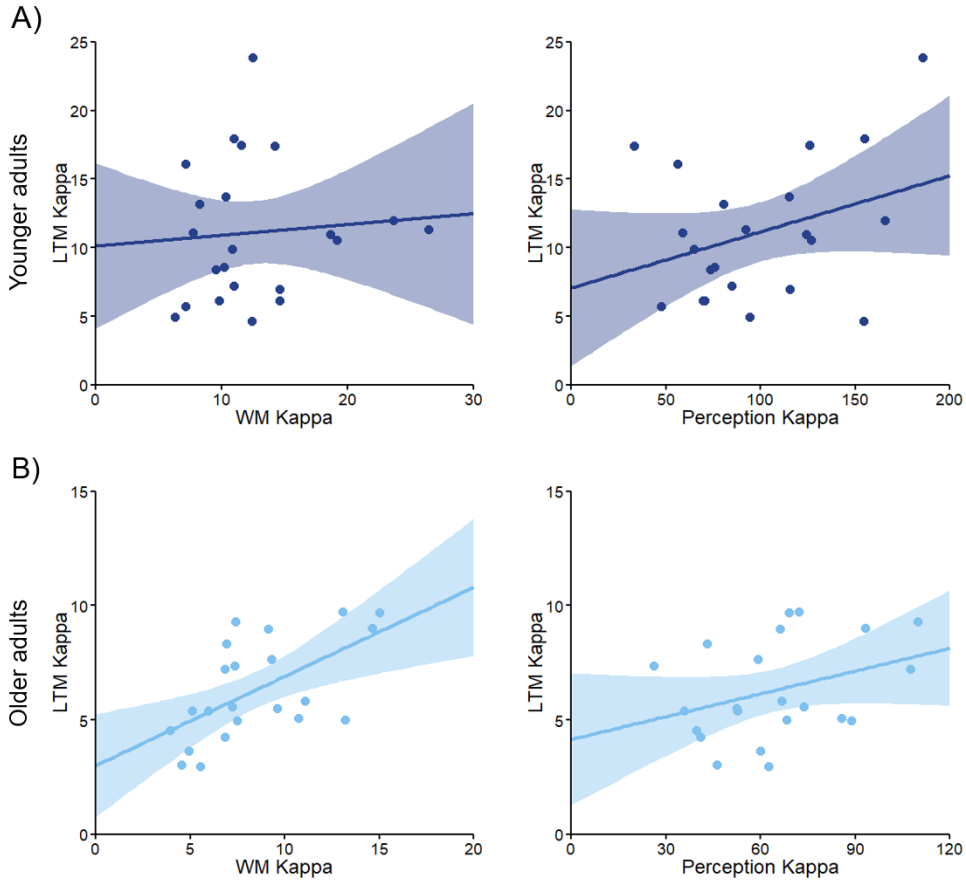

Figure 4. Relationship between LTM and WM precision, and LTM and perceptual precision in the A) younger and B) older adults. Note the different scaling of axes between the age groups.

Discussion

The present experiment examined whether age-related declines in the precision of episodic memory retrieval may be partially, or fully, explained by age-related decreases

in the fidelity of perception and/or working memory. Consistent with findings from Chapter 2, I here observed significant age-related declines in the precision of LTM retrieval for object colours. Additionally, age-related decreases in precision were evident in the older group in both the perceptual and the working memory task. In contrast, no significant age differences in the probability of successful target reports were detected in any of the three tasks. However, given the weak evidence provided by the Bayesian analyses in favour of these null findings, the selectivity of precision deficits in the current tasks remains unclear. Examination of the relationships between perceptual, WM and LTM indicated a significant contribution of WM precision to individual differences in the precision of LTM retrieval in older age. However, age-related declines in the precision of LTM still persisted after controlling for variability in the fidelity of both perception and WM. Together, these findings suggest a contribution of decreases in WM precision to declines in the precision of LTM in older age, but indicate that the age-related reductions in LTM precision cannot fully be explained by differences in the fidelity of information processed at lower levels, suggesting additional degradation of information retained in LTM.

The current result of reduced precision of WM retrieval in older age is consistent with previous findings demonstrating age-related decreases in the fidelity of short-term memory retrieval (Noack et al., 2012; Peich et al., 2013; Pertzov et al., 2015). While previous studies have employed simple shape stimuli such as coloured squares (Noack et al., 2012) and bars (Peich et al., 2013), as well as more complex but unfamiliar object stimuli (Pertzov et al., 2015), the current results further extend the findings of age-related loss of WM precision to features bound to familiar objects. Interestingly, in a previous study employing continuous assessment of working memory retrieval, age-related increases in binding errors (i.e., mistakenly reporting the cued feature of an uncued object from the same encoding display), in addition to decreases in memory precision, were observed (Peich et al., 2013). In contrast, in the current experiment, the model with von Mises and uniform components was found to provide a better fit for participants' working memory (as well as perceptual and long-term memory) performance than a model further incorporating von Mises distributions around the non-target feature values from the same encoding display. Therefore, evidence for the presence of binding errors in either of the age groups was not observed in the current WM, or the LTM and perception, tasks. It may be that this discrepancy between the current and previous findings can be partially

explained by differences in stimuli used. In contrast to the simple shape stimuli employed Peich and colleagues (2013), the object stimuli used in the current experiment may have resulted in enhanced performance because participants could draw on each object's rich, semantic representation, with which to bind the individual target features. This hypothesis is in line with previous reports demonstrating a benefit of real-word object stimuli for working memory performance (Brady, Störmer, Alvarez, 2016), as well as preserved ability to utilize semantic information to support memory functioning in older age (Crespo-Garcia, Cantero, & Atienza, 2012; Mohanty, Naveh-Benjamin, & Ratneshwar, 2016; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005).

In addition to the mean level declines in WM precision detected in the older group, variability in WM precision was a significant predictor of the precision of LTM retrieval in the older adults. This is in line with previous findings demonstrating a relationship between WM and LTM performance in older age (Bender & Raz, 2012; Hertzog et al., 2003; Hultsch et al., 1990; Park et al., 2002, 1996). However, while the contribution of WM to age-related LTM deficits has often been interpreted in light of reduced processing resources (e.g., Bender & Raz, 2012; Hertzog et al., 2003; Park et al., 2002), as well as binding deficits (Bartsch et al., 2019; Chen & Naveh-Benjamin, 2012), the current experiment provided novel evidence for a contribution of reduced precision of WM representations to declines in the quality of LTM retrieval in older age. This relationship may reflect an influence of WM on the formation of long-term memories (Blumenfeld & Ranganath, 2006; Davachi et al., 2001; Ranganath et al., 2005), where the precision of long-term memory representations may be constrained by the fidelity of this information in working memory during encoding. Alternatively this relationship could arise via a common mechanism, such as decreased signal-to-noise ratio of neural processing (Li et al., 2001; Welford, 1981), or attentional limitations at encoding (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Naveh-Benjamin, Craik, Perretta, & Tonev, 2000), constraining the fidelity of mnemonic representations over both short and long term in older age.

Interestingly, no significant relationship between WM and LTM precision was detected in the current data in the younger adult group. However, the Bayes factor analyses did not provide strong evidence in favour of these null results, and furthermore no significant differences in the relationship between WM and LTM precision were detected between the age groups. It is possible that the failure to detect such effects could reflect ceiling

effects in memory precision in the younger adults. Whether WM precision might predict the precision of LTM retrieval in younger adults also therefore remains to be determined.

In addition to declines in memory precision, the fidelity of reconstructing the object colours in the perceptual task exhibited age-related declines also. This is in accordance with previous reports displaying age-related changes in colour discrimination (Fiorentini, Porciatti, Morrone, & Burr, 1996; Knoblauch, Vital-Durand, & Barbur, 2001). Despite significant age-related declines, variability in perceptual fidelity was not a significant predictor of the precision of LTM retrieval in the older, or younger, group. Indeed, in contrast to the memory tasks, the fidelity of colour reports in the perception task was high in both age groups. Given the limited power of the current sample size to detect smaller effects (such as $R^2 \sim 0.1$ observed for the relationship between perceptual and LTM precision in the current data), as well as the weak evidence in support of the null finding observed in the Bayesian analysis, a subtler contribution of perceptual fidelity to the fidelity of LTM memory retrieval cannot be excluded. Indeed, a trend for a positive relationship between perceptual precision and WM precision was observed in both age groups, suggesting that the fidelity of perceptual processing may be related to the fidelity of short-term memory retrieval, even if not of long-term memory. It may also be that tasks assessing the fidelity of more complex perceptual representations, rather than single object attributes, may better predict LTM performance in older age (Trelle et al., 2017). Furthermore, although the lack of response time limit should have minimized the contribution of potential age differences in sensorimotor accuracy to performance differences in the perceptual, and the memory tasks, a potential contribution of sensorimotor decreases to the observed age differences cannot be excluded. However, controlling for perceptual task performance in the memory precision analyses should have minimised any influence of perceptual or sensorimotor differences.

Critically, the results of the current experiment demonstrated that significant age-related declines in the precision of LTM retrieval persisted after controlling for individual differences in the precision of perception and WM representations. This finding indicates that age-related declines in the fidelity of information processed at lower levels could not fully account for the age-related deficit in LTM precision. These results are in line with previous studies demonstrating that while WM deficits may contribute to age-related declines in LTM performance, they cannot solely account for the LTM impairments (e.g., Bartsch et al., 2019; Stine & Wingfield, 1987). For instance, a recent study demonstrated

that despite matching WM binding performance between younger and older adults, significant declines in LTM performance on an associative retrieval task still persisted (Bartsch et al., 2019). Consistent with this, the current findings suggest additional age-related degradation of information retained in LTM over and above that explained by age differences in WM precision. An interesting question for future studies to address is whether this decline in memory fidelity may reflect a loss of memory precision over time, and/or additional noise arising during retrieval.

To conclude, the findings from the current experiment demonstrated age-related declines in the fidelity of object colour representations across perception, WM and LTM. While variability in WM precision predicted the precision of LTM retrieval in the older group, differences in perceptual processing were not a significant contributor to individual differences in the fidelity of LTM retrieval. Importantly, significant age differences in the precision of LTM retrieval persisted after controlling for variability in the fidelity of both perception and WM, suggesting additional age-related degradation of memory precision during storage and/or retrieval from LTM. The experiment presented in the next chapter will use fMRI to more directly assess the contribution of age-related changes during memory encoding and retrieval to declines in the precision of episodic memory.

Chapter 4: Encoding and retrieval contributions to age-related changes in the success and precision of episodic memory

The behavioural experiments described in the previous chapters showed evidence for differential effects of healthy ageing on the success and precision of episodic memory, however the neural mechanisms underlying age-related changes in these two memory components are yet to be characterized. Previous findings from younger adults have suggested retrieval activity in dissociable brain regions to support the success and precision of episodic memory, with the binary success of memory retrieval scaling with hippocampal activity and the graded precision of retrieved memories with activity in the angular gyrus (Richter, Cooper et al., 2016). However, less is known about whether separable encoding mechanisms may also contribute to the later accessibility and fidelity of episodic memories, and if the neural activity underlying these two aspects of episodic memory differs in older age. The experiment presented in the current chapter used functional magnetic resonance imaging (fMRI) combined with a continuous report task, adapted from the behavioural experiments described in previous chapters, to investigate age-related changes in the encoding and retrieval activity supporting the success and precision of episodic memory. The experiment aimed to assess 1) whether age-related decreases in retrieval success and memory precision may be associated with distinct neural changes in the hippocampus and angular gyrus during memory retrieval, 2) whether distinct encoding mechanisms may support the later success and precision of episodic memory, and 3) if the encoding activity contributing to later memory success and precision differs between younger and older adults.

Introduction

Recently, there has been growing interest in the neural basis of episodic memory precision in younger adults (Cooper & Ritchey, 2019; Montchal, Reagh, & Yassa, 2019; Nilakantan et al., 2017; Richter, Cooper et al., 2016; Stevenson et al., 2018). However, little is known about the neural changes that might underlie age-related deficits in the fidelity of episodic memory retrieval. Episodic memory retrieval is thought to rely on a network of subcortical and cortical brain regions, including the medial temporal lobe, medial prefrontal cortex, and medial and lateral parietal cortices (Ranganath & Ritchey, 2012; Rugg & Vilberg, 2013). While previous studies using categorical measures of

memory performance (e.g., correct/incorrect source memory, remember/know) have often observed regions within this network to co-activate during successful recollection (Duarte, Henson, & Graham, 2011; Hayama, Vilberg, & Rugg, 2012; Kim, 2010; Yonelinas, 2005), more recent evidence using continuous measures of retrieval performance has suggested dissociable roles for regions of this network in distinct aspect of episodic memory retrieval (Richter, Cooper et al., 2016). Specifically, Richter, Cooper and colleagues (2016) demonstrated that while hippocampal activity was increased when participants successfully retrieved information about a study event versus when they failed to do so, activity in the angular gyrus tracked the precision of participants' successfully retrieved memories on a continuous scale (Richter, Cooper et al., 2016). Consistent with these findings, others have shown parietal event-related potentials (ERPs) to be sensitive to not only the success of episodic memory retrieval but also to the quality of the retrieved information (Murray, Howie, & Donaldson, 2015). Moreover, transcranial simulation of the lateral parietal cortex has been observed to selectively enhance the precision of episodic recollection (Nilakantan et al., 2017), providing further evidence for the role of this region in supporting the precision of episodic memory retrieval.

The proposed roles of the hippocampus and the angular gyrus in the success and precision of memory retrieval, respectively (Richter, Cooper et al., 2016), are consistent with previous accounts of hippocampal and parietal contributions to episodic memory retrieval. In response to a partial cue, the hippocampus is thought to initiate memory retrieval via the mechanism of pattern completion, providing a thresholded memory signal denoting instances where a cue either succeeds or fails to elicit recollection (Norman, 2010; Yonelinas, 2002). When retrieval succeeds, the hippocampus is thought to facilitate the reinstatement of the retrieved content in the distributed cortical regions originally encoding the information (Bosch, Jehee, Fernandez, & Doeller, 2014; McClelland et al., 1995; Staresina et al., 2012; Treves & Rolls, 1994). The angular gyrus has been proposed to play a role in the online maintenance and representation of the retrieved memories, integrating information across the multiple domain-specific cortical regions (Bonnici et al., 2016; Rugg & King, 2018; Shimamura, 2011). In addition to memory precision, activity in the angular gyrus has also been observed to correlate with the detail and vividness of episodic memory retrieval (Bonnici et al., 2016; Kuhl & Chun, 2014; Vilberg & Rugg, 2007, 2009), consistent with the view of this region supporting

qualitative aspects of memory retrieval. However, others have also highlighted a potential role for the medial temporal lobes in episodic memory precision, in particular for the retrieval of spatial and temporal aspects of previous experiences (Montchal et al., 2019; Nilakantan et al., 2018; Stevenson et al., 2018).

Previous neuroimaging investigations have demonstrated age-related decreases in both hippocampal (Daselaar et al., 2006; Dennis et al., 2008; Giovanello & Schacter, 2012; Cansino et al., 2015; Tsukiura et al., 2011) and parietal (Angel et al., 2013; Daselaar et al., 2006; Duarte et al., 2010) retrieval activity associated with comparisons between successful and unsuccessful memory retrieval. Age-related reductions in hippocampal activity have often been linked to deficits in retrieving associations between units of information (e.g., Kukolja, Thiel, Wilms, Mirzazade, & Fink, 2009), or in engaging in recollection-based retrieval (e.g., Daselaar et al., 2006). Parietal declines have also been linked to age-related recollection decreases (e.g., Angel et al., 2013; Daselaar et al., 2006), however, their specific functional role, and whether they may reflect a contribution distinct from hippocampal decreases, is yet to be established.

In addition to retrieval impairments, deficient encoding of information into memory is thought to play a role in age-related episodic memory decline (Craik & Rose, 2012). In younger adults, successful retrieval of episodic memories has been shown to be associated with increased activity in the medial temporal, prefrontal, and occipitotemporal regions during encoding (Kim, 2011; Paller & Wagner, 2002; Spaniol et al., 2009). Of these regions, the hippocampus is thought to bind distinct units of information together into a coherent memory representation (Davachi, 2006; Moscovitch et al., 2016; Staresina & Davachi, 2008), while the posterior cortical regions are thought to be involved in the perceptual processing of the encoded material (Garoff, Slotnick, & Schacter, 2005; Kim & Cabeza, 2007), and the lateral prefrontal cortex in orchestrating strategic encoding processes prioritising information relevant for current task goals (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). In contrast to regions displaying positive subsequent memory effects (i.e., increased encoding activity for subsequently remembered information), decreases in encoding activity in the ventrolateral parietal cortex are typically associated with subsequent memory success (Daselaar et al., 2009; Uncapher & Wagner, 2009). These negative subsequent memory effects may reflect a shift in attentional focus from internally-oriented processes to

externally-oriented cognition during memory encoding (Daselaar et al., 2004; Daselaar et al., 2009).

Despite some work indicating that the encoding correlates of successful memory may display a degree of specificity to the type of information encoded (e.g., object vs. scene information) (Staresina, Duncan, & Davachi, 2011), as well as the type of retrieval process later engaged (e.g., recollection vs. familiarity, or free recall vs. recognition) (Ranganath et al., 2004; Staresina & Davachi, 2006), the specific encoding substrates supporting the later access to memory and memory fidelity are currently underspecified. Indeed, the majority of previous studies investigating the neural basis of memory precision have focused on examining retrieval, rather than encoding, mechanisms (Montchal et al., 2019; Murray et al., 2015; Nilakantan et al., 2017; Richter et al., 2016; Stevenson et al., 2018, but see Cooper & Ritchey, 2019). In addition to being dissociable at retrieval (Richter, Cooper et al., 2016), it is possible that distinct encoding mechanisms may support the later success and precision of memory retrieval. While the hippocampus may support the later successful retrieval of associations between an object and its features (Davachi, 2006), mnemonic fidelity of object features might be more dependent on the cortical regions representing this information (Garoff et al., 2005). Whether in addition to supporting memory fidelity during retrieval, encoding activity in the parietal cortex may be contribute to later memory quality (e.g., Tibon et al., 2019), is currently unclear. Furthermore, the prefrontal cortex may support later memory fidelity by mediating top-down allocation of attentional resources to encoding of goal-relevant stimulus features, as well as later memory accessibility via the employment of deep and elaborative encoding strategies enabling the formation of strong associations between an object and its features (Blumenfeld & Ranganath, 2007; Chun & Turk-Browne, 2007).

Age-related decreases in encoding activity that differentiates successful and unsuccessful memory formation have typically been observed in visual regions (Maillet & Rajah, 2014a; Park et al., 2013; Wang & Cabeza, 2016), whereas in the prefrontal cortex age-related increases in subsequent memory effects have frequently been observed (Dennis, Kim et al., 2007; Duverne, Motamedinia, & Rugg, 2009; Gutchess et al., 2005; Maillet & Rajah, 2014a; Morcom et al., 2003). The age-related over-recruitment of prefrontal cortex has often been viewed as compensatory (Davis et al., 2008), however more recent findings argue against this interpretation (Morcom & Friston, 2012; Morcom & Henson, 2018). Indeed, age-related decreases in prefrontal activity associated with later successful

memory retrieval have also been frequently reported, in particular for the encoding of associative memories (Dennis, Hayes, et al., 2008; Dulas & Duarte, 2011; Vidal-Piñeiro et al., 2018).

Despite the prevalent notion of hippocampal binding deficits playing a key role in age-related memory decline (e.g., Shing et al., 2010), results regarding functional changes in this region during episodic encoding have been somewhat inconsistent. Both hippocampal decreases (Dennis, Daselaar, & Cabeza, 2007; Dennis, Hayes et al., 2008; Dennis, Kim et al, 2007) and increases (Dulas & Duarte, 2011) for successful memory encoding have been previously reported, with two recent larger scale studies finding no effect of age on the magnitude of hippocampal subsequent memory effects across the lifespan (De Chastelaine et al., 2016; Vidal-Piñeiro et al., 2018). Diminished negative subsequent memory effects in the parietal cortex have, on the other hand, been more consistently observed in older age (e.g., De Chastelaine et al., 2015; Maillet & Rajah, 2014a; Miller et al., 2008; Park et al., 2013), potentially reflecting deficient reallocation of cognitive resources to memory encoding in older age (De Chastelaine et al., 2015; De Chastelaine, Wang, Minton, Muftuler, & Rugg, 2011).

The fMRI experiment presented in the current chapter sought to gain a more detailed understanding of the neural basis of age-related episodic memory decline. While previous investigations have provided evidence for age-related differences in both encoding and retrieval activity underlying episodic memory, such studies have typically employed only binary or categorical measures of memory. Accordingly, the knowledge of the precise role of these changes in distinct aspects of episodic memory function is still limited. Indeed, to fully understand the specific role of age-related functional changes in different brain regions, it is important to deconstruct memory performance into its constituent parts.

In the current experiment, young and healthy older adults completed a version of the continuous report task in the MRI scanner. This enabled the examination of age-related changes in both encoding and retrieval activity associated with the (subsequent) success and precision of memory retrieval. During retrieval, consistent with previous results from younger adults (Richter, Cooper et al., 2016), hippocampal activity was expected to be associated with the binary success of memory retrieval, while activity in the angular gyrus was predicted to correlate with the precision of retrieved memories. Behavioural

reductions in the success and precision of memory retrieval in older age may thus be accompanied by decreases in retrieval activity in the hippocampus and angular gyrus, respectively. Furthermore, at encoding, age-related decreases in hippocampal activity may be evident for memory success, whereas age-related declines in memory precision may be more dependent on the integrity of encoding processes in the ventral visual regions. Moreover, it is possible that encoding alterations in the angular gyrus may play a role in the decreased precision of episodic memory retrieval in older age. Age-related encoding decreases in the prefrontal cortex may further contribute to decreases in both memory components due to the diminished employment of strategic encoding processes enhancing both the fidelity and accessibility of memory representations.

In addition to these hypothesized regional differences, the selectivity of neural activity underlying the success and precision of memory retrieval may differ between the age groups as older age has often been observed to be associated with loss of specificity, or dedifferentiation, of neural function (Goh, 2011; Koen & Rugg, 2019). For instance, while younger adults recruit differential neural circuits for explicit versus implicit memory, as well as for episodic versus autobiographical retrieval, the specificity of neural activity underlying these cognitive processes has been observed to be reduced in older age (Dennis & Cabeza, 2011; St-Laurent et al., 2011). Thus, while the younger adults may recruit distinct encoding and retrieval substrates for the (subsequent) success and precision of episodic memory, neural activity underlying these two aspects of memory retrieval may be less dissociable in older age (Goh, 2011; Koen & Rugg, 2019).

Methods

Participants

Twenty-one younger (18-29 years old) and 24 older adults (60-75 years old) took part in the current experiment. None of the participants had taken part in the experiments described in the previous chapters. All participants were right-handed, native English-speakers, had normal or corrected-to-normal vision, no colour blindness, and no current or historical diagnosis of any neurological, psychiatric, or developmental disorder, or learning difficulty. Participants further indicated no current use of any psychoactive medication, and no medical or other contradictions to MRI scanning (e.g., metal implants, claustrophobia). Two older adults did not complete the full scan session and

were excluded from the analysis. One older adult was further excluded due to low visual acuity (as indicated by a visual acuity test prior the scan), and one younger and one older adult due to excessive movement in the scanner (> 4mm), leaving 20 younger adults and 20 older adults to contribute to the present analyses. Demographic information for the 40 participants is displayed in Table 1. All older volunteers scored within the healthy range (≥ 26, *M*: 28.00, *SD*: 1.32) on the MoCA (Nasreddine et al., 2005) screening test for mild cognitive impairment. The groups did not differ in terms of number of years of formal education completed, $t(38) = 0.29$, $p = .783$, $d = 0.09$, however the older adults scored significantly higher than the younger adults on the SILVS (Zachary & Shipley, 1986) measure of crystallized intelligence, $t(38) = 4.24$, $p < .001$, $d = 1.34$.

Participants were recruited via the University of Cambridge Memory Lab volunteer database, University of Cambridge Psychology Department Sona volunteer recruitment system (Sona Systems, Ltd), and community advertisements. All participants were reimbursed £30 for the scan session, as well as for any travel expenses occurred, and gave written informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee.

Table 1. *Participant demographic information: means (standard deviations).*

	Younger adults	Older adults
N	20	20
Age	22.10 (3.10)	70.20 (4.19)
Gender (N)	8 M, 12 F	7 M, 13 F
Years of education	16.90 (2.79)	16.60 (3.94)
SILVS	32.50 (3.91)	37.50 (2.70)
MoCA	n/a	28.00 (1.32)

Note. M = males, F = females.

Materials

Stimuli for the memory task consisted of 180 scene and 180 object images. The scene images, depicting outdoor landscapes, were obtained from an existing scene stimuli set (Richter, Cooper et al., 2016) and Google image search. The object images were obtained from an existing object stimuli set (Brady et al., 2013) and consisted of distinct everyday

objects that had been converted to the same initial colour hue. One object image was randomly paired with each scene image forming a set of 180 trial-unique study displays (size: 750 x 750 pixels) (see Figure 1). For each display, the location and colour of the object were randomly chosen from circular parameter spaces (0-360 degrees). All participants viewed the same encoding displays during the study phase.

Design and procedure

The memory task consisted of 9 study-test blocks (see Figure 1) divided over 9 functional runs (one study and one test phase per run). In each task block, participants were first presented with 20 stimuli displays in a row (stimulus duration: 5s), and were instructed to try to memorize the location and colour of each object the best they could. The study and test phases were separated by a 10s delay, during which a "Get Ready" message was displayed on a black screen. In the test phase, participants were asked to reconstruct *either* the location *or* the colour of each object previously studied (one feature question per object, 20 retrieval trials per block). For each question, the test object reappeared on its associated background with the word "Location" or "Colour" presented in the centre of the background to indicate the type of feature question asked on that trial. The initial appearance of the questioned feature at test was randomly chosen from a circular parameter space (0-360 degrees), and the appearance of the unquestioned feature remained unchanged from study to test. In other words, for location questions, the test object reappeared in its original colour, but in a randomly selected location, whereas for colour questions the test object reappeared in its original location but in a randomly chosen colour. Participants were able to change the location or the colour of the object by moving a slider left and right around a 360-degree response dial using their middle and index finger on a button box, and were instructed to try and recreate the object's original features as accurately as they could. Participants confirmed their answer by pressing a third key on the button box with their thumb. The retrieval phase was self-paced with a minimum trial length of 7s and a maximum trial length of 11s. If the participant responded in under 6.7s, the retrieval display remained on the screen until 7s had passed before moving on to the next question. If the participant responded in over 6.7s, the retrieval display remained on the screen for another 300ms before moving on to the next question. The maximum trial length of 11s was selected based on older adults'

mean reaction time + 2 *SDs* in a self-paced pilot version of the task to give sufficient response time for the older adults. Excluding one older participant who reported difficulty in reaching the thumb button (percentage of trials where no response was confirmed: 70%; note that this participant had comparable memory performance to the remaining older adults), the percentage of trials where response selection was not confirmed in time was very low in each age group (young adults *M*: 1.36%, *SD* 1.77%, older adults *M*: 2.92%, *SD*: 3.14%), though there was a trend for a significant difference between the young and older adults, $t(37) = 1.93$, $p = .062$. Furthermore, although mean response times were faster in the younger group (*M:* 5.64, *SD:* 0.68) than in the older group (*M:* 6.49, *SD:* 0.64), $t(38) = 4.12$, $p < .001$, $d = 1.30$, both groups on average responded well under the 11s limit. In the case a participant failed to confirm their answer within the maximum allotted time, their last position on the response wheel was recorded as their answer.

The type of feature question asked for each object was randomised across displays, but constant across participants. The allocation of stimuli displays to task blocks was randomised across participants, and the order of study and test trials within each block pseudorandomised with the constraint of no more than four encoding or retrieval trials in a row for which the same type of feature question was (subsequently) asked. A total of 90 location and 90 colour questions were asked across the task, with 10 questions of each type per task block. Study and test trials were separated by a fixation cross with jittered duration between 0.4s and 2.4s (mean ISI duration: 1s) drawn from an approximate Poisson distribution. After five task blocks, participants were given a 10-minute break from the memory task in the scanner, during which a diffusion-weighted structural scan was acquired.

Prior to the scan, all participants filled in a consent and MRI screening form, and completed practice trials of the memory task. After the scan, participants filled in a post-experiment questionnaire. The older adults further completed the MoCA (Nasreddine et al., 2005) in a separate behavioural testing session prior to the MRI scan.

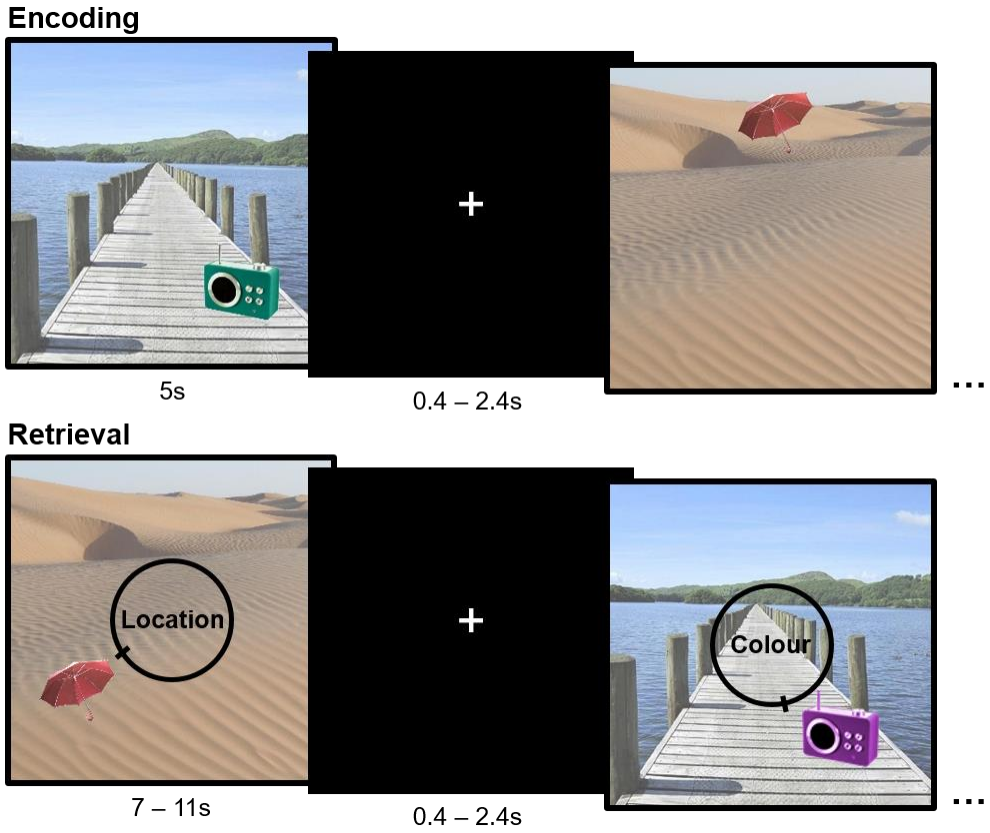

Figure 1. Examples of study and test trials of the memory task completed in the scanner. Participants viewed stimuli displays consisting of one object overlaid on a scene background (stimulus duration: 5s). The location and colour of the object at study were randomly chosen from circular parameter spaces (0-360 degrees). At test, participants recreated *either* the location *or* the colour of each studied object using a 360-degree continuous response dial.

Behavioural analysis

Retrieval error on each trial was calculated as the angular deviation between the participant's response value and the studied target feature value (0 ± 180 degrees). To distinguish between the success and precision of memory retrieval, a mixture model (Bays et al., 2009; Zhang & Luck, 2008) was fitted to each participant's retrieval error data. This model consisted of a von Mises distribution (circular equivalent of a Gaussian distribution) centred at the target feature value and a circular uniform distribution, capturing variability in successful target retrieval and the likelihood of guessing responses, respectively. Retrieval success was defined as the probability of responses

stemming from the target von Mises distribution (*pT*) and retrieval precision as the concentration parameter (*K*) of the target von Mises distribution. These two parameters of memory performance were estimated separately for each participant. Due to the low number of guess trials it was not possible to separate the two feature conditions (location and colour) for fMRI analyses, (cf., Cooper et al., 2017; Richter, Cooper et al., 2016), however behavioural performance is reported also separately for each feature condition.

MRI acquisition

MRI scanning took place at the University of Cambridge Medical Research Council Cognition and Brain Sciences Unit using a 3T Siemens Tim Trio scanner (Siemens, Germany) with a 32-channel head coil. For each participant, a high resolution whole brain anatomical image was acquired using a T1-weighted 3D magnetization prepared rapid gradient echo (MPRAGE) sequence (repetition time (TR): 2.25s, echo time (TE): 3ms, flip angle = 9°, field of view (FOV): 256 x 256 x 192mm, resolution: 1mm isotropic, GRAPPA acceleration factor 2). Functional data were acquired over 9 runs each comprising one task block (one study and one test phase), using a single-shot echoplanar imaging (EPI) sequence (TR: 2s, TE: 30ms, flip angle° = 78, FOV: 192 x 192mm, resolution: 3mm isotropic). Each volume consisted of 32 sequential oblique-axial slices (interslice gap: 0.75mm) acquired parallel to the anterior commissure – posterior commissure transverse plane. The mean number of volumes acquired per functional run was 162.28 (*SD*: 8.69) and did not significantly differ between the age groups (younger adults: 161.60, *SD*: 9.63, older adults: 164.95, *SD*: 7.51, $t(38) = 1.23$, $p = .227$).

fMRI preprocessing

Data preprocessing and analysis was performed with Statistical Parametric Mapping (SPM) 12 (https://www.fil.ion.ucl.ac.uk/spm/) implemented in MATLAB R2016a. The first five volumes of each functional run were discarded to allow for T1 equilibration. Furthermore, any additional volumes collected after each task block had finished were discarded for each participant so that the last volume of each run corresponded to a time point of 2s after the last fixation cross. The functional images were spatially realigned to the mean image to correct for head motion and temporally interpolated to the middle slice

to correct for differences in slice acquisition time. The anatomical image was coregistered to the mean EPI image, bias-corrected and segmented into different tissue classes (grey matter, white matter, cerebrospinal fluid). These segmentations were used to create a study-specific structural template image using the DARTEL (Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra) toolbox (Ashburner, 2007). The functional data was normalized to MNI space using DARTEL and spatially smoothed with an isotropic 8mm full-width at half-maximum (FWHF) Gaussian kernel.

fMRI analysis

To distinguish between successful memory retrieval and guessing on a trial-wise basis, the mixture model (von Mises + uniform distribution) was fitted to all retrieval errors across all participants (7200 trials in total) in order to calculate a cut-off point where the probability of participants' responses stemming from the target von Mises distribution was less than 5% (cf., Richter, Cooper et al., 2016). This cut-off point was established as +/- 59 degrees in the current data and was then used to classify each encoding and retrieval trial as successful (absolute retrieval error $\leq$ 59 degrees) or unsuccessful (absolute retrieval error > 59 degrees). For the successful encoding and retrieval trials, a trial-specific measure of memory precision was further calculated as 180 – participant's absolute retrieval error on that trial for higher values (smaller error) to reflect higher precision (range: 121 – 180). Memory precision was not calculated for unsuccessfully retrieved trials as responses in this condition were randomly distributed and did not carry meaningful information about memory quality. The trials were further separated by task type (encoding vs. retrieval), and the successful trials were separated by the type of feature tested (location vs. colour). Due to the low number of guessing responses per feature condition, it was not possible to model unsuccessful trials separately for each feature condition. Unsuccessful trials were therefore collapsed across the two feature conditions.

For each participant, a first level General Linear Model (GLM) was constructed containing six regressors corresponding to each event of interest (3 encoding events: successful location encoding, successful colour encoding, unsuccessful encoding; 3 retrieval events: successful location retrieval, successful colour retrieval, unsuccessful retrieval). For the successful encoding and retrieval trials, trial-specific estimates of

memory precision were further included as parametric modulators comprising four additional regressors in the model. The precision parametric modulators were rescaled to the range of 0 – 1 (0 = absolute error of 121, 1 = absolute error of 180) to enable the direct comparison of retrieval success and precision effects, and then mean centred for each participant. Neural activity corresponding to the regressors of interest was modelled with a boxcar function convolved with the canonical hemodynamic response function (HRF). Encoding trials were modelled with a duration of 5s. Retrieval trials were modelled with participant's trial-specific response time, or by a duration of 7s if participant's response time did not exceed 7s to ensure that the retrieval event duration corresponded to the duration that the retrieval display remained on the screen. As the cognitive and neural processes of interest were assumed to occur throughout the retrieval event (cf., Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008), and the older adults on average displayed higher reaction times than the younger adults (see the Results section), retrieval trials were modelled with variable duration to ensure that the whole retrieval event was captured for both age groups. Of note, it is possible that this approach could have masked effects related to memory precision if event duration and memory precision were highly correlated. However, across participants the trial-wise correlation between these two variables did not reach significance during location retrieval in either the young, r = -.07, z = - .07, $t(19) = 1.98$, p = .063, or the older adults, r = -.06, z = -.06, $t(19) = 1.50$, p = .149 (participant-specific correlations transformed to Fisher's z before averaging). For colour trials, a small significant negative correlation was detected in both the young, r = -.07, z = -.07, $t(19) = 2.48$, p = .023, and the older adults, r = -.10, z = -.10, $t(19) = 3.64$, p = .002, however the majority of variance in these two measures was still unrelated. Importantly, the correlations did not significantly differ between the age groups for either location, $t(38) = 0.35$, p = .731, or colour, $t(38) = 0.58$, p = .569, retrieval.

Furthermore, the six participant-specific movement parameters estimated during realignment (3 rigid-body translations, 3 rotations) were included as covariates in the first level model to capture any residual movement-related artefacts. Due to the small number of guessing trials in each functional run, data from all functional runs were concatenated for each participant (as often done when classifying trials based on memory performance, c.f., De Chastelaine et al., 2016) and 9 constant block regressors were included as additional covariates. Autocorrelation in the data was estimated with an

AR(1) model and a temporal high pass filter with a 1/128 Hz cut-off was used to eliminate low frequency noise. First level subject-specific parameter estimates were submitted to second level random effects analyses.

Contrasts

The contrasts for the fMRI analysis focused on identifying regions where encoding and/or retrieval activity predicted the success and/or precision of memory retrieval across the age groups, as well as regions that displayed age differences in the relationship between brain activity and these two aspects of memory retrieval. To examine retrieval activity associated with the success of memory retrieval, successful retrieval trials were contrasted to trials where memory retrieval failed (*retrieval success effects*). To identify retrieval activity associated with the precision of memory retrieval, correlations between blood-oxygen-level-dependent (BOLD) signal and the precision parametric modulator were examined (i.e., linear relationship between BOLD signal and precision parametric modulator) (*retrieval precision effects*).

Similarly, for encoding, trials where memory retrieval subsequently succeeded were contrasted to trials where memory retrieval later failed in order to examine encoding activity predicting the later success of memory retrieval (*subsequent retrieval success effects*). To identify encoding activity associated with later memory precision, correlations between BOLD signal and the precision parametric modulator were examined (*subsequent precision effects*).

For the analysis of encoding activity both positive subsequent memory effects, reflecting increased encoding activity for trials that were later successfully retrieved or highly precise (successful > unsuccessful; positive correlation with precision parametric modulator), as well as negative subsequent memory effects, reflecting decreased encoding activity for trials that were later successfully retrieved or highly precise (successful < unsuccessful; negative correlation with precision parametric modulator) were examined as negative subsequent memory effects have previously been observed in one of the regions of interest (ROI), the ventrolateral parietal cortex (Daselaar et al., 2009; Uncapher & Wagner, 2009), and have been shown to be sensitive to ageing (Park et al., 2013). There were no a priori hypotheses regarding negative retrieval effects. Therefore the retrieval analyses focused on positive retrieval effects (successful >

unsuccessful; positive correlation with precision parametric modulator). Age differences in encoding and retrieval activity associated with the success and precision of memory retrieval were assessed with two-sample t-tests.

Regions of interest

The analyses focused on a set of a priori ROIs, including the hippocampus (HC), angular gyrus (AnG), inferior frontal gyrus (IFG) and fusiform gyrus (FFG). The hippocampus and the angular gyrus were chosen based on previous evidence suggesting distinct contributions of retrieval activity in these two regions to the success and precision of episodic memory, respectively (Richter, Cooper et al., 2016), while the inferior frontal and fusiform gyri were selected based on meta-analytic evidence indicating them as key regions displaying subsequent memory effects for visual information (Kim, 2011), as well as due to frequent reports of age-related encoding differences in the inferior frontal (e.g., Morcom et al., 2010; De Chastelaine et al., 2016b) and fusiform cortex (Maillet & Rajah, 2014a; Li et al., 2015). Each ROI comprised the whole anatomical region and was defined by the Automated Anatomical Labelling (AAL) atlas. Separate ROIs for the left and right hemisphere region were created as the lateralization of cognitive processing is often reported to be reduced in older age (Cabeza, 2002).

Statistical significance of the results within each anatomical ROI was assessed using small-volume correction with a peak-level familywise error (FWE) –corrected (based on random field theory) threshold of $p < .05$, correcting for the number of voxels in each ROI. In addition to the ROI analyses, exploratory whole brain analyses were conducted to identify any additional regions displaying age differences in the current paradigm. To assess the statistical significance of results from the whole brain analysis, a peak-level FWE whole brain-corrected threshold of $p < .05$ in combination with a voxel extent of a minimum of 5 contiguous voxels was used. Note that the alpha-level for the ROI analysis was not corrected for the number of ROIs included in the analysis.

Results

Behavioural results

Distributions of participants' retrieval errors (angular deviation between participant's response value and target feature value) across trials in each age group are displayed in Figure 2. A mixed ANOVA with the factors of age group (young vs. old) and feature condition (location vs. colour) indicated a significant main effect of age group, $F(1, 38) = 20.93$, $p < .001$, *partial* $\eta^2 = 0.36$, on mean absolute error (see Table 2). Although significant age differences in mean absolute error were observed in both the location, $t(38) = 2.98$, $p = .005$, $d = 0.94$, and the colour, $t(38) = 5.44$, $p < .001$, $d = 1.72$, condition, a significant interaction between age group and feature condition, $F(1, 38) = 4.73$, $p = .036$, *partial* $\eta^2 = 0.11$, indicated greater age-related increases in absolute error in the colour condition.

Furthermore, a mixed ANOVA with the factors of age group (young vs. old) and feature condition (location vs. colour) indicated a significant main effect of age group, $F(1, 38) = 15.19$, $p < .001$ *partial* $\eta^2 = 0.29$, on mean reaction time (see Table 2). Older adults took significantly longer to respond than the younger adults in both the location, $t(38) = 4.74$, $p < .001$, $d = 1.50$, and the colour condition, $t(38) = 2.43$, $p = .020$, $d = 0.77$. A significant interaction between age group and feature condition, $F(1, 38) = 8.93$, $p = .005$, *partial* $\eta^2 = 0.19$, indicated greater age-related increases in reaction time in the location condition.

Table 2. *Mean absolute error (degrees) and reaction time (s) in each age group and feature condition. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	Absolute error	RT	Absolute error	RT
Location	24.08 (13.64)	5.16 (0.74)	36.98 (13.74)	6.22 (0.67)
Colour	32.72 (13.55)	6.24 (0.66)	53.31 (10.14)	6.78 (0.73)

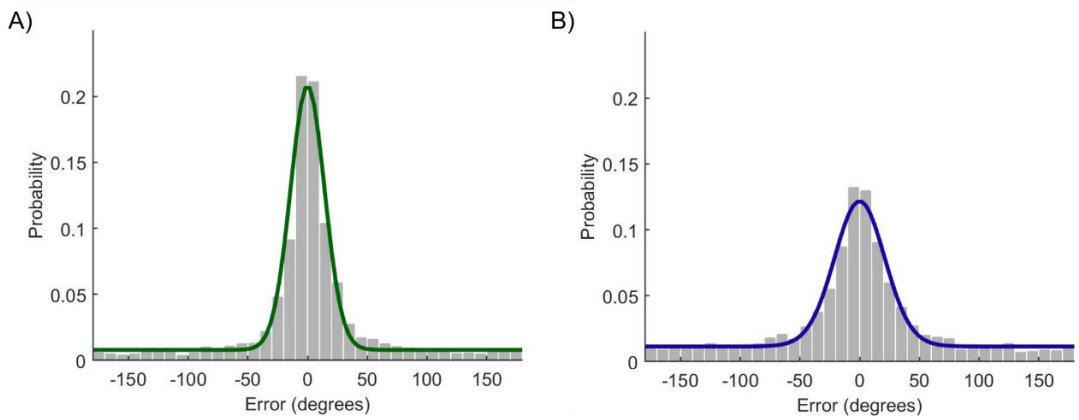

Figure 2. Distribution of retrieval errors (response – target) across all participants and retrieval trials in the A) younger and B) older group (across 3600 trials per group). Coloured lines (green: younger adults, blue: older adults) illustrate response probabilities predicted by the mixture model (von Mises + uniform distribution) fitted to aggregate data from each age group for visualization. The older adults displayed both greater variability in target responses (reflected in the broader Gaussian distribution) and increased probability of guessing responses (reflected in the increased height of the uniform distribution).

Comparison of the model-estimated success (*pT*), and precision (*K*) of memory retrieval computed across the feature conditions indicated that both the probability of successful memory retrieval, $t(38) = 2.57$, $p = .014$, $d = 0.81$, and the precision of memory retrieval, $t(38) = 4.63$, $p < .001$, $d = 1.47$, were significantly reduced in the older relative to the younger group in the current experiment (see Figure 3 and Table 3). Although the effect size for the age-related difference in memory precision was numerically greater than for success (consistent with the results reported in previous chapters), direct comparison of age differences in retrieval success and precision (scores on both measures z-scored for this analysis) did not provide evidence for a significantly greater deficit in memory precision, $F(1, 38) = 1.47$, $p = .233$.

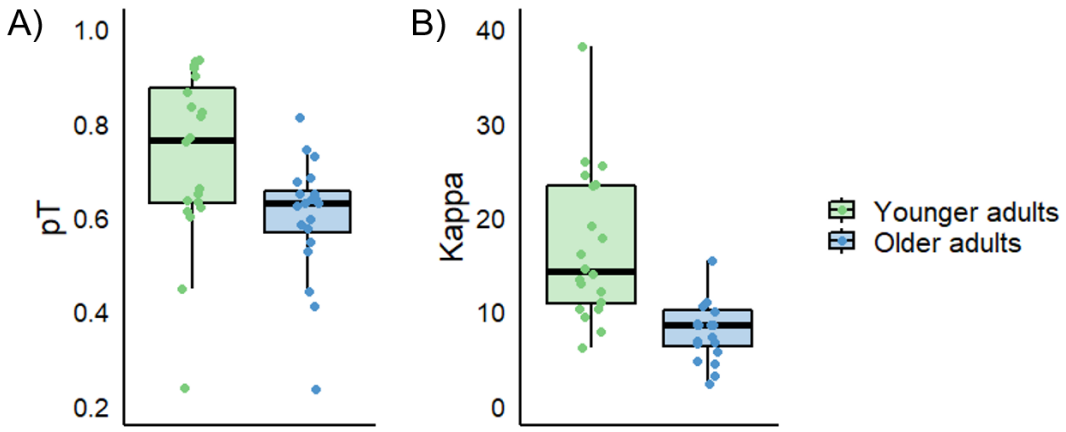

Figure 3. Distribution of the model-estimated A) probability of successful memory retrieval (*pT*) and B) memory precision (*K*) in the younger and older adults. Boxplots display the median and upper and lower quartiles, and error bars the largest/smallest value within 1.5 interquartile range from the upper/lower quartile. Jittered data points display individual participant parameter estimates.

Although for the purposes of the fMRI analysis it was not possible to separate the two feature conditions, on the behavioural level analysis of feature-specific estimates of the probability of successful memory retrieval (*pT*) and memory precision (*K*) was possible. Examination of the feature-specific estimates of the probability of successful memory retrieval (*pT*) with a mixed ANOVA with the factors of age group (young vs. old) and feature condition (location vs. colour) indicated a significant main effect of age group, $F(1, 38) = 11.45$, $p = .002$, *partial* $\eta^2 = 0.23$, and a significant interaction between age group and feature condition, $F(1, 38) = 4.72$, $p = .036$, *partial* $\eta^2 = 0.11$ (see Table 3). While the older adults displayed a significantly lower probability of successful memory retrieval in the colour condition, $t(38) = 3.87$, $p < .001$, $d = 1.22$, age differences in retrieval success in the location condition did not reach significance, $t(38) = 1.80$, $p = .081$. Similarly, the investigation of feature-specific estimates of memory precision with a mixed ANOVA with the factors of age group (young vs. old) and feature condition (location vs. colour) indicated a significant main effect of age group, $F(1, 38) = 15.88$, $p < .001$, *partial* $\eta^2 = 0.30$, and a significant interaction between age group and feature condition, $F(1, 38) = 11.29$, $p = .002$, *partial* $\eta^2 = 0.23$. The older adults exhibited significantly lower precision of memory retrieval in both the location, $t(38) = 3.77$, $p <$

.001, d = 1.19, and the colour condition, $t(38) = 2.76$, p = .009, d = 0.87, with greater age-related declines evident in the location condition.

Direct comparison of age differences in the success and precision of memory retrieval in each feature condition (estimates z-scored) with mixed ANOVAs including the factors of age group (young vs. old) and measure (retrieval success vs. precision) did not provide evidence for significantly greater age differences in the precision of memory retrieval in either the location, $F(1, 38) = 2.03$, p = .163, or the colour, $F(1, 38) = 0.37$, p = .547, condition.

Table 3. *Mean model-estimated probability of successful memory retrieval (pT) and memory precision (K) computed across features and for each feature condition separately. Standard deviations reported in parentheses.*

	Younger adults		Older adults	
	pT	Kappa	pT	Kappa
All	0.76 (0.14)	16.47 (7.66)	0.60 (0.13)	7.98 (3.09)
Location	0.78 (0.15)	35.36 (27.11)	0.69 (0.16)	11.48 (8.20)
Colour	0.76 (0.15)	9.81 (5.10)	0.55 (0.18)	6.02 (3.43)

fMRI results

Retrieval activity associated with memory success and precision across participants

Across the age groups, significant increases in retrieval activity for successful memory retrieval (successful > unsuccessful) were observed in all the ROIs (see Table 4). Of these regions, the bilateral hippocampus, left angular gyrus, right inferior frontal gyrus, and bilateral fusiform gyri also displayed a significant positive relationship between retrieval activity and the precision of memory retrieval (linear increase in BOLD with increase in precision parametric modulator) (see Table 4). A trend for a positive relationship between memory precision and retrieval activity was observed across participants in the left inferior frontal gyrus also, $t(38) = 3.99$, p = .061, whereas no

significant retrieval precision effects were detected in the right angular gyrus (*t*s < 2.89, *p*s > .244).

Table 4. *Regions displaying a significant relationship between retrieval activity and the success and/or precision of memory retrieval across the age groups in the ROI analysis.*

Region	x	y	z	t	p
Successful > unsuccessful					
L hippocampus	-30	-18	-12	6.42	< .001
R hippocampus	18	-3	-15	5.07	.001
L angular gyrus	-39	-57	21	5.20	.001
R angular gyrus	42	-45	36	4.04	.021
L inferior frontal gyrus	-60	6	12	5.24	.003
R inferior frontal gyrus	57	9	9	7.03	< .001
L fusiform gyrus	-30	-33	-27	5.85	< .001
R fusiform gyrus	48	-66	-18	5.22	.001
Positive relationship with precision					
L hippocampus	-30	-18	-15	5.64	< .001
R hippocampus	24	-15	-12	4.58	.003
L angular gyrus	-54	-66	33	5.97	< .001
R inferior frontal gyrus	30	30	-21	4.67	.011
L fusiform gyrus	-33	-24	-18	4.05	.028
R fusiform gyrus	45	-48	-21	4.30	.016

Note. L = left, R = right.

Age differences in retrieval activity associated with memory success and precision

Investigation of age differences in the retrieval activity associated with the success of memory retrieval indicated significantly decreased retrieval success effects in the older group in the left hippocampus (see Table 5 and Figure 4). Although hippocampal activity was increased for successful memory retrieval when compared to guessing in both age groups (younger adults: $t(19) = 6.58$, $p < .001$, peak: -33, -18, -12; older adults: $t(19) = 4.06$, $p = .034$, peak: -30, -18, -15), the magnitude of this effect was significantly decreased in the older group. No significant age differences in retrieval success effects were observed in the other ROIs (although note that a marginal reduction was evident in

the left angular gyrus, $t(38) = 3.31$, $p = .076$, peak: -51, -60, 24; other ts < 3.29, ps > .273).

Retrieval activity associated with memory precision, on the other hand, was significantly reduced in the older group in the left angular gyrus (see Table 5 and Figure 4). While activity in the left angular gyrus significantly predicted the precision of memory retrieval in the younger group, $t(19) = 5.38$, $p = .003$, peak: -54, -66, 33, this effect did not reach significance in the older group alone, $t(19) = 3.20$, $p = .154$. No significant age differences in retrieval precision effects were detected in the other ROIs (ts < 2.86, ps > .186).

Table 5. *Regions displaying significant age differences in retrieval success and retrieval precision effects in the ROI analysis.*

Region	**x**	**y**	**z**	**t**	**p**
Retrieval success					
Younger adults > older adults					
L hippocampus	-18	-6	-12	4.17	.009
Retrieval precision					
Younger adults > older adults					
L angular gyrus	-48	-72	33	3.87	.021

Note. L = left, R= right.

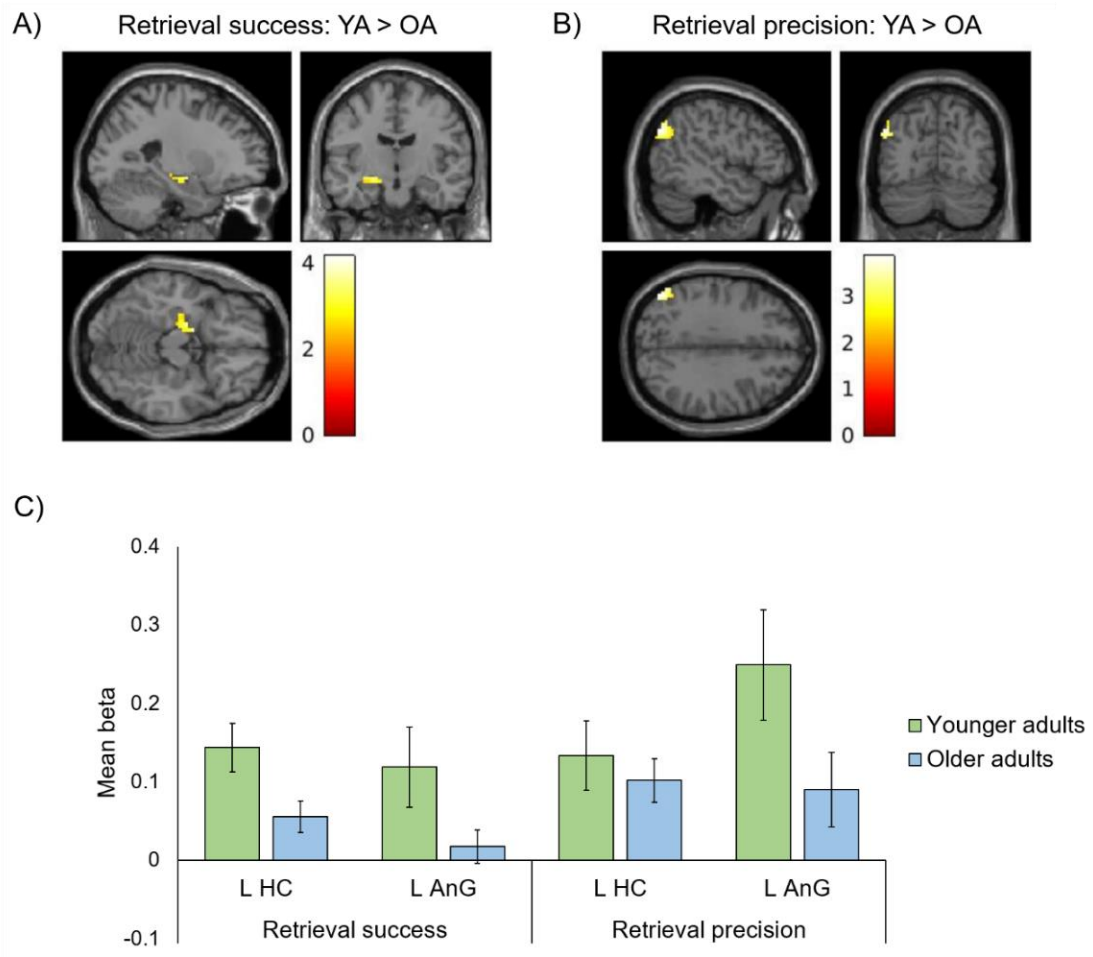

Figure 4. Age differences in A) hippocampal retrieval success effects and B) angular gyrus retrieval precision effects (visualized at an uncorrected threshold of $p < .01$, masked with the anatomical ROI image of the left A) hippocampus and B) angular gyrus). C) Mean betas for the retrieval success and retrieval precision effects in the left hippocampus and left angular gyrus in young and older adults (extracted from the left HC and left AnG anatomical ROI for each participant). Error bars display ± 1 *SEM*. YA = younger adults; OA = older adults.

Direct comparison of retrieval success and retrieval precision effects

To examine whether age differences in the retrieval activity underlying the success and precision of memory retrieval were specific to the hippocampus and angular gyrus, respectively, mean beta-values for the retrieval success and retrieval precision contrasts were extracted for each participant from the left hippocampal and left angular gyrus anatomical ROI. A mixed ANOVA indicated no significant three-way interaction

between age group (young vs. old), memory measure (retrieval success vs. precision) and brain region (left HC vs. left AnG), $F(1, 38) = 2.00$, $p = .166$, nor a significant two-way interaction between age group and region for either retrieval success, $F(1, 38) = 0.06$, $p = .809$, or retrieval precision, $F(1, 38) = 2.26$, $p = .141$. Therefore, no evidence for significantly disproportionate age-related deficits in the retrieval activity underlying one aspect of memory retrieval were observed in either of these two regions. However, consistent with previous results (Richter, Cooper et al., 2016) the analysis indicated a two-way interaction between memory measure and region, $F(1, 38) = 4.24$, $p = .046$, *partial* $\eta^2 = 0.10$, across the age groups. This appeared to be driven by significantly greater angular gyrus sensitivity to memory precision than retrieval success, $t(39) = 2.71$, $p = .010$, $d = .43$, while no significant differences between hippocampal retrieval success and retrieval precision effects were detected, $t(39) = 0.61$, $p = .542$. As indicated by the lack of a three-way interaction between age group, memory measure and brain region presented above, the selectivity of retrieval activity underlying these two memory components did not significantly differ between the young and older adults.

Encoding activity associated with subsequent memory success and precision across participants

As for successful memory retrieval, increases in brain activity for successful encoding of object features were widely observed across the ROIs. Apart from the left hippocampus (ts < 2.91, ps > .151), significant increases in encoding activity for trials that were subsequently successfully retrieved in comparison to those that were later forgotten (successful > unsuccessful) were observed across participants in all the other ROIs (see Table 6). Of these regions, increased encoding activity in the right angular gyrus, bilateral inferior frontal, and bilateral fusiform gyri also predicted greater subsequent precision of memory retrieval across the participants (see Table 6) (all other ts < 2.66, ps > .269).

In contrast, negative subsequent memory effects, reflecting decreases in encoding activity for trials that were later successfully retrieved or highly precise, were observed across participants in the angular gyrus only (other ts < 3.39, ps > .235) (see Table 6). Greater encoding deactivation in the right angular gyrus was associated with the subsequent success of memory retrieval (note that a marginal effect was observed in the left angular gyrus also, $t(38) = 3.38$, $p = .059$), and greater encoding deactivation in the

bilateral angular gyrus with greater precision of later memory retrieval. Of note, the peaks of these negative subsequent memory effects differed from those exhibiting positive subsequent memory effects within the anatomical angular gyrus ROI (see Figure 5 for positive and negative subsequent memory effects for each age group and memory measure visualized at an uncorrected threshold). Although most frequently negative, also positive subsequent memory effects have previously been reported in the ventrolateral parietal cortex (see Uncapher & Wagner, 2009 for review).

Table 6. *Regions displaying a significant relationship between encoding activity and the subsequent success and/or precision of memory retrieval across the age groups in the ROI analysis.*

Region	**x**	**y**	**z**	**t**	**p**
Successful > unsuccessful					
R hippocampus	33	-24	-15	3.84	.019
L angular gyrus	-33	-66	42	3.65	.032
R angular gyrus	30	-60	48	6.51	< .001
L inferior frontal gyrus	-45	30	18	8.29	< .001
R inferior frontal gyrus	51	39	15	6.74	< .001
L fusiform gyrus	-39	-63	-12	9.75	< .001
R fusiform gyrus	30	-57	-12	7.50	< .001
Successful < unsuccessful					
R angular gyrus	54	-63	33	5.04	.001
Positive relationship with precision					
R angular gyrus	26	-63	48	4.65	.004
L inferior frontal gyrus	-45	3	27	5.56	.001
R inferior frontal gyrus	45	6	24	4.63	.013
L fusiform gyrus	-45	-57	-15	6.36	< .001
R fusiform gyrus	42	-54	-15	5.89	< .001
Negative relationship with precision					
L angular gyrus	-54	-63	33	4.56	.004
R angular gyrus	48	-51	24	5.16	.001

Note. L = left, R = right.

Age differences in encoding activity associated with subsequent memory success and precision

Investigation of age differences in the encoding activity predicting the later success of memory retrieval yielded significant age-related reductions in the bilateral inferior frontal and fusiform gyri (other *t*s < 3.07, *p*s > .161) (see Table 7 and Figures 5 and 6). In the younger adults, successful memory encoding was associated with significant increases in bilateral inferior frontal gyri (left: $t(19) = 7.84$, $p = .002$, peak: -39, 30, 18; right: $t(19) = 5.85$, $p = .006$, peak: 51, 39, 15) and bilateral fusiform gyri (left $t(19) = 10.87$, $p < .001$, peak: -39, -63, -12; *right*: $t(19) = 7.96$, $p < .001$, peak: 33, -30, -21), while in the older group only the left inferior frontal activity significantly differed between successful and unsuccessful encoding trials, $t(19) = 4.58$, $p = .045$, peak: -51, 36, 3 (other *t*s < 3.48, *p*s > .173).

Reductions in subsequent precision effects, on the other hand, were observed in the older group in the left fusiform gyrus only (other *t*s < 3.20, *p*s > .327) (see Table 7 and Figures 5 and 6). Although fusiform encoding activity significantly predicted later memory precision in both the younger, $t(19) = 6.53$, $p = .001$, peak: -39, -54, -9, and older adults alone, $t(19) = 4.28$, $p = .046$, peak: -39, -78, -18, the magnitude of this effect was reduced significantly in the older group (see Table 7).

Age-related increases (reflecting reduced or lack of deactivation) in negative subsequent memory effects were observed in the angular gyrus (see Table 7 and Figures 5 and 6). For encoding activity negatively associated with the subsequent success of memory retrieval, significant age-related differences were observed in the bilateral angular gyrus. Where in younger adults greater encoding deactivation of the right angular gyrus was associated with the later success of memory retrieval, $t(19) = 4.66$, $p = .018$, peak: 54, -63, 33, encoding activity in this region did not predict the success of memory retrieval in the older group alone (*t*s < 3.45, $p > .126$). Although significant age differences in the negative subsequent retrieval success effects were observed in the left angular gyrus, encoding activity in this region did not significantly differ for subsequent successful and unsuccessful memory retrieval in either the young (*t*s < 3.13, *p*s > .168) or older (*t*s < 3.26, *p*s > .115) adults alone.

Similarly, significant increases in negative subsequent precision effects were observed in the older group in the right angular gyrus (note that a marginal effect observed in left

angular gyrus also, $t(38) = 3.26$, $p = .086$). Where in younger adults greater deactivation of the right angular gyrus at encoding was associated with higher subsequent precision of memory retrieval, $t(19) = 5.56$, $p = .005$, peak: 51, -48, 24, activity in this region did not significantly predict later memory precision in the older adults alone (ts < 3.69, ps > .090).

Table 7. *Regions displaying significant age differences in subsequent retrieval success and/or precision effects in the ROI analysis.*

Region	x	y	z	t	p
Subsequent retrieval success					
Younger adults > older adults					
L inferior frontal gyrus	-39	30	15	5.10	.003
R inferior frontal gyrus	45	9	24	4.32	.024
L fusiform gyrus	-39	-63	-12	6.19	< .001
R fusiform gyrus	30	-57	-9	4.44	.010
Younger adults < older adults					
L angular gyrus	-51	-72	30	3.71	.027
R angular gyrus	45	-54	33	4.51	.005
Subsequent precision					
Younger adults > older adults					
L fusiform gyrus	-42	-54	-12	3.86	.048
Younger adults < older adults					
R angular gyrus	54	-51	24	4.56	.006

Note. L = left, R = right.

Direct comparison of subsequent retrieval success and subsequent precision effects

To examine whether disproportionate age differences in encoding activity associated with either aspect of later memory retrieval were observed in any of the regions of interest, mean beta-values for the subsequent retrieval success and subsequent precision contrasts were extracted for each participant from each anatomical ROI. The interaction between age group (young vs. old) and memory measure (retrieval success vs. precision) did not reach significance in any of the ROIs displaying significant age differences in the

encoding activity predicting later memory performance (*F*s < 1.41, *p*s > .242). The results therefore did not provide evidence for significantly disproportionate age-related changes in the encoding activity associated with the later success or precision of memory retrieval in any of the regions of interest. Furthermore, no significant differences between subsequent success and subsequent precision effects were detected in any of the regions of interest, *F*s < .060, *p*s > .443.

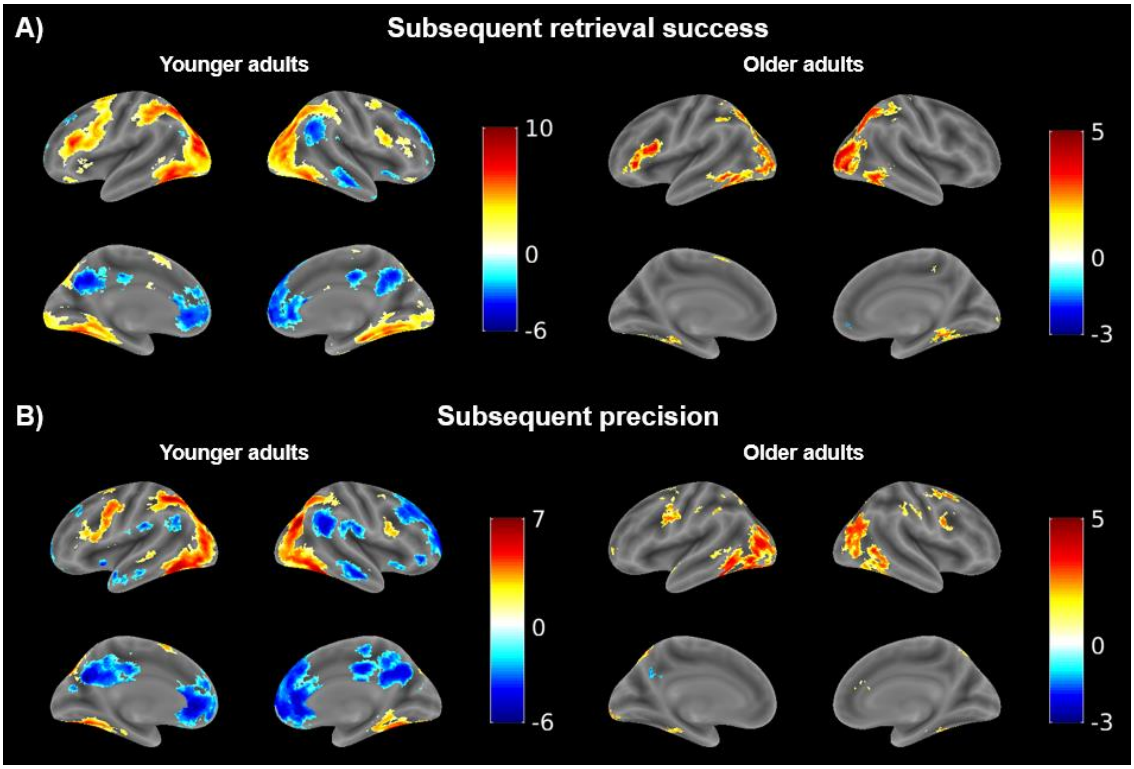

Figure 5. Encoding activity scaling with the subsequent A) success and B) precision of memory retrieval in each age group. Visualized at an uncorrected threshold of p < .01 with a minimum cluster size of 10 voxels.

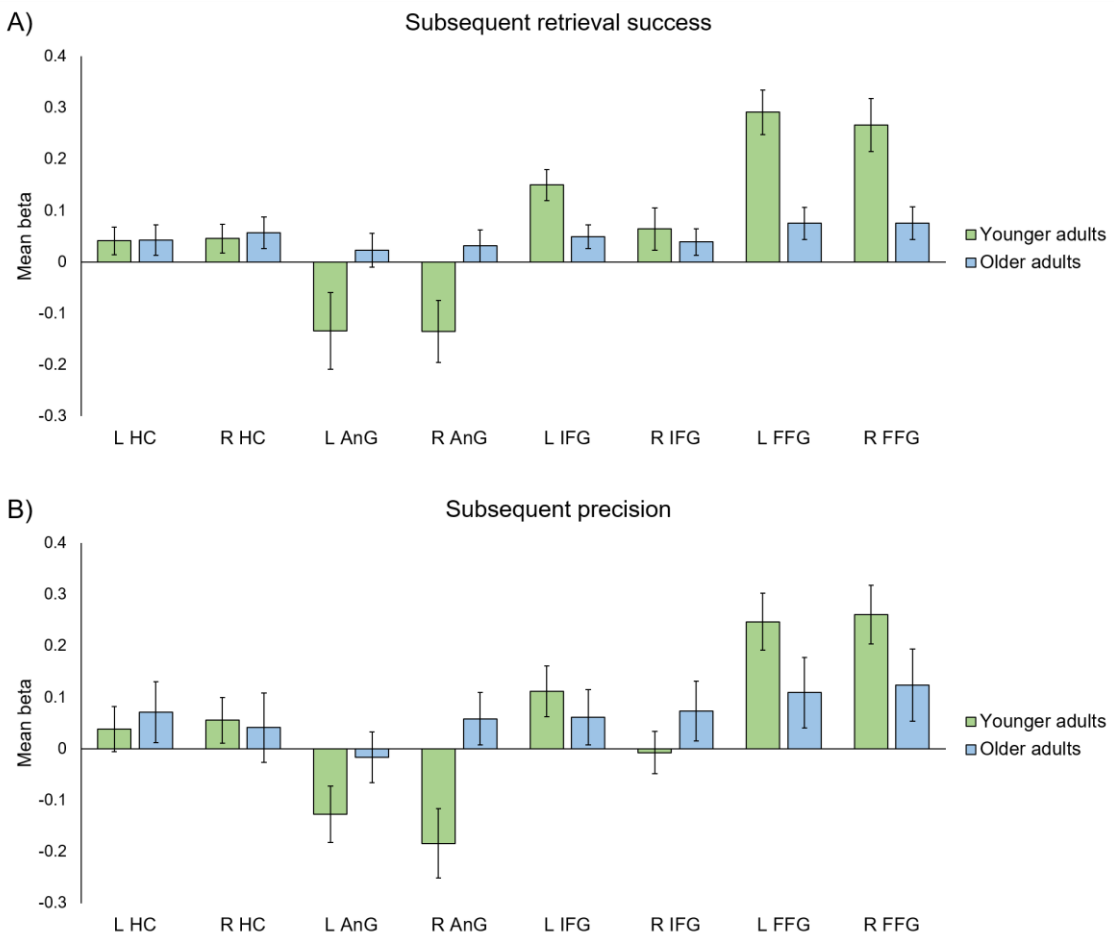

Figure 6. Mean beta-values for A) subsequent retrieval success and B) subsequent precision effects in the young and older adults (mean betas extracted from each anatomical ROI for each participant). Error bars display ± 1 *SEM*.

Age differences in the lateralization of prefrontal subsequent memory effects

Given previous evidence for reduced lateralization of prefrontal activity in older age (e.g., Cabeza, 2002; Morcom et al., 2003), I further examined whether the lateralization of subsequent success and/or precision effects in the inferior frontal gyrus differed between the age groups. A mixed ANOVA with the factors of age group (young vs. old) and hemisphere (left vs. right) indicated a significant interaction between hemisphere and age group for both subsequent success, $F(1, 38) = 7.93$, $p = .008$, *partial* $\eta^2 = 0.17$, and subsequent precision, $F(1, 38) = 6.99$, $p = .012$, *partial* $\eta^2 = 0.16$, effects. Whereas in the younger adults greater left than right IFG subsequent memory effects were observed for both the later success, $t(19) = 3.15$, $p = .002$, $d = 0.79$, and precision, $t(19) = 2.57$, $p = .019$, $d = 0.58$, of memory retrieval, the left and right IFG encoding activity

associated with the subsequent success, $t(19) = 0.89$, $p = .386$, or precision, $t(19) = 0.66$, $p = .515$, of memory retrieval did not significantly differ in the older group. Furthermore, age differences in prefrontal lateralization did not significantly differ between the subsequent success and subsequent precision effects, $F(1, 38) = 1.18$, $p = .285$.

Whole brain analyses

In addition to the ROI analyses, exploratory whole brain analyses were conducted to identify any additional regions displaying age-related differences in activity associated with the success or precision of episodic memory. Examination of age differences in the retrieval activity predicting memory success and precision did not yield any significant clusters at the whole brain level. Consistent with the findings from the ROI analyses, subsequent retrieval success effects were significantly reduced in the older group in comparison to the younger group in a cluster spanning the inferior temporal gyrus and fusiform gyrus. Furthermore, subsequent precision effects were increased in the older in comparison to the younger group in the anterior cingulate cortex (due to a lack of negative subsequent precision effects in the older group in this region) (see Table 8).

Table 8. *Significant age differences in subsequent memory effects across the whole brain, assessed at a peak-level FWE-corrected significance threshold of p < .05 with a minimum cluster extent of 5 contiguous voxels.*

Region	**Voxels**	**x**	**y**	**z**	**t**
Subsequent retrieval success					
Younger adults > Older adults					
L inferior temporal gyrus	35	-48	-60	-9	6.46
L fusiform gyrus		-45	-51	-15	5.53
Subsequent memory precision					
Older adults > Younger adults					
R anterior cingulate gyrus	6	12	42	6	5.67

Note. L = left, R = right.

Discussion

The experiment presented in the current chapter aimed to assess the neural basis of age-related decreases in the success and precision of episodic memory. In the current experiment, both the probability of successful memory retrieval and memory precision were observed to be significantly reduced in older in comparison to younger adults. These behavioural decreases were accompanied by age-related changes in both encoding and retrieval activity supporting the accessibility and fidelity of episodic memories. During retrieval, the older group displayed diminished retrieval success effects compared to the younger adults in the hippocampus, while retrieval precision effects were reduced in the older adults in the angular gyrus. At encoding, age-related decreases in encoding activity predicting both the later success and precision of memory retrieval were evident in the fusiform gyrus, whereas reductions in subsequent retrieval success effects only were evident in the inferior frontal gyrus. Furthermore, while in the younger group greater encoding deactivation of the angular gyrus was associated with the later success and precision of memory retrieval, these negative subsequent memory effects were diminished in the older group for both memory components. Together, these findings provide evidence for both encoding and retrieval contributions to age-related declines in the success and precision of episodic memory retrieval.

Although retrieval activity in hippocampal, prefrontal, ventral visual, and lateral parietal regions was found to correlate with memory precision across participants, significant age-related reductions in the relationship between retrieval activity and memory precision were only observed in the left angular gyrus. This observation aligns with previous evidence from younger adults implicating the lateral parietal cortex in the fidelity of episodic memory retrieval (Murray et al., 2015; Nilakantan et al., 2017; Richter, Cooper et al., 2016). Age-related reductions in parietal activity associated with successful memory retrieval have been reported in previous studies (Angel et al., 2013; Daselaar et al., 2006; Duarte et al., 2010, but see Wang et al., 2016), in particular for the retrieval of associative memories (reviewed in Wang & Cabeza, 2016). These decreases have often been interpreted as reflecting deficits in episodic recollection (e.g., Angel et al., 2013; Daselaar et al., 2006), but the understanding of their precise contribution to age-related memory decline has so far been limited. As previous studies have not distinguished between activity associated with the success of memory retrieval and the precision of retrieved information, it is possible that parietal decreases evident in

previous studies may at least partly reflect age-related losses of memory fidelity, as observed in the current experiment.

Significant age-related reductions in retrieval activity associated with the binary success of memory retrieval, on the other hand, were observed in the current experiment only in the hippocampus. This is consistent with previous findings from younger adults implicating this region in supporting the success of memory retrieval specifically (Richter, Cooper et al., 2016). Indeed, the hippocampus is thought to support the successful recovery of stored memory representations and to facilitate the subsequent reinstatement of the retrieved information in cortical regions (McClelland et al., 1995; Norman & O'Reilly, 2003). Age-related declines in hippocampal retrieval activity have frequently been reported in the literature (Daselaar et al., 2006; Dennis, Hayes et al., 2008; Giovanello & Schacter, 2012; Kukolja et al., 2009; Cansino et al., 2015), and have often been related to deficits in successful associative (e.g., Kukolja et al., 2009) or recollection-based (e.g., Daselaar et al., 2006) retrieval. These accounts align well with findings from the current experiment, where the contrast between retrieval success and failure reflected the successful retrieval of associations between an object and its features, a process thought to rely on recollection (Yonelinas, 2002). Interestingly, more recent work has proposed that hippocampal deterioration may also underlie age-related deficits in memory precision (Nilakantan et al., 2018). In the current experiment no significant age differences in the hippocampal retrieval (or encoding) activity associated with the precision of episodic memory were observed, seeming to contradict the view of a predominantly hippocampal basis for the age-related reductions in the precision of episodic memory retrieval.

However, it is important to note that the current results did not provide evidence for disproportionate age-related declines in the activity associated with the success or precision of memory retrieval in the hippocampus or the angular gyrus, respectively. Indeed, activity associated with successful memory retrieval was also marginally reduced in the older group in the angular gyrus. It therefore remains to be established how regionally specific age-related declines in the brain activity underlying these two aspects of memory retrieval are, or whether they reflect a broader, network-wide dysfunction.

Consistent with the notion that impoverished encoding of memory traces may contribute to age-related episodic memory decline (Craik & Rose, 2012), encoding activity

supporting both the later successful retrieval and memory fidelity was observed to differ between the young and older adults. In the fusiform gyrus, age-related reductions were observed for encoding activity associated with both the later success and precision of memory retrieval. Consistent with this finding, previous studies have commonly identified age-related decreases in subsequent memory effects in the ventral visual cortex (Maillet & Rajah, 2014a; Wang & Cabeza, 2016). Furthermore, the quality of neural representations corresponding to different visual stimuli has also been observed to exhibit age-related decreases in visual regions during both perception and memory encoding (Carp et al., 2011; Trelle et al., 2019; Zheng et al., 2018), suggesting age-related reductions in the fidelity of perceptual and memory encoding processes supported by these regions. Indeed, the current results suggest that impoverished encoding of sensory information into lasting and precise memory representations in visual regions may contribute to age-related reductions in the accessibility and fidelity of this information during later retrieval.

In addition to age-related decreases in subsequent retrieval success and precision effects observed in the fusiform gyrus, age-related decreases in encoding activity predicting the subsequent success (but not precision) of memory retrieval were evident in the inferior frontal gyrus, consistent with previous reports of age-related decreases in left prefrontal activity associated with successful associative memory formation (e.g., Dulas & Duarte, 2011; reviewed in Wang & Cabeza, 2016). The age-related decreases in prefrontal subsequent retrieval success effects in the current experiment may reflect the diminished employment of strategic encoding operations required for the formation of strong bindings between an object and its features. Consistent with this interpretation, age-related memory declines have been proposed to partly result from a reduced ability to initiate deep and elaborative encoding strategies facilitating later successful remembering (Naveh-Benjamin, Brav, & Levy, 2007).

Interestingly, many previous studies have also demonstrated age-related increases in prefrontal subsequent memory effects, often contralateral to regions recruited for successful encoding in younger adults (e.g., Morcom et al., 2003; Persson et al., 2006). In the current experiment, no significant age-related increases in subsequent memory effects were observed in the right inferior frontal gyrus. However, the examination of age differences in the lateralization of subsequent memory effects indicated reduced lateralization of encoding activity associated with both the later success and precision of

memory retrieval in the older group. Whereas in the younger group greater subsequent success and precision effects were observed in the left, in comparison to the right, inferior frontal gyrus, encoding activity associated with either of these two aspect of memory retrieval did not significantly differ between the two hemispheres in the older group. The current results thus align with previous accounts proposing reduced hemispheric lateralization of prefrontal activity in older age (Cabeza, 2002).

Despite encoding activity in the hippocampus predicting the later success of memory retrieval, no significant age differences in subsequent retrieval success effects were observed in this region. Although prior accounts have often proposed a role of hippocampal binding deficits in age-related memory impairments (e.g., Shing et al., 2010), decreases in encoding activity in this region have not been consistently observed. For instance, two recent larger scale studies demonstrated age-invariant subsequent memory effects in the hippocampus (De Chastelaine et al., 2016; Vidal-Piñeiro et al., 2018), consistent with the findings observed in the current experiment. Indeed, these prior findings in combination with the results observed in the current experiment may suggest a greater role for hippocampal retrieval, rather than encoding, deficits in age-related episodic memory declines.

In contrast to the activity increases observed during retrieval, greater encoding deactivation in the right angular gyrus predicted the later success and precision of memory retrieval. This is consistent with previous reports of an "encoding/retrieval flip" in memory-related brain activity in this region (Daselaar et al., 2009). Consistent with previous findings of diminished negative subsequent memory effects in older age in the lateral and medial parietal cortex (De Chastelaine et al., 2015; Maillet & Rajah, 2014a; Miller et al., 2008; Park et al., 2013), negative subsequent memory effects in the angular gyrus were reduced in the older group for both later success and precision of memory retrieval in the current experiment. Given the overlap between negative subsequent memory and task-negative effects in the default mode network, age-related reductions in negative subsequent memory effects have been proposed to reflect decreased suppression of activity in this network and the reduced reallocation of cognitive resources to externally-oriented encoding processes (De Chastelaine et al., 2015, 2011; Miller et al., 2008). However, whether age-related changes in negative subsequent memory effects are critical for memory performance, or may reflect more domain-general changes in the modulation of default-mode network activity in response to task demands, remains to be

clarified (Rugg, 2016; Vidal-Piñeiro et al., 2018). Although age-related differences in negative subsequent memory effects did not reach significance in other regions when assessed at a whole brain level, at an uncorrected threshold the older adults appeared to display an absence of negative subsequent memory effects in other regions overlapping with the default mode network also (see Figure 5), consistent with previous findings (Park et al., 2013).

In addition to the age-related differences in encoding and retrieval mechanisms supporting the success and precision of episodic memory, the current experiment sought to assess whether distinct encoding processes may support the later success and precision of memory retrieval. Apart from the hippocampus, both significant subsequent retrieval success and subsequent precision effects were detected in all regions of interest across the participants, and direct comparison of the subsequent memory effects for these two memory components did not yield significant differences in any of the regions of interest. The current findings thus provided little evidence for differentiation of encoding mechanisms supporting these two aspects of memory retrieval. Instead, the findings suggest that encoding activity in similar brain regions may support both later memory access and fidelity. Furthermore, no disproportionate age differences in the encoding activity relating to either aspect of memory retrieval were evident across the regions of interest.

In addition to analyses of regional activity associated with the success and precision of memory retrieval, future analyses of the current data will investigate age differences in the network interactions supporting the success and precision of memory retrieval. Previous evidence has demonstrated age-related alterations in the functional connectivity of both memory encoding (Foster, Picklesimer, Mulligan, & Giovanello, 2016; Grady, McIntosh, & Craik, 2003; Oh & Jagust, 2013) and retrieval (King, de Chastelaine, & Rugg, 2018; Monge, Stanley, Geib, Davis, & Cabeza, 2018; Tsukiura et al., 2011) networks, potentially playing a role in the memory reductions observed in the current paradigm. Of particular interest for future analyses are age-related changes in the integrity of hippocampal-parietal functional connectivity during memory retrieval, as well as hippocampal-visual and hippocampal-prefrontal connections during encoding. Another interesting question for future studies to address, but not afforded by the current design, is the potential contribution of reduced fidelity of neural representations to the age-related declines in memory precision. The reduced subsequent precision effects in

the fusiform gyrus and reduced retrieval precision effects in the angular gyrus observed in the current analyses are particularly interesting in light of previous evidence highlighting the of the occipitotemporal cortex and the angular gyrus in representing mnemonic content during encoding and retrieval, respectively (Favila, Samide, Sweigart, & Kuhl, 2018). Interestingly, some previous evidence has demonstrated intact fidelity of neural representations in the lateral parietal cortex during memory retrieval in older age (Wang et al., 2016). However, that study examined the reinstatement of activity patterns corresponding to two different encoding tasks implemented for word and picture stimuli, therefore assessing only coarse discriminations between different categories of stimuli and encoding contexts. It is possible that more fine-grained representation of retrieved content in the ventrolateral parietal cortex may be compromised in older age and contribute to the precision deficits observed in the current experiments.

In conclusion, the experiment presented in the current chapter provided evidence for both encoding and retrieval contributions to the age-related declines in the success and precision of memory retrieval. During retrieval, age differences were localised to the posterior-medial episodic memory network, with older adults displaying reduced retrieval success effects in the hippocampus and decreased retrieval precision effects in the angular gyrus. During encoding, on the other hand, subsequent retrieval success and precision effects were reduced in the older group in the fusiform gyrus, while prefrontal decreases were evident for subsequent retrieval success only. Furthermore, the older group displayed a lack of negative subsequent retrieval success and precision effects in the angular gyrus. Overall, these findings suggest distinct encoding and retrieval contributions to age-related decreases in the success and precision of episodic memory retrieval, and highlight that rather than reflecting a single cause, age-related memory deficits likely emerge due to functional declines in multiple interacting brain regions.

Chapter 5: Neuroanatomical correlates of the success and precision of episodic memory retrieval in older age

In Chapter 4, I observed age-related changes in the brain activity underlying the success and precision of episodic memory retrieval. In addition to changes in brain function, healthy ageing is associated with declines in the structural integrity of brain regions underpinning episodic memory; an important determinant of individual differences in memory abilities across older individuals (Fjell & Walhovd, 2010; Nyberg et al., 2012). Although prior studies have linked variation in structural integrity of the brain to individual differences in episodic memory performance in older age, our current understanding of the more specific brain structure-behaviour relationships remains limited. The experiment presented in the current chapter used voxel-based morphometry (VBM) (Ashburner & Friston, 2000) to assess the neuroanatomical correlates of variation in two separable aspects of episodic memory; namely the success and precision of memory retrieval, in older age. Results from this experiment demonstrated a positive relationship between lateral parietal grey matter (GM) volume and memory precision across older adults, providing novel insight into the structural basis of individual differences in memory quality. This finding was further consistent with the age-related functional decreases observed for precision-related activity in the angular gyrus in Chapter 4, thus highlighting the importance of both structural and functional integrity of this region in the fidelity of episodic recollection.

Introduction

Healthy ageing is associated with various neurobiological changes affecting the integrity of grey and white matter of the brain. In terms of brain morphology, the total grey matter volume of the brain as well as regional volumes have been shown to decrease with advancing age (Good et al., 2001; Peelle, Cusack, & Henson, 2012; Raz et al., 1997; Raz et al., 2004, 2005; Resnick et al., 2003). Although age-related grey matter decreases have been widely documented across the cortex (Fjell, Walhovd, et al., 2009; Fjell et al., 2014; Walhovd et al., 2011; Ziegler et al., 2012), considerable regional variability in the rate and trajectory of these declines exists (Fjell & Walhovd, 2010). In particular, prefrontal grey matter has been highlighted as being especially vulnerable to age-related declines in both cross-sectional and longitudinal studies (Allen et al., 2005; Fjell, Walhovd, et al.,

2009; Fjell, Westlye, et al., 2009; Raz et al., 1997; Raz et al., 2004; Resnick et al., 2003), however the lateral parietal and temporal regions also display pronounced age-related decreases (Fjell, Walhovd, et al., 2009; Fjell, Westlye, et al., 2009; Fjell et al., 2014; Good et al., 2001; Resnick et al., 2003; Ziegler et al., 2012). Furthermore, non-linear trajectories of age-related grey matter loss have been documented in some subcortical regions (Walhovd et al., 2011; Ziegler et al., 2012). In particular, grey matter in the hippocampus appears to remain relatively preserved until midlife, after which accelerated decline becomes evident (Coupé et al., 2017; Nobis et al., 2019; Walhovd et al., 2005; Ziegler et al., 2012).

In addition to mean level cognitive declines, ageing is often thought to lead to increased inter-individual variability in cognitive performance (Nelson & Dannefer, 1992; Christensen et al., 1999; Hultsch, MacDonald, & Dixon, 2002, but see Green, Shafto, Matthews, Cam-Can, & White, 2015; Salthouse, 2012). Indeed, substantial variability in age-related episodic memory changes has been reported in many studies, with some older individuals exhibiting only modest or a lack of decrease in their memory abilities, while others display marked declines (reviewed in Nyberg et al., 2012; Nyberg & Pudas, 2019). Individual differences in memory performance in older age are thought to be at least partly attributable to variation in the structural integrity of the brain (Fjell & Walhovd, 2010). According to the brain maintenance hypothesis, preserved structural, functional and neurochemical integrity of the brain underlies the maintenance of memory abilities in older age (Nyberg et al., 2012). In line with this proposal, several studies have displayed a positive relationship between brain structure and general cognitive performance as well as more specific cognitive domains, such as memory ability (reviewed in Kaup, Mirzakhanian, Jeste, & Eyler, 2011; Raz & Rodrigue, 2006; Salthouse, 2011).

Focusing on the structural correlates of variability in episodic memory specifically, a common finding in previous studies has been a relationship between hippocampal volume and episodic memory performance in older age. Evidence from both cross-sectional studies with older adult (Fleischman et al., 2014; Hedden et al., 2016; Ward et al., 2015) and lifespan samples (Henson et al., 2016) as well as longitudinal studies (Fjell, McEvoy, Holland, Dale, & Walhovd, 2013; Gorbach et al., 2017; Kramer et al., 2007; Leong et al., 2017; Persson et al., 2012) has linked decreases in hippocampal volume to reductions in episodic memory performance. In a recent study, it was found that while

the majority of the variance in episodic memory performance across older adults was shared among different brain markers (~60%), hippocampal volume explained the largest unique proportion of variance (~ 8%) (Hedden et al., 2016). Several studies have also linked prefrontal volume to inter-individual differences in memory performance in older age (e.g., Becker et al., 2015; Fleischman et al., 2014; Head et al., 2008; Kalpouzos et al., 2009). In line with the role of the prefrontal cortex in supporting memory control processes (Simons & Spiers, 2003), this relationship has been shown to be mediated by age-related reductions in executive functions, specifically working memory and inhibitory control (Head et al., 2008). Consistent with this finding, others have also linked differences in prefrontal volume and thickness to variation in specific memory control processes, such as memory inhibition (Eich, Razlighi, & Stern, 2017) and the use of efficient encoding (Husa et al., 2017) and retrieval strategies (Kirchhoff, Gordon, & Head, 2014) in older age.

Although prominent age-related grey matter loss has often been reported in the lateral parietal cortex (e.g., Fjell et al., 2014; Good et al., 2001; Resnick et al., 2003; Ziegler et al., 2012), evidence linking variation in parietal grey matter integrity to individual differences in episodic memory has been relatively scarce. A study by Walhovd et al. (2006) observed parietal cortical thickness to correlate with episodic memory recall after several months delay in a lifespan adult sample, even after controlling for the effects of variation in hippocampal volume, suggesting a possible contribution separable to that of the hippocampus. However, no such relationship was observed in that study at shorter recall delays. Furthermore, a more recent study investigating the brain characteristics of "super-agers", i.e., older adults exhibiting youth-like memory performance, demonstrated that whereas cortical thickness of the angular gyrus in this group was comparable to that of younger adults, decreases in angular gyrus thickness were evident in a more typical older adult group also showing reduced memory performance (Sun et al., 2016). While this finding suggests that preserved integrity of the angular gyrus may play a role in the maintenance of memory function in older age, no direct relationship between individual differences in angular gyrus thickness and memory performance was observed in that study (Sun et al., 2016). The exact contribution of parietal grey matter integrity to individual differences in episodic memory performance in older age therefore remains to be clarified.

Although previous studies have highlighted regions in which structural integrity correlates with individual differences in memory performance in older age, the exact contribution of these regions to specific mnemonic processes remains to be characterized. In the majority of previous studies, the structural basis of individual differences in memory performance has been assessed with standard neuropsychological tests or composite memory measures, unable to disentangle the effects of brain structure variability on specific memory processes. Some evidence has begun to unravel more detailed structure-behaviour relationships by examining whether, for instance, variability in different retrieval processes, such as item and associative recognition (Becker et al., 2015; Henson et al., 2016), or recollection and familiarity (Yonelinas et al., 2007), may depend on different neuroanatomical substrates. However, the structural correlates of the precision of episodic memory retrieval, and whether they may differ from the correlates of successful memory retrieval, are currently unknown.

The experiment presented in the current chapter thus aimed to assess the relationship between variability in regional grey matter volume and individual differences in the success and precision of episodic memory retrieval in older age. For this purpose, structural neuroimaging and behavioural data was acquired for 51 older adults. Twenty of these older adults had taken part in the functional neuroimaging experiment described in Chapter 4, while a structural scan was acquired for an additional 31 participants. Both groups of participants completed the same continuous report task, with the older adults participating in the fMRI experiment completing this task inside of the MRI scanner, and the older adults participating in the structural study completing the memory task outside of the MRI scanner. All participants completed the continuous report task described in Chapter 4, assessing retrieval of object locations and colours. VBM analyses were performed to examine the relationship between regional grey matter volume and the success and precision of memory retrieval (taking into account the different testing environments).

Given the proposed roles of the hippocampus and the angular gyrus in the success and precision of episodic memory retrieval, respectively (Richter, Cooper et al., 2016), as well as the age-related functional differences observed in these regions for each aspect of memory retrieval in Chapter 4, grey matter volume in the angular gyrus was expected to predict variation in memory precision, while hippocampal grey matter volume was predicted to relate to variability in the probability of successful memory retrieval.

Furthermore, motivated by the age-related encoding activity differences observed in the prefrontal and fusiform cortex in Chapter 4, as well as prior evidence indicating a contribution of grey matter differences in these regions to episodic memory performance in older age (Becker et al., 2015; Head et al., 2008; Murphy et al., 2010), the relationship between local grey matter volume and the success and precision of memory retrieval were assessed in these regions also. Given the contribution of encoding activity in the fusiform gyrus to both later success and precision of memory retrieval in Chapter 4, and the known role of this region in object perception and memory (Bar et al., 2001; Haxby et al., 2001), reductions in fusiform grey matter volume may be associated with decreases in both the success and precision of episodic memory retrieval. Similarly, variation in prefrontal volume may be associated with individual differences in both the success and precision of memory retrieval via its role in strategic encoding processes that enable the formation of both detailed and accessible memory traces (Blumenfeld & Ranganath, 2007), as well as in facilitating access to goal-relevant features of stored memories during retrieval (Badre & Wagner, 2007).

Methods

Participants

Fifty-one healthy older adults between the ages of 60 and 87 took part in the present experiment. All participants were right-handed, fluent English-speakers, had normal or corrected-to-normal vision, no colour blindness, and no current or historical diagnosis of any neurological, psychiatric, or developmental disorder, or learning difficulty. Participants reported no current use of any psychoactive medication, and no medical or other contradictions to MRI scanning (e.g., metal implants, claustrophobia). All participants scored within the healthy range (≥ 26) on the MoCA (Nasreddine et al., 2005) screening test for mild cognitive impairment. Outliers with a retrieval success (*pT*) or precision (*K*) estimate more than three *SD*s from the group mean were excluded from the analyses, leading to exclusion of two participants. Demographic information for the remaining 49 participants is displayed in Table 1. Twenty of the participants had completed the memory task inside the MRI scanner in the fMRI experiment described in Chapter 4. For the remaining 29 participants, only a structural scan was acquired and the memory task was completed outside of the MRI scanner. The two groups of participants

did not significantly differ in terms of age, $t(47) = 0.20$, $p = .839$, number of years of formal education completed, $t(47) = 0.16$, $p = .870$, MoCA scores, $t(47) = 1.59$, $p = .119$, or scores on the SILVS measure of crystallised intelligence (Zachary & Shipley, 1986), $t(47) = 0.54$, $p = .590$.

Participants were recruited via the University of Cambridge Memory Lab volunteer database and community advertisements. All participants were reimbursed £30 for their participation as well as for any travel expenses occurred, and gave written informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee.

Table 1. *Participant demographic information: means (standard deviations).*

	Mean (SD)
N	49
Age	70.94 (5.32)
Gender (N)	18 M, 31 F
Education	16.29 (4.75)
SILVS	36.98 (1.91)
MoCA	28.51 (1.34)

Note. M = males, F = females.

Materials

Stimuli for the memory task were the same as described in Chapter 4, consisting of 180 outdoor scene images (obtained from Richter, Cooper et al., 2016 and Google image search) and 180 images of colour-rotated everyday objects (obtained from Brady et al., 2013) randomly paired to form a total of 180 trial-unique study displays. For each study display, the location and colour of the object were randomly chosen from a circular parameter space (0-360 degrees). All participants viewed the same encoding displays.

Design and procedure

Experimental procedures for the older adults completing the memory task in the MRI scanner are described in detail in Chapter 4. The memory task completed by the older

adults participating in the structural imaging part of the study was identical to that described in Chapter 4. To briefly recapitulate, the task comprised 9 study-test blocks in total, in each of which participants first viewed 20 stimuli displays in a row (stimulus duration: 5s) and then reconstructed *either* the location *or* the colour of each studied object as precisely as they could. At test, the initial appearance of the questioned feature was randomly chosen from a circular space (0-360 degrees), while the appearance of the other feature remained unchanged from study to test. Participants completing the task outside of the scanner were able to change the location and the colour of the object by moving a slider around the continuous response dial with the left and right arrow keys on a computer keyboard, and pressed the space bar to confirm their answer, while participants taking part in the functional imaging experiment used a scanner compatible button box to make their responses. The retrieval phase was self-paced with the constraints of a minimum trial duration of 7s and a maximum trial duration of 11s.

Participants completed a total of 180 retrieval trials (90 for each feature). The type of feature question asked for each object was randomised across displays but constant across participants. The allocation of stimuli displays to task blocks was randomised across participants, and the order of study and test trials within each block pseudorandomised with the constraint of no more than four encoding or retrieval trials presented in a row for which the same type of feature question was (subsequently) asked. The encoding and retrieval phases were separated by a 10s delay. The encoding and retrieval trials were separated by a central fixation cross with a jittered duration between 0.4s and 2.4s (mean ISI duration: 1s) drawn from an approximate Poisson distribution.

MRI scanning for participants in the structural study involved the acquisition of a standard T1-weighted whole brain anatomical image, a whole brain diffusion-weighted image, a T2-weighted high-resolution structural image of the medial temporal lobes, and an 8-minute functional resting state scan. The present analyses were conducted on the T1-weighted whole brain anatomical images only, and data from the other scans will be explored in future analyses. For participants taking part in the functional imaging study, a standard T1-weighted whole brain anatomical image was acquired prior to the functional runs. At the beginning of the MRI session, all participants filled in a consent form and an MRI screening form. The MoCA and SILVS were completed in a separate behavioural testing session for all participants.

Behavioural analysis

On each trial, participant's retrieval error was calculated as the angular deviation between their response value and the studied feature value (0 ± 180 degrees). As in previous chapters, a probabilistic mixture model (Bays et al., 2009; Zhang & Luck, 2008) was fitted to each participant's retrieval error data to distinguish between the success and precision of memory retrieval. The model consisted of a von Mises distribution (a circular equivalent of a Gaussian distribution) centred at the target feature value and a circular uniform distribution, capturing variability in successful target retrieval and the likelihood of randomly distributed guessing responses, respectively. The probability of successful memory retrieval was defined as the probability of responses stemming from the target von Mises distribution (*pT*) and the precision of memory retrieval as the concentration parameter (*K*) of the target von Mises distribution. These two parameters of memory performance were estimated separately for each participant.

In contrast to the fMRI experiment described in Chapter 4, in the current experiment it was possible to examine the neural correlates of memory performance in each feature condition separately as the analysis required only computation of the overall success and precision of memory retrieval across trials, for which a relatively low number of unsuccessful trials was not a problem (c.f., Sutterer & Awh, 2016). However, initial analyses did not reveal significant differences in the relationship between regional GM volume and memory performance between the two feature conditions in any of the ROIs (retrieval success: ts < 2.82, ps > .382; memory precision: ts < 2.96, ps > .201), or across the whole brain (retrieval success: ts < 3.92, ps > .669; memory precision: ts < 3.95, ps > .644). Therefore, as in the functional imaging experiment described in Chapter 4, estimates of memory performances for the VBM analyses were computed collapsing data across the two feature conditions.

MRI acquisition

The MRI scanning took place at the University of Cambridge Medical Research Council Cognition and Brain Sciences Unit using a 3T Siemens Tim Trio scanner (Siemens, Germany) with a 32-channel head coil. The present analyses were conducted on high resolution whole brain anatomical images, which were acquired using a T1-weighted 3D MPRAGE sequence (TR: 2.25s, TE: 3ms, flip angle = 9°, FOV: 256 x 256 x 192mm,

resolution: 1mm isotropic, GRAPPA acceleration factor 2). The acquisition parameters were identical for the participants taking part in the fMRI experiment and in the structural experiment only.

VBM analysis

Preprocessing and analysis of the structural images was performed with SPM 12 (https://www.fil.ion.ucl.ac.uk/spm/) implemented on MATLAB R2016a. Each anatomical image was first visually examined for artefacts and gross anatomical abnormalities (no participants excluded due to this), and the origin of the image was manually reset to the anterior commissure. The anatomical images were then segmented into GM, white matter (WM) and cerebrospinal fluid (CSF), and these segmentations were used to create a study-specific structural template image using the DARTEL toolbox (Ashburner, 2007). The segmented native space grey matter images were normalised to MNI space using the DARTEL toolbox and spatially smoothed with an isotropic 8mm FWHF Gaussian kernel, with modulation applied to preserve the total amount of GM within each voxel. For each participant, total intracranial volume (TIV) was computed as the sum of total GM, WM and CSF estimates.

The normalized and smoothed grey matter images were analysed using VBM (Ashburner & Friston, 2000) in order to identify local GM correlates of variability in the success (pT) and precision (K) of episodic memory retrieval. Two separate general linear models were constructed to examine the relationship of GM volume to memory performance across the participants; one for examining the correlations between GM volume and the probability of successful retrieval (pT), and one for assessing the relationship between GM volume and memory precision (K). For both models, participant age, gender and years of formal education completed were included as covariates of no interest. Furthermore, TIV was added as an additional covariate of no interest in the model in order to examine regionally specific effects beyond variation in head size (Peelle et al., 2012).

Regions of interest

The main regions of interest for the VBM analyses were the same as used in the analysis of functional data described in Chapter 4: the hippocampus, the angular gyrus, the inferior frontal gyrus, and the fusiform gyrus. Each anatomical region of interest was defined with the Automatic Anatomical Labelling atlas, and mask images for the left and right hemisphere regions were created separately. Statistical significance of the relationships between GM volume and memory performance (*pT* and/or *K*) in each region of interest was determined with a small volume FWE-corrected (based on random field theory) peak-level threshold of $p < .05$. Exploratory whole brain analyses with a FWE-corrected peak-level threshold of $p < .05$ were conducted to identify any additional brain regions displaying a relationship between GM volume and memory performance in the current paradigm (*pT* and/or *K*).

Results

Behavioural results

The distribution of retrieval errors across all participants and trials is displayed in Figure 1A. Mean absolute error across the participants and feature conditions was 39.70 degrees (*SD*: 9.60). Absolute error was significantly lower in the location (*M*: 31.60, *SD*: 10.55) in comparison to the colour condition (*M*: 47.70, *SD*: 10.75), $t(48) = 12.20$, $p < .001$, $d = 1.74$. Similarly, across participants reaction times were significantly lower in the location (*M*: 6.24 s, *SD*: 0.73 s) in comparison to the colour condition (*M*: 6.73, *SD*: 0.69), $t(47) = 6.20$ $p < .001$, $d = .90$ (note that reaction time data from one participant was excluded from this analysis due to a missing reaction time estimate for the location condition, see methods section of Chapter 4 for more details).

Across features, the mean probability of successful memory retrieval (*pT*) across the older adults was 0.67 (*SD*: 0.12), and the mean precision of successful memory retrieval (*K*) was 7.86 (*SD*: 3.10). Examination of feature-specific model-estimates of memory performance indicated that both the probability of successful memory retrieval, $t(48) = 3.42$, $p = .001$, $d = 0.49$, and the precision of memory retrieval, $t(48) = 6.40$, $p < .001$, $d = 0.91$, were higher in the location (*pT M*: 0.74, *SD*: 0.14; *Kappa M*: 13.71, *SD*: 8.83) in comparison to the colour (*pT M*: 0.65, *SD*: 0.17; *Kappa M*: 5.20, *SD*: 2.68) condition.

However, as noted in the methods section, no significant differences in the grey matter correlates of memory performance were detected between the two feature conditions, and therefore the VBM analyses were conducted on estimates of retrieval success and memory precision computed across the feature conditions described above. Considerable inter-individual variability was evident in estimates of both probability of successful memory retrieval and the precision of memory retrieval (see Figure 1B and 1C), thus allowing for the investigation of GM volume correlates of this variability. The probability of retrieval success and memory precision did not significantly correlate across the older adults, r = .04, p = .778, highlighting the possibility that different neuroanatomical correlates may be related to variability in each measure.

Of note, across features the probability of successful memory retrieval was significantly lower in the group of participants who performed the memory task inside the MRI scanner (*M*: 0.63, *SD*: 0.10) than in those participants who performed the task outside of the scanner (*M*: 0.71, *SD*: 0.12), $t(47) = 2.53$, $p = .015$, $d = 0.73$. Given that the two participant groups did not significantly differ in terms of the demographic variables (age, education, MoCA or SILVS), this difference was likely due to the distractibility of the MRI scanning environment (see Gutchess & Park, 2006). Memory precision did not significantly differ between the two groups of participants (in scanner *M*: 7.78, *SD*: 3.01, outside of scanner *M*: 7.91 *SD*: 3.20), $t(47) = 0.14$, $p = .888$. To account for the group difference in retrieval success, testing environment (in the scanner vs. outside of the scanner) was added as an additional covariate of no interest in all VBM analyses. Controlling for this covariate resulted in a similar lack of significant correlation between the probability of successful memory retrieval and the precision of memory retrieval across the older adults, partial r = .04, p = .806, as reported above.

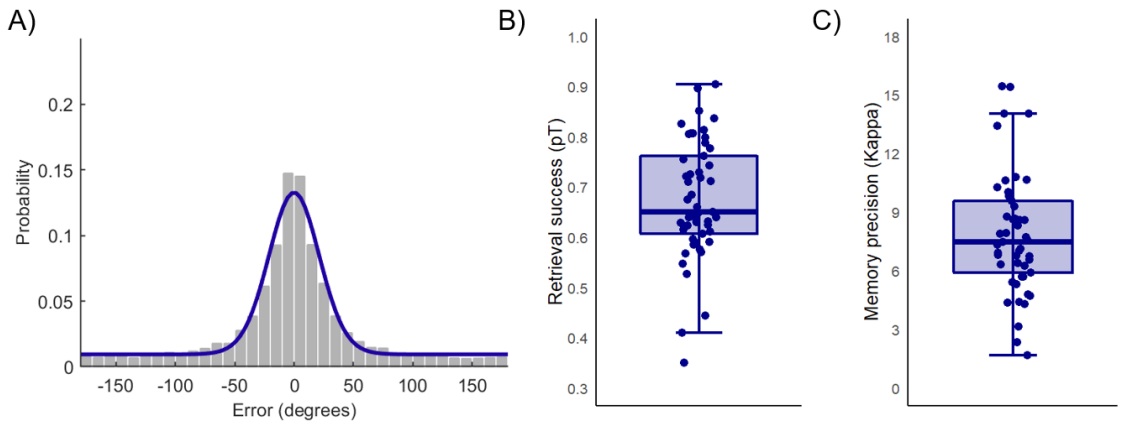

Figure 1. A) Distribution of retrieval errors across all participants and retrieval trials (8820 trials in total). Blue line displays the response probabilities predicted by the mixture model (von Mises + uniform distribution, fitted to aggregate data for visualization). Boxplots display the median and upper and lower quartiles of B) probability of successful memory retrieval (*pT*), and C) memory precision (*K*). Error bars displaying the largest/smallest value within 1.5 interquartile range from the upper/lower quartile, and jittered data points display the individual participant parameter estimates.

VBM results

VBM analyses were performed to identify brain regions displaying a significant relationship between GM volume and the success and/or precision of memory retrieval, after controlling for the effects of age, gender, education, and testing environment (in/outside scanner). The analysis of GM volume correlates of the probability of successful memory retrieval (*pT*) indicated a marginal effect in the right fusiform gyrus, $t(42) = 3.80$, $p = .051$, peak: 40, -28, -18, where there was a trend for greater grey matter volume to be associated with higher success of memory retrieval across participants. No significant or marginal relationships between GM volume and the success of memory retrieval were detected in the other regions of interest, including the hippocampus (*t*s < 2.67, *p*s >. 459), or in the exploratory whole brain analyses (*t*s > 3.80, *p*s > .763).

Examination of the GM correlates of the precision of memory retrieval (*K*), on the other hand, indicated a significant relationship between GM volume and memory precision in the left angular gyrus, $t(42) = 3.75$, $p = .026$, peak: -46, -68, 24, where greater GM volume was associated with higher precision of memory retrieval (see Figure 2). The relationship between regional GM volume and memory precision did not reach significance in the

other ROIs (*t*s < 3.61, *p*s > .121), however, on the whole brain level, a marginal positive relationship between GM volume and memory precision was evident in left inferior temporal gyrus also, $t(42) = 5.05$, $p = .059$, peak: 50, -57, -9. No other significant or marginal effects were observed at the whole brain level (*t*s < 4.63, *p*s > .170).

To examine whether the observed relationship between GM volume and memory performance in the left angular gyrus was specific to the precision of memory retrieval, the probability of successful memory retrieval was included as an additional covariate of no interest in the general linear model (retrieval success and precision estimates z-scored for this model). The relationship between memory precision and GM volume in the left angular gyrus remained significant after controlling for variation in the probability of successful memory retrieval, $t(41) = 3.75$, $p = .026$, peak: -48, -68, 24, indicating a contribution of angular gyrus GM volume to individual differences in memory precision over and above of any variance shared with differences in the probability of successful memory retrieval. Interestingly, the angular gyrus region where a relationship between grey matter volume and memory precision was observed in the current VBM analysis appeared to overlap with the region displaying age-related differences in retrieval activity associated with memory precision in the fMRI analysis described in Chapter 4 (see Figure 2C).

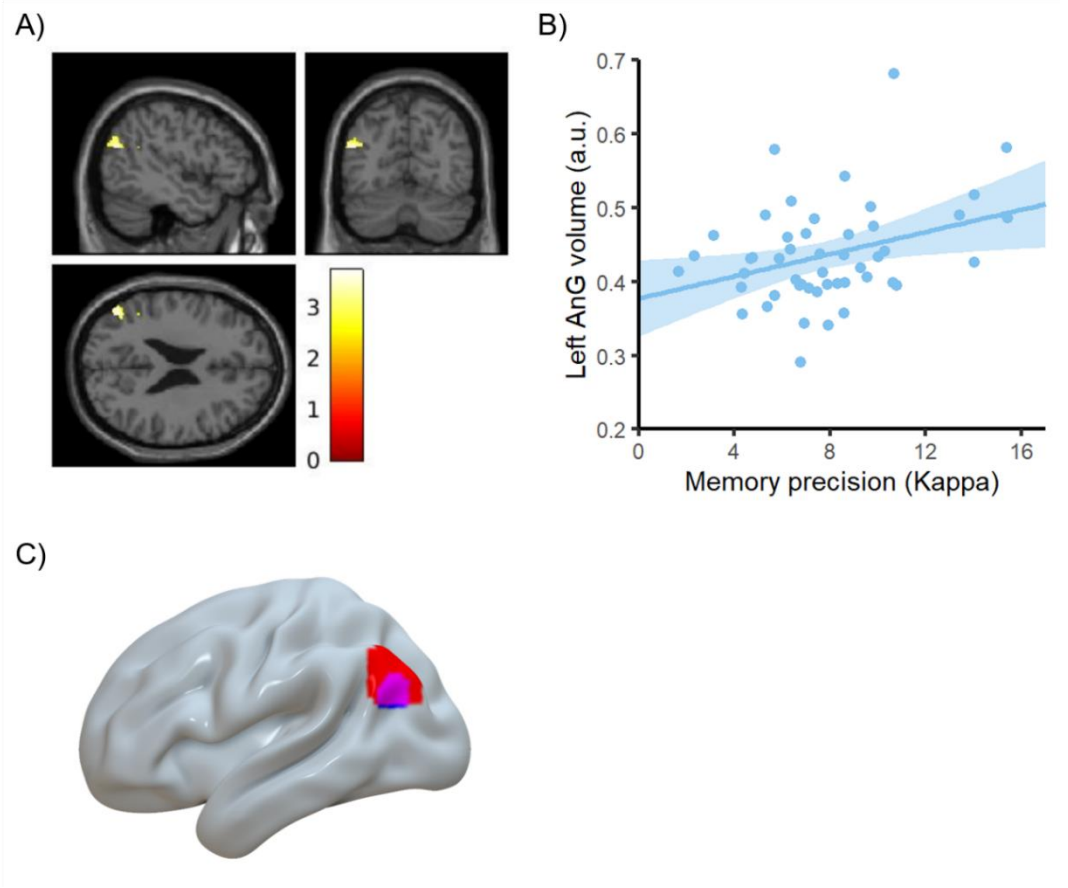

Figure 2. A) Grey matter volume in the angular gyrus correlated with the precision of memory retrieval across participants (effect masked with the left angular gyrus ROI and displayed at p < .01 uncorrected threshold for visualization). B) Relationship between the left angular gyrus GM volume (arbitrary units, a.u.) and memory precision (*K*) across the older participants. For visualisation, GM volumes were extracted from the cluster (*p* < .001 uncorrected, *k* = 54) associated with the peak angular gyrus voxel displaying a relationship with the precision of memory retrieval (x, y, z = -46, -68, 24). C) Overlap (purple) between the angular gyrus region displaying age differences in retrieval activity associated with memory precision in Chapter 4 (red) and the angular gyrus region demonstrating a relationship between grey matter volume and memory precision in the current VBM analysis (blue). Both effects are visualized at an uncorrected threshold of *p* < .001.

Discussion

The present chapter aimed to assess the relationship between variation in regional grey matter volume and individual differences in the success and precision of episodic memory retrieval in older age. Consistent with the age-related functional differences observed for precision-related activity in the angular gyrus in Chapter 4, I here observed a relationship between individual variability in left angular gyrus grey matter volume and the precision of memory retrieval in older age. Interestingly, no significant relationship between hippocampal volume and the probability of retrieval success was observed. Furthermore, no significant relationships between grey matter volume and the probability of successful memory retrieval were detected in other regions of interest, or across the whole brain, although a marginal positive relationship was present in the fusiform gyrus.

Although prior studies have often observed age-related grey matter declines in the lateral parietal cortex (Fjell et al., 2014; Good et al., 2001; Resnick et al., 2003; Ziegler et al., 2012), evidence relating structural integrity of this region to individual differences in episodic memory in older age has been limited. While some studies have linked parietal white matter integrity to variation in episodic memory in older age (Leong et al., 2017; Lockhart et al., 2012; Ziegler et al., 2010), evidence for a contribution of grey matter integrity in this region has less often been observed (Walhovd et al., 2006). The limited evidence for a relationship between parietal grey matter integrity and episodic memory performance may be partially explained by the lack of inclusion of this area as a region of interest in many studies (reviewed in Kaup et al., 2011), as well as the choice of memory measures in previous investigations. In particular, the majority of previous studies have employed standardized neuropsychological measures and/or composite scores of episodic memory, potentially insensitive for detecting variation in more qualitative aspects of memory retrieval as afforded by the current paradigm. Interestingly, in the current data the relationship between angular gyrus grey matter volume and memory precision persisted even after controlling for variation in the probability of successful memory retrieval, suggesting a contribution separable of any relationship shared with individual differences in the probability of successful memory retrieval.

The relationship between hippocampal grey matter volume and the probability of successful memory retrieval on the other hand did not reach significance in the current

study. Although findings of a relationship between hippocampal volume and episodic memory performance have been reported before (e.g., Gorbach et al., 2017; Hedden et al., 2016; Henson et al., 2016; Persson et al., 2012), not all previous studies have consistently detected such a relationship (Becker et al., 2015; Rajah, Kromas, Han, & Pruessner, 2010; Tisserand, Visser, Van Boxtel, & Jolles, 2000; Van Petten, 2004). The lack of a significant relationship in the current dataset may reflect the moderate sample size of the current study for detection of such individual differences, in particular for relatively small and complex structures such as the hippocampus (Good et al., 2001). Moreover, given the functional and structural heterogeneity of the hippocampal formation (Moscovitch et al., 2016; Strange, Witter, Lein, & Moser, 2014), it is possible that variability in different subcomponents of episodic memory retrieval may map onto structural differences in distinct hippocampal subfields (see Stevenson et al., 2018) undetected in the current analysis.

Outside the hippocampus, there was a trend for a positive relationship between fusiform gyrus grey matter volume and the probability of successful memory retrieval (p = .051 FWE SVC). While the primary sensory cortices are typically considered to be more resistant to age-related grey matter loss (Allen et al., 2005; Raz et al., 2004, 2005), higher order regions, such as the fusiform cortex, typically display greater age-related decreases (McGinnis et al., 2011; Nosheny et al., 2019). Changes in cortical thickness of the right fusiform gyrus have been previously observed to be associated with longitudinal decline in episodic memory performance in older age (Murphy et al., 2010), and in improvements in episodic memory performance in older adults following visualization-based memory training (Engvig et al., 2010). Given the results of Chapter 4 linking fusiform activity decreases at encoding with age-related reductions in memory success, one possibility is that structural integrity of this region may contribute to encoding processes enhancing the later accessibility of visual information from memory. However, given that this relationship did not reach statistical significance in the current study, further research is needed to assess the reliability of this finding.

The current results highlighted a relationship between grey matter volume of the lateral parietal cortex and memory precision in older age, however the basis of this relationship remains to be specified. Given the evidence for age-related grey matter losses in the lateral parietal cortex (Good et al., 2001; Lemaître et al., 2005; Resnick et al., 2003; Ziegler et al., 2012), it is possible that this relationship may reflect individual differences

in the extent of age-related structural declines in this region, or alternatively, this relationship may reflect more stable individual differences in grey matter volume present across the lifespan. Future studies incorporating lifespan samples and longitudinal approaches are required to address this matter. Future analyses can further distinguish whether this relationship between angular gyrus grey matter volume and memory performance may reflect variability in cortical thickness, surface area, or both (Ashburner & Friston, 2000; Hutton, Draganski, Ashburner, & Weiskopf, 2009). Indeed, some previous evidence has suggested these two grey matter components may exhibit differential age-related decline (Lemaitre et al., 2012; Storsve et al., 2014).

In addition to the relationships between regional grey matter volume and memory performance observed in the current experiment, and in previous studies (Becker et al., 2015; Head et al., 2008; Henson et al., 2016; Persson et al., 2012), previous research has demonstrated a contribution of white matter integrity of the frontal, temporal and parietal regions to variability in episodic memory performance in older age (Charlton, Barrick, Markus, & Morris, 2013; Metzler-Baddeley, Jones, Belaroussi, Aggleton, & O'Sullivan, 2011; Lockhart et al., 2012; Ziegler et al., 2010). Interestingly, in younger adults variability in the integrity of white matter tracts connecting the medial temporal lobe and the lateral parietal cortex has been found to predict individual differences in the retrieval of detailed memories (Wais, Jahanikia, Steiner, Stark, & Gazzaley, 2017), suggesting a potential role for the structural integrity of this pathway in individual differences in the precision of memory retrieval in older age also. In order to gain a more complete picture of the multifaceted structural basis of individual differences in episodic memory in older age, future analyses of the diffusion-weighted imaging data acquired for the current sample will examine the contribution of variability in white matter integrity of the episodic memory network to differences in the rate of successful memory retrieval and memory precision in older age.

In conclusion, findings of the current experiment provided novel evidence for a relationship between the structural integrity of the lateral parietal cortex and memory precision in older age. Critically, the relationship between angular gyrus grey matter volume and memory precision persisted after controlling for individual differences in the probability of successful memory retrieval, indicating a contribution beyond any relationship shared with individual differences in retrieval success. In contrast, significant grey matter correlates of individual differences in the probability of successful

memory retrieval were not observed in the current experiment, although the results indicated a trend for a positive relationship between grey matter volume in the fusiform cortex and the probability of successful memory retrieval in older age. To extend these findings, future analyses will explore the contribution of individual differences in structural connectivity within the episodic memory network to variability in the success and precision of memory retrieval in older age.

Chapter 6: General Discussion

The research presented in this thesis aimed to gain a more detailed understanding of the specific components underlying episodic memory decline in older age. Across the experiments presented in this thesis, I used continuous measures of memory retrieval in combination with mixture modelling of participants' retrieval errors to disentangle the effects of healthy ageing on two aspects of episodic memory retrieval: the probability of successfully retrieving information from memory, and the precision of the retrieved information. In addition to examining the effects of healthy ageing on these two aspects of memory retrieval, I also sought to identify the cognitive and neural changes underlying age-related decreases in each of these components. Using behavioural task manipulations and neuroimaging, I investigated the role of perceptual and working memory decreases and declines in the functional and structural integrity of the brain in the age-related changes in the success and precision of episodic memory retrieval. Converging findings across the experiments highlighted a role for impoverished precision of memory representations in the age-related episodic memory decline. The present chapter will summarize findings from each of the experimental chapters, discuss their theoretical implications and provide directions for future research.

Summary of findings

Findings from the current experiments provided consistent evidence for an age-related decline in the precision of episodic memory retrieval. Across four experiments, varying in the specific task design employed, the fidelity of older adults' successful memory retrieval was consistently reduced in comparison to that of the younger adults. In the two behavioural experiments presented in Chapter 2, I first examined the effects of healthy ageing on retrieval of different object features from long-term memory. Age-related reductions in memory precision were observed across retrieval of different perceptual aspects of the encoded stimulus, specifically locations, colours and orientations of the studied objects. In contrast to memory precision, significant age-related decreases in the probability of successful memory retrieval were detected only in the orientation condition of Experiment 2, which was also the condition resulting in the lowest probability of successful memory retrieval in the younger adults, potentially suggesting an effect of task difficulty in the age-related decreases in successful memory retrieval.

In Chapter 3, I investigated whether potential age-related reductions in the fidelity of perception or working memory may play a role in the LTM precision decreases observed in older age. In this experiment, significant age-related reductions in the precision of object colour reports were observed across perception, WM and LTM. The probability of reporting the target colour, on the other hand, did not significantly differ between the age groups in any of the three tasks. Consistent with prior evidence implicating working memory decreases in age-related episodic memory impairments (e.g., Bender & Raz, 2012; Hultsch et al., 1990), I observed the fidelity of WM retrieval to predict individual differences in the precision of LTM retrieval in the older group. However, controlling for variation in the precision of both working memory, and perception, did not fully account for the age-related deficit in the precision of long-term memory, suggesting additional age-related loss of memory fidelity during long-term memory storage or retrieval.

In the fMRI experiment presented in Chapter 4, I sought to more directly assess the potential contribution of both encoding and retrieval deficits to the age-related declines in the success and precision of episodic memory retrieval. In this experiment, younger and older adults completed a version of the continuous report task inside of the MRI scanner. This enabled the investigation of age differences in both encoding and retrieval activity associated with the (subsequent) success and precision of memory retrieval. Behaviourally, both the success and precision of memory retrieval were significantly reduced in the older group in this experiment. Analysis of the fMRI data further suggested distinct encoding and retrieval contributions to the age-related changes in each of these two memory components. During memory retrieval, I observed that the relationship between hippocampal activity and the binary success of memory retrieval was reduced in the older group, whereas age-related decreases in the relationship between retrieval activity and the graded precision of memory retrieval were observed in the angular gyrus. Furthermore, alterations in the encoding activity supporting the later success and precision of memory retrieval were observed in the older group in both the ventral visual and prefrontal cortex. Whereas the older group displayed reduced subsequent retrieval success and precision effects in the fusiform gyrus, age-related reductions in the inferior frontal gyrus were only evident for encoding activity predicting the later success of memory retrieval. Contrary to the pattern of activity observed during

retrieval, at encoding greater deactivation of the angular gyrus predicted later success and precision of memory retrieval in the young, but not older adults.

The final experimental chapter of the current thesis assessed the contribution of variability in the structural integrity of brain regions underpinning episodic memory to individual differences in the success and precision of episodic memory retrieval in older age. The voxel-based morphometry analysis presented in this chapter revealed a positive relationship between grey matter volume in the angular gyrus and the fidelity of memory retrieval in older age. This relationship persisted after controlling for variability in the probability of successful memory retrieval, suggesting a contribution over and above of any relationship shared with retrieval success. The findings of this experiment thus provided further evidence for the role of neural differences in the angular gyrus in memory precision in older age.

Age differences in memory performance across experiments

Each of the experiments presented in the current thesis employed a continuous report task to characterize age-related differences in memory performance. However, due to differences in the specific research question addressed, the exact task design varied across the experiments and may have impacted the age differences observed. Procedural differences across the current experiments are summarized in Table 1, and the mean mixture model parameters in each age group and experimental condition are presented in Figure 1. While age differences in memory precision were consistently observed across the experimental conditions, significant age-related decreases in the probability of successful memory retrieval were detected only in the orientation condition of Experiment 2 in Chapter 2, and in the colour condition of the fMRI experiment presented in Chapter 4 (but note that the difference in retrieval success was marginal in the location condition of this experiment also, and significant when modelling data across the feature conditions).

It is possible that the distractibility of the MRI scanning environment may have had a greater impact on older adults' memory performance, potentially contributing to the age differences in retrieval success observed in the fMRI experiment presented in Chapter 4. Indeed, previous research has demonstrated that the MRI environment can disproportionately affect older adults' long-term memory performance (Gutchess &

Park, 2006). Consistent with this potential explanation, Figure 1 suggests that the mean probability of successful memory retrieval in the older group who completed the same memory task outside of the scanner in the structural imaging experiment in Chapter 5 appears to be more comparable to that of the younger adult group in Chapter 4. However, since a separate younger adult group was not tested with the same experimental procedure outside of the scanner, the effect of the MRI environment on age differences in retrieval success cannot be directly evaluated. Indeed, it is possible that other procedural differences between the memory task used in Chapter 4 and the task versions used in the previous behavioural experiments may have also influenced the age differences observed. For instance, encoding blocks in Chapter 4 were longer than in the previous behavioural experiments (see Table 1). Given the previously-demonstrated susceptibility of older adults' memory performance to interference (Campbell, Hasher, & Thomas, 2010; Wilson, Potter, & Cowell, 2018; Yassa & Stark, 2011), this may have impacted the age differences observed in successful memory retrieval in Chapter 4.

Significant age differences in retrieval success were also evident in the orientation condition of the second behavioural experiment presented in Chapter 2. This was also the condition with the numerically lowest probability of successful memory retrieval in the younger adults across the experiments presented in the current thesis. Prior findings in a younger population have similarly demonstrated orientation to have the lowest probability of successful memory retrieval out of the three feature conditions tested in the current thesis (Cooper et al., 2017), however it is unclear why exactly the orientation condition would result in the lowest performance. While the object stimuli in this experiment were not pre-experimentally associated with a certain colour, or a background location, many of the objects can be thought of having a canonical 'upright' orientation. It is possible that this may have influenced the ease at which orientation information could be encoded to and/or retrieved from memory. Furthermore, given the demanding nature of the task, it is possible that the participants, and the older adults in particular, may have prioritized the encoding of location and colour information, resulting in a lower probability of successful retrieval of object orientations.

Although age differences in memory precision were consistently detected across the experimental conditions, Figure 1 suggests particularly prominent age-related differences in the location conditions of Chapter 4 and Experiment 1 of Chapter 2. In these two experiments, the object stimuli were presented on a scene background, whereas

an abstract texture background or a grey background was used in the other experiments. The presence of a contextually and visually richer scene background may have enabled the younger adults to encode object locations with greater precision, for instance by using specific landmarks in the background image (e.g., the hat was located next to the window), whereas the older adults may have not been able to benefit from such encoding strategies to the same extent (Craik & Rose, 2012). Alternatively, it is possible that the scene background could have hindered performance in the older group due to greater presence of irrelevant information. Indeed, reduced attentional resources are thought to impair the ability to inhibit irrelevant information in older age (e.g., Ryan, Leung, Turk-Browne, & Hasher, 2007)**.** However, a descriptively similar pattern of greater age-related differences in memory precision for object colours encoded on a scene background (Chapter 4) is not suggested by Figure 1, which may have been expected if the presence of a scene background distracted from the encoding of target features.

Findings across the experiments presented in this thesis thus suggest that experimental manipulations may influence age differences in the success and precision of episodic memory retrieval, however it is important to note that the current experiments were not designed to systematically explore the effects of these factors. The experiments presented in the current thesis each differ in various factors (see Table 1), making it difficult to distinguish the effects of a particular manipulation on memory performance. A more systematic approach is required to elucidate the effects of different experimental manipulations, such as block length or the number of features to encode, on age-related differences in the success and precision of episodic memory retrieval. Of particular interest is the investigation of factors influencing age differences in retrieval success, which were detected only in some conditions of the current experiments. Importantly, age differences in memory precision were consistently observed across the experiments, suggesting that these differences were robust to the exact experimental manipulation employed.

Table 1. *Differences in experimental design across the experiments.*

	Chapter 2 Experiment 1	Chapter 2 Experiment 2	Chapter 3	Chapter 4	Chapter 5
Features tested	Location	Location, Colour, Orientation	Colour	Location, Colour	Location, Colour
N retrieval trials	120	240 (80 per feature)	120	180 (90 per feature)	180 (90 per feature)
N blocks	5	10	8	9	9
N displays encoded per block	12	4	5	20	20
N objects encoded per display	3	3	3	1	1
N features encoded per object	1	3	1	2	2
N features retrieved per object	1	3	1	1	1
Encoding duration	9s	12s	9s	5s	5s
Retrieval duration	Unlimited	Unlimited	Unlimited	11s	11s
Background stimuli	Scene	Texture	Grey	Scene	Scene
In / outside scanner	Out	Out	Out	In	Out

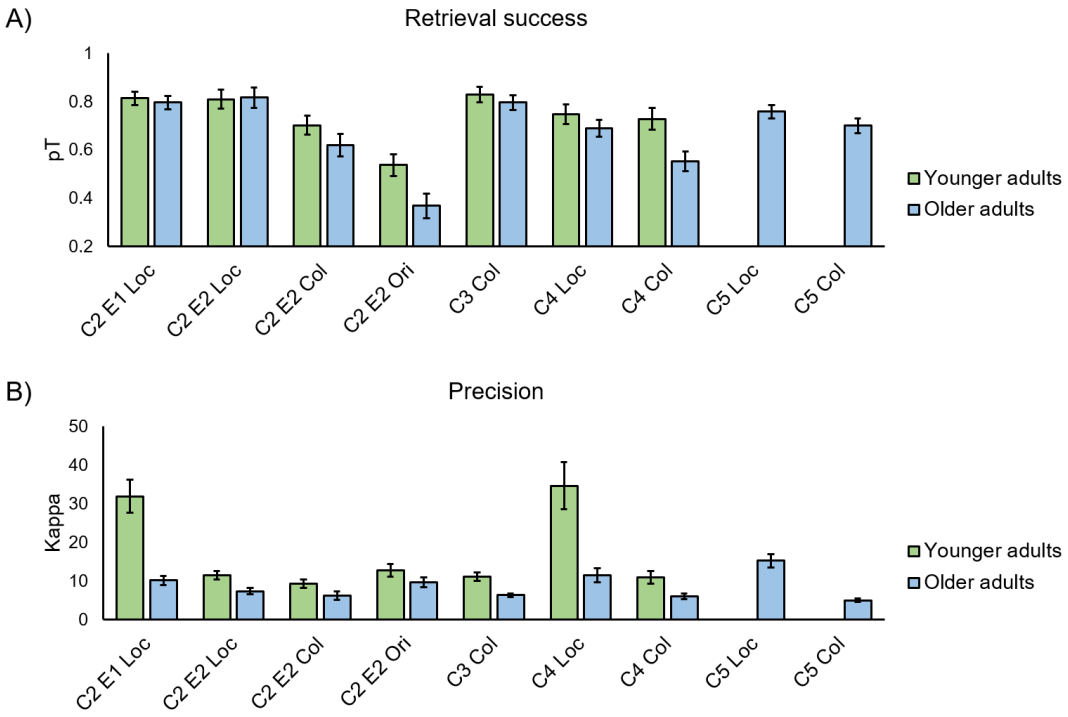

Figure 1. Mean model-estimated A) probability of successful memory retrieval, and B) precision of memory retrieval in each age group and experimental condition. Error bars display ± 1 SEM. Note that for Chapter 5, the estimates include only older adults who completed the memory task outside of the MRI scanner (N = 29). C = Chapter; E = Experiment; Loc = Location; Col = Colour; Ori = Orientation.

Implications for the cognitive basis of age-related memory decline

The current findings of reduced precision of memory retrieval in older age align with several previous reports of age-related reductions in the quality or specificity of information retained in memory (Kensinger & Schacter, 1999; Levine et al., 2002; Trelle et al., 2017). However, in many previous studies the assessment of age-related changes in memory quality has relied on binary or categorical measures of memory accuracy, or participants' metacognitive judgements about the confidence or vividness of their memory retrieval. The degree to which these measures truly reflect changes in memory fidelity, and not changes in other aspects of retrieval performance, has been difficult to distinguish. The research presented in the current thesis employed a more novel approach to the assessment of age-related changes in memory quality; a continuous report task requiring participants to reconstruct perceptual attributes of studied stimuli on a fine-grained, analogue scale. These types of measures are becoming increasingly popular for the assessment of episodic memory function in younger adults (e.g., Brady et al., 2013; Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Richter, Cooper et al., 2016), and have recently also been adopted for the examination of age-related changes in short-term and long-term memory (Nilakantan et al., 2018; Peich et al., 2013; Pertzov et al., 2015). The employment of this method allowed for a more direct assessment of memory fidelity in older age, as well as for the separation of age-related changes in retrieval precision from other potential sources of memory reductions (but see Schurgin et al., 2018), such as decreases in the probability of successful retrieval or the misbinding of object features. Indeed, in the current experiments, age-related reductions in memory precision were observed irrespective of the presence or absence of age-related declines in the probability of successful memory retrieval, suggesting that a decline in memory precision may be a consistent property of memory function in older age.

Reductions in the precision with which information can be encoded to and retrieved from memory may provide a possible explanation for several types of memory errors typically observed in older age. For instance, older adults typically display a greater tendency for false recognition of material perceptually, and/or conceptually, similar to items that have been previously studied (e.g., Stark et al., 2013; Trelle et al., 2017; Yassa et al., 2011). These age-related increases in false recognition of perceptually similar material might be explained by a loss of memory fidelity leading to representations of similar events becoming less distinctive in memory. Reduced memory precision may also result in

changes in the cognitive strategies employed during memory retrieval. Younger adults have been demonstrated to combine both item-specific (i.e., colour of the target item) and gist-based (i.e., average colour of all items from the same category as the target item) information when making a mnemonic decision (Brady, Schacter, & Alvarez, 2018). Gist-based information tends to be weighted more when there is greater uncertainty about the item-specific information, as indexed by participants' lower confidence in their item-specific memory (Brady et al., 2018). Thus, in addition to resulting in less distinctive memory representations of similar events, reduced precision of memory representations may increase susceptibility to false recognition by means of increasing reliance on gist-based information due to noisy item-specific memory traces (see Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997).

Furthermore, the precision of memory representations and the accessibility of these representations may interact during retrieval. In particular, it is possible that greater fidelity of a memory representations may make the representation more likely to be successfully retrieved from memory. Reduced memory fidelity may therefore partly explain the prominent age differences observed on tasks requiring controlled access of information from memory in the absence of environmental support (Craik & McDowd, 1987; Danckert & Craik, 2013; Rhodes et al., 2019). The common finding of greater vulnerability to age-related decline of recall in comparison to recognition (Craik & McDowd, 1987; Danckert & Craik, 2013; Rhodes et al., 2019) may partly reflect a greater influence of impoverished memory fidelity on tasks where the encoded stimulus is not readily available at test. However, the lack of correlation between the probability of successful retrieval and memory precision observed across the older adults in Chapter 5 suggests that decreases in memory precision may not always be coupled with reductions in the success of memory retrieval.

Another typical finding in the literature regarding age-related memory reductions is the prominent decline of associative retrieval in older age (Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995). Studies investigating age-related declines in associative memory have typically focused on age-related reductions in the probability of successfully retrieving an association between units of information (e.g., Cansino et al., 2018; Naveh-Benjamin, 2000), however the current results indicate that the precision with which event features can be bound and retrieved from memory also exhibits age-related decreases. Reduced memory precision may partly account for the

age-related associative memory deficits observed in categorical memory tasks, in particular when they require discrimination between similar memory traces. For instance, decreased memory precision is likely to contribute to age-related deficits on source memory tasks requiring the discrimination of two, or more, similar sources of memories, such as voices of speakers of the same gender (Simons et al., 2004) or quadrants of object locations presented on a computer screen (Cansino et al., 2018; Kukolja et al., 2009).

Importantly, the current results do not imply that memory reductions in older age solely result from reductions in the fidelity of retained memory representations. Significant reductions in the probability of successful memory retrieval were also observed in the older group in the orientation condition of Chapter 2 and in the colour condition (and when modelling performance across features) of Chapter 4. Thus at least in some circumstances, older age is also associated with a reduced probability of accessing information from memory. In Chapter 2, significant age-related reductions in the probability of successful memory retrieval were observed only in the orientation condition, but not the location or colour conditions, suggesting that these reductions could be driven by forgetting of particular associations between an object and its features. This is consistent with the notion of vulnerability of associative retrieval to age-related decline (Naveh-Benjamin, 2000; Old & Naveh-Benjamin, 2008). However, future studies separating the contributions of memory for object identity and its associated features are required to distinguish the relative contribution of declines in item and associative memory to reductions in the probability of successful memory retrieval in older age.

Implications for the neural basis of age-related memory decline

In addition to elucidating the cognitive basis of age-related episodic memory impairments, the findings presented here contribute to a more detailed understanding of the neural changes underlying age-related episodic memory declines. In particular, the functional and structural neuroimaging experiments presented in Chapters 4 and 5 highlighted the role of the ventrolateral parietal cortex, more specifically the angular gyrus, in episodic memory precision in older age. Chapter 4 demonstrated an age-related decrease in the relationship between retrieval-related BOLD activity and memory precision in the angular gyrus, whereas the VBM analysis presented in Chapter 5

provided evidence for a relationship between variation in angular gyrus grey matter volume and individual differences in memory precision in older age. There was considerable overlap in the angular gyrus region identified in these two analyses, providing converging evidence for a contribution of both the functional and structural integrity of the lateral parietal cortex to memory fidelity in older age.

The findings implicating the angular gyrus in the age-related reductions in memory precision are consistent with increasing evidence from younger adults demonstrating a role for the lateral parietal cortex in supporting the quality and detail of episodic memory retrieval (Kuhl & Chun, 2014; Murray et al., 2015; Richter, Cooper et al., 2016; Vilberg & Rugg, 2007, 2009). In addition to scaling with the objective precision of memory retrieval (Richter, Cooper et al., 2016), retrieval activity in the angular gyrus has been demonstrated to be associated with the subjective vividness of retrieved memories (Kuhl & Chun, 2014; Tibon et al., 2019), as well as the amount of details recollected from memory (Vilberg & Rugg, 2007, 2009). Furthermore, individuals with lateral parietal lesions typically display reduced memory confidence and less frequently report their memory retrieval to be accompanied by the subjective experience of remembering a past event, despite a lack of pronounced objective memory impairments (Davidson et al., 2008; Simons et al., 2010). These findings suggest that the richness and detail of episodic memory retrieval may be affected by parietal lesions, leading to reduced subjective ratings of retrieval quality. Interestingly, transcranial magnetic simulation of the lateral parietal cortex during memory retrieval has recently been shown to enhance the precision of episodic recollection in younger adults (Nilakantan et al., 2017). Whether this approach may also be able to alleviate the memory precision declines exhibited by older adults can be explored in future studies.

In the fMRI experiment presented in Chapter 4, the relationship between retrieval activity in the angular gyrus and the graded precision of memory retrieval did not reach significance in the older group alone. However, a recent electroencephalography study has provided evidence for a functional role of the parietal cortex in the precision of episodic memory retrieval in older age (Murray, Ouyang, & Donaldson, 2019). Murray and colleagues (2019) observed ERPs over the parietal cortex to be sensitive to the precision of recollected information in older adults, similar to findings previously observed in younger adults (Murray et al., 2015). These findings, in combination with the current observation of a relationship between the structural integrity of the angular

gyrus and variability in memory precision in older age, suggest that this region may nevertheless continue to support the precision of episodic memory retrieval in older age. However, as no younger control group was included in the Murray et al. (2019) study, it remains to be established whether a similar reduction in the sensitivity of parietal ERPs to memory precision may be evident in older age as observed for BOLD activity in the angular gyrus in Chapter 4.

In contrast to the current findings implicating the lateral parietal cortex in the age-related declines in memory fidelity, others have proposed a greater role for the hippocampus in the reductions in episodic memory precision observed in older age (Holden, Hoebel, Loftis, & Gilbert, 2012; Nilakantan et al., 2018; Stark et al., 2010; Yassa & Stark, 2011). Nilakantan and colleagues (2018) reported that patients with medial temporal lobes lesions and healthy older adults both exhibited declines in the precision, but not success, of spatial recollection. In particular, declines in retrieval precision were prominent for patients whose lesions included the hippocampus, leading the authors to propose that hippocampal deficits may also underlie the age-related changes in episodic memory precision (Nilakantan et al., 2018). However, the contribution of structural and/or functional declines in the hippocampus, or elsewhere in the brain, to the precision deficits observed in healthy older adults was not directly assessed in that study, meaning that the possible involvement of reduced angular gyrus function could not be assessed.

In contrast, the research presented in the current thesis enabled a more direct evaluation of this proposal by assessing the extent to which the memory precision deficits exhibited by older adults may be associated with alterations in encoding or retrieval activity in the hippocampus, and/or grey matter integrity of this region. In Chapter 4, I observed hippocampal retrieval (but not encoding) activity to correlate with the precision of memory retrieval across young and older participants, consistent with the proposal that this region might also play a role in episodic memory precision (Nilakantan et al., 2018; Stevenson et al., 2018; Yonelinas, 2013). However, no significant age differences in the relationship between hippocampal BOLD activity and memory precision were observed, nor did variability in structural integrity of the hippocampus significantly predict individual differences in memory precision across the older adults in Chapter 5. Thus, the current results failed to provide evidence for a primarily hippocampal basis of age-related reductions in memory precision. However, given the moderate sample sizes of the current neuroimaging experiments, further research is required to establish whether

the hippocampus may also play a role in the memory precision deficits observed in older age (see Yassa & Stark, 2011). Furthermore, given the role of the hippocampus in facilitating the reinstatement of cortical memory traces (McClelland et al., 1995; Norman & O'Reilly, 2003; Treves & Rolls, 1994), it is possible that reduced fidelity of hippocampal inputs to cortical regions, including the angular gyrus, may have contributed to the precision deficits observed in older age, even if no significant age differences in the relationship between univariate activity and memory precision were evident. This possibility will be examined in future analyses investigating the integrity of hippocampal-cortical functional connectivity in older age.

The current results, however, provided evidence for a decreased relationship between hippocampal retrieval activity and the success of memory retrieval in older age, consistent with prior reports (e.g., Cansino et al., 2015; Tsukiura et al., 2011). The age differences observed for retrieval success and precision-related activity in the hippocampus and the angular gyrus, respectively, align with the proposed roles of these two regions in episodic memory retrieval (Diana, Yonelinas, & Ranganath, 2007; Richter, Cooper et al., 2016; Rugg & King, 2018; Sestieri, Shulman, & Corbetta, 2017). Computational models of hippocampal function suggest that at the time of retrieval, the hippocampus enables the recovery of stored memories via the mechanism of pattern completion (O'Reilly & McClelland, 1994; Norman & O'Reilly, 2003)**.** The recurrent collateral connectivity of the CA3 subfield of the hippocampus is thought to allow for retrieval of a complete memory representation (i.e., pattern) in response to a partial, or degraded, cue (O'Reilly & McClelland, 1994; Treves & Rolls, 1994; reviewed in Hunsaker & Kesner, 2013). As a consequence of hippocampal pattern separation, assigning distinct memory representations to similar inputs, lure items are thought to rarely lead to pattern completion (Norman, 2010; Norman & O'Reilly, 2003). The hippocampal memory signal can thus be viewed as thresholded, where above a certain criteria only studied items will elicit memory retrieval (Norman, 2010; Norman & O'Reilly, 2003).

The finding of reduced hippocampal retrieval success effects in the older group in Chapter 4 highlights the possibility that age-related changes in the probability of successful memory retrieval may be partly underpinned by an impaired hippocampal retrieval mechanism. Interestingly, prior accounts have proposed ageing to impair hippocampal pattern separation and to be associated with an increased tendency for

pattern completion (Wilson, Gallagher, Eichenbaum, & Tanila, 2006; Yassa & Stark, 2011). Findings demonstrating age-related impairments in mnemonic discrimination of studied items from perceptually similar lures have been taken as evidence to support this proposal (e.g., Holden et al., 2012; Ly et al., 2013; Stark et al., 2010; Yassa et al., 2011). However, distinguishing the processes of pattern separation and pattern completion from behavioural data alone in such paradigms is difficult (Hunsaker & Kesner, 2013; Molitor, Ko, Hussey, & Ally, 2014). Another approach for the assessment of pattern completion in older age has been taken by studies investigating the effect of cue completeness on memory performance (Paleja & Spaniol, 2013; Vieweg, Riemer, Berron, & Wolbers, 2019; Vieweg, Stangl, Howard, & Wolbers, 2015). Although demonstrating an age-related bias toward pattern completion, these studies have also provided evidence for a deficit in pattern completion in older age (Vieweg et al., 2019, 2015). Specifically, reducing the amount of cue completeness (by masking a studied scene serving as a retrieval cue) has been shown to disproportionately impair scene recognition performance in older adults (Vieweg et al., 2019, 2015). It is thus possible that age-related impairments in hippocampal pattern completion may in part contribute to a decreased likelihood of successful memory retrieval in older age.

After successful reinstatement of the hippocampal memory representation, the hippocampus is thought to drive the reinstatement of the retrieved information in the cortical regions originally encoding the event (Danker & Anderson, 2010; Treves & Rolls, 1994). Cortical reinstatement is thought to vary in the degree of detail or precision of the reinstated memories (Danker, Tompary, & Davachi, 2017; McClelland & Goddard, 1996). Accounts of the role of the posterior parietal lobe in episodic memory retrieval suggest that this region may be involved in the online maintenance of the retrieved content after hippocampal pattern completion has occurred (Rugg & King, 2018; Sestieri et al., 2017; Vilberg & Rugg, 2008; Wagner et al., 2005), integrating information from multiple modality-specific cortical regions into a coherent memory representation (Bonnici et al., 2016; Shimamura, 2011). This proposal has been supported by evidence showing sustained activity associated with successful episodic memory retrieval in the angular gyrus, in contrast to a more transient response observed in the medial temporal lobes (Vilberg & Rugg, 2012).

Given the proposed role of the angular gyrus in the online maintenance of retrieved information (e.g., Rugg & King, 2018; Vilberg & Rugg, 2008), one possibility is that the

age-related declines in memory precision observed in the current thesis may in part reflect greater noise in the representation of retrieved content in this region. Computational accounts of cognitive ageing have proposed age-related neuromodulatory declines to decrease the signal-to-noise ratio of neural signalling, reducing the fidelity of cortical representations (Li et al., 2001; Li & Rieckmann, 2014). In line with this proposal, functional neuroimaging studies have demonstrated reduced fidelity of cortical reinstatement in older age (e.g., Abdulrahman et al., 2017; St-Laurent et al., 2014; but see Wang et al., 2016), but these decreases have not yet been directly evaluated in relation to memory precision. Future studies employing multivariate approaches to the analysis of fMRI data would therefore be useful in order to examine the role of age-related changes in the fidelity of cortical reinstatement in the angular gyrus, and elsewhere in the brain, in the age-related changes in the precision of episodic memory retrieval.

In addition to changes during memory retrieval, the current data suggest encoding contributions to the age-related decreases in the success and precision of episodic memory retrieval. In Chapter 4, the relationship between encoding activity in the fusiform gyrus and the subsequent success and precision of memory retrieval was reduced in the older group, consistent with prior findings displaying age-related reductions in subsequent memory effects in the ventral visual cortex (Maillet & Rajah, 2014a; Park et al., 2013). Indeed, decreases in BOLD activity are frequently observed in visual regions during episodic memory encoding, as well as across other cognitive tasks (Cabeza et al., 2004; Li et al., 2015; Spreng et al., 2010). Furthermore, the selectivity of neural responses in visual regions has been shown to exhibit age-related declines (Carp et al., 2011; Goh et al., 2010; Park et al., 2012). Activity in the fusiform gyrus, in particular, has been observed to display reduced category- and item-specificity during visual perception in older age (Goh et al., 2010; Park et al., 2012), suggesting age-related decreases in the fidelity of perceptual processes supported by this region. It is possible that age-related declines in the ventral visual cortex may contribute to impoverished encoding of visual information into memory, impacting both the later likelihood of this information being successfully retrieved as well as the fidelity with which it can be reinstated.

Furthermore, the current results indicated a reduced relationship between encoding activity in the inferior frontal gyrus and the later success of memory retrieval in the older group, consistent with prior reports of decreased prefrontal subsequent memory effects

in older age (Dulas & Duarte, 2011; Vidal-Piñeiro et al., 2018, Wang & Cabeza, 2016). The prefrontal cortex is considered critical for supporting memory control processes directing the encoding of information in a goal-relevant manner (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). Indeed, memory declines in older age are thought to in part result from decreased ability to engage in strategic encoding processes maintained by the prefrontal cortex (Craik & Rose, 2012; Shing et al., 2010). The current findings thus highlight the possibility that such decreases may have impacted the efficiency with which feature and object information were bound to a durable memory representation (Shing et al., 2010), affecting the likelihood of later successful retrieval of these associations. Furthermore, prior research has often demonstrated age-related increases in subsequent memory effects in the right prefrontal cortex (e.g., Gutchess et al., 2005; Morcom et al., 2003). In the current fMRI experiment, no significant age-related increases in the right prefrontal encoding activity associated with later success, or precision, of memory retrieval were observed. However, the analysis of age differences in the hemispheric lateralization of prefrontal encoding activity provided evidence for reduced lateralization of both subsequent success and subsequent precision effects in older age. The current findings are thus consistent with the proposal of age-related reductions in prefrontal functional lateralization (Cabeza, 2002), potentially reflecting loss of neural specificity or increased neural inefficiency in older age (Morcom & Henson, 2018).

In addition to a diminished relationship between retrieval activity and the graded precision of episodic memory retrieval, the older adults also displayed a reduced relationship between encoding activity and both the subsequent precision and success of memory retrieval in the angular gyrus in Chapter 4. Where in younger adults, greater deactivation of the angular gyrus at encoding predicted later success and precision of memory retrieval, no such effects were detected in the older group. In contrast to the enhanced activation typically observed during successful retrieval, negative subsequent memory effects in the ventrolateral parietal cortex, and other regions of the default-mode network, are often observed in younger adults (Daselaar et al., 2009; Kim, 2011; Uncapher & Wagner, 2009). These effects are typically diminished in older age (De Chastelaine et al., 2015; Park et al., 2013), and have been proposed to reflect inefficient suppression of internally-oriented cognition and irrelevant thoughts detrimental for memory encoding (De Chastelaine et al., 2011; De Chastelaine et al., 2015; Miller et al.,

2008). This interpretation aligns with the proposed involvement of the angular gyrus, along with other regions of the DMN, in tasks requiring the representation of internally generated information, such as the contents of memory retrieval (Buckner & DiNicola, 2019). In turn, deactivation in these regions is thought to occur when the current task requires the representation of externally constrained information, such as during the encoding of perceptual information (Buckner & DiNicola, 2019). However, it should be noted that the finding that episodic memories can be successfully acquired even in the absence of reliable negative subsequent memory effects, such as observed in the case of healthy older adults in Chapter 4 and in previous studies (e.g., De Chastelaine et al., 2011), has raised questions regarding the functional significance of the negative subsequent memory effects for successful memory formation (Rugg, 2016). Thus, the precise role of decreased memory-related deactivations in the ventrolateral parietal cortex during encoding in the age-related episodic memory deficits remains to be clarified.

The neuroimaging results observed in the current thesis thus suggest both encoding and retrieval contributions to age-related changes in the success and precision of memory retrieval. However, it is important to note that although significant age differences in the encoding and retrieval activity underlying the success and precision of memory retrieval were detected in partly distinct brain regions, direct comparison of age differences in these effects did not provide evidence for significantly disproportionate functional changes associated with either aspect of memory retrieval in any of the regions of interest. Indeed, in many of the regions of interest encoding and/or retrieval activity correlated with both the success and precision of memory retrieval across participants. How regionally specific the age-related changes in the encoding and retrieval correlates of these two aspects of memory retrieval are, therefore, remains to be clarified.

Mixture modelling of LTM retrieval

Throughout the experiments presented in this thesis I used a mixture modelling approach to characterize age differences in memory performance. In each experiment a two-component mixture model consisting of a von Mises distribution centred at the target feature value and a circular uniform distribution was fitted to participants' retrieval error data to estimate two parameters of memory performance: the probability of successfully

retrieving information about the target feature from memory (*pT*), and the precision of the retrieved information (*K*). This model assumes that two distinct sources of error contribute to participants' retrieval performance: variability, i.e. noise, in successful retrieval of target features, and the presence of guessing responses where memory retrieval has failed to bring any diagnostic information about the target to mind.

This mixture model was originally developed to account for the distribution of recall errors in continuous report tasks of WM (Zhang & Luck, 2008), but has since been shown to also characterize the pattern of retrieval errors observed in LTM (e.g., Brady et al., 2013; Richter, Cooper et al., 2016, although note that some LTM models use a different distribution for the successful component, e.g., Harlow & Donaldson, 2013). Studies utilizing this analysis approach in LTM have yielded novel insights regarding the cognitive and neural substrates of episodic memory (e.g., Cooper & Ritchey, 2019; Richter, Cooper et al., 2016; Stevenson et al., 2018), and have demonstrated that the two mixture model parameters can be differentially affected by both experimental manipulations (e.g., Sutterer & Awh, 2016; Xie & Zhang, 2017, 2018) and neurological conditions (Cooper et al., 2017; Nilakantan et al., 2018).

However, it should be noted that the validity of this two-component mixture model has been questioned in both WM (Bays et al., 2009; Fougnie et al., 2012; Schurgin et al., 2018; van den Berg et al., 2012) and LTM (Schurgin et al., 2018). In WM, alternative models propose responses resembling random guessing to reflect low precision of memory retrieval emerging from variability in the fidelity with which stimuli is encoded across trials (van den Berg et al., 2012), or non-target reports resulting from misbinding of features across items (Bays et al., 2009). In the current experiments, I compared the standard von Mises and uniform mixture model to a model further incorporating a non-target error component (Bays et al., 2009), but, consistent with previous work in younger adults (Richter, Cooper et al., 2016), found the von Mises and uniform model to better characterize both younger and older adults' memory performance in the current experiments.

Interestingly, recent work has further suggested that a simpler, single parameter signal detection model may better characterize memory performance in both WM and LTM continuous report tasks (Schurgin et al., 2018). Using data from a perceptual discrimination task, Schurgin et al. (2018) showed that by taking into account the non-

linear relationship between physical and psychological stimulus spaces, participants' retrieval performance on a continuous report paradigm could be characterized by one parameter corresponding to memory strength (*d'*). According to their Target Confusability Competition (TCC) model, recall errors in continuous report tasks arise from a noisy memory-match signal, the strength of which for each distractor value in the continuous response space depends on the psychophysical similarity of the distractor to the target. Response errors resembling random guesses arise in this model due to distractors far from the target being equally confusable to the target item (i.e., participants are unable to determine whether a distractor 120 degrees or 180 degrees from the target is closer to the target), not due to a separate guessing state.

Schurgin et al. (2018) provided evidence to show that the TCC model fit better than the more complex von Mises and uniform mixture model for several WM datasets, as well as for data from a LTM object colour retrieval task (but note that the model was fit to item hits only, whereas item memory was not assessed separately from feature retrieval in the experiments presented in the current thesis). In terms of the mixture model parameters, the TCC model would predict a change in memory strength to result in correlated changes in both memory precision and the probability of guessing responses. Thus, it remains to be further evaluated how well this model can account for previous findings from LTM demonstrating selective increases or decreases in one of these parameters (e.g., Cooper et al., 2017; Nilakantan et al., 2018; Xie & Zhang, 2018). Furthermore, it is unclear how well this model fits with existing accounts of hippocampal memory retrieval; a region considered as the key substrate of episodic memory, and typically not characterized by a familiarity-like retrieval mechanism (Norman, 2010; Norman & O'Reilly, 2003, but see Wais, Wixted, Hopkins, & Squire, 2006). Due to requirement for additional perceptual discrimination data, it was not possible to evaluate the TCC model in the experiments presented in the current thesis, however future studies incorporating an estimation of the psychophysical scaling function can address whether changes in this function, and/or in memory strength could account for the pattern of age-related memory changes observed in the current thesis. Indeed, while the current mixture model provides a method for statistically decomposing sources of retrieval error, further research is needed to develop a more mechanistic account of the distribution of retrieval errors in LTM (see Bays 2014, 2015 and Taylor & Bays, 2019 for a neural-level implementation of WM retrieval).

Outstanding questions and future directions

Together, the findings presented in this thesis provided evidence for age-related declines in the probability of successful memory retrieval in some circumstances and, more consistently, the precision of retrieved memory representations; however future work is required to fully uncover the neurocognitive basis of age-related changes in each of these aspects of memory retrieval, and the degree of which they may reflect dissociable or shared neurocognitive mechanisms. In particular, it remains to be established whether encoding and retrieval deficits are sufficient to explain the age-related reductions in memory precision, or whether the fidelity of the underlying memory representations also exhibits greater decay over time in older age. Evidence from younger adults has shown greater loss of memory precision over long versus short study-test delays (Harlow & Donaldson, 2013), suggesting that encoding and retrieval factors may be insufficient to fully explain variability in memory fidelity. Accordingly, it may be that forgetting in older age is characterized by accelerated loss of the fidelity of retained information, contributing to the retrieval precision declines observed in the current experiments.

It is also possible that the fidelity of memory retrieval in older age might have been affected by perceptual interference present at test. The continuous report task used here allowed for a test object to be viewed across varying degrees of perceptual similarity to the original encoded value. As older adults' memory retrieval has been observed to be susceptible to perceptual interference (Ly et al., 2013; Pidgeon & Morcom, 2014; Wilson et al., 2018), it is possible that the test format might have partially contributed to the memory precision declines observed in older age. Interestingly, in short-term memory, moderate, in contrast to high or low, levels of perceptual similarity have been observed to decrease the precision of memory retrieval in younger adults (Sun et al., 2017). Future studies should address whether a greater susceptibility to interference may contribute to the precision reductions observed in older age, as well as the type of interference that is most detrimental. However, the observation in Chapter 3 that reductions in episodic memory precision were not fully accounted for by age-related deficits present in the working memory task suggests that interference at test was unlikely to be the sole factor contributing to age-related declines in memory precision, given that the test format was identical between the working memory and long-term memory tasks used in Chapter 3.

In contrast to episodic retrieval, semantic memory is thought to remain relatively spared in older age (Rönnlund et al., 2005), and has been observed to benefit episodic memory retrieval, sometimes reducing age differences in episodic memory performance (Mohanty et al., 2016; Naveh-Benjamin et al., 2005). It is possible that the semantically rich material used in the current paradigms, such as everyday objects and landscape scenes, could have resulted in enhanced memory performance in older age. In addition to the potential benefit from semantic memory, the reinstatement of aspects of the encoding context may have also enhanced participants' memory performance in the paradigms used here. In particular, in Chapter 2, the background on which the object was originally presented at encoding was also present during retrieval. In Chapter 3, although a grey background was used across the trials, the object reappeared at test in the same location as it had been presented in during encoding. In Chapters 4 and 5 both the associated background and the encoded value of the uncued feature were reinstated at test. Although prominent age-related declines in contextual memory are often evident (Old & Naveh-Benjamin, 2008; Spencer & Raz, 1995), reinstatement of contextual aspects of the studied stimuli, such as the background the stimuli was associated with, has been observed to increase retrieval performance in older age (Craik & Schloerscheidt, 2011). An interesting question for future studies to assess is, therefore, whether greater age differences in the probability of successful memory retrieval and/or the precision of retrieved information might be observed under conditions where minimal encoding and retrieval support is provided.

Although successful memory retrieval and memory precision can be viewed as theoretically distinct memory components (e.g., Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Richter, Cooper et al., 2016), it is important to consider whether age-related changes in these two components could arise via a single mechanism (see also Schurgin et al., 2018). In the current thesis, age-related declines in memory precision were consistently detected across the experiments, however evidence for significantly disproportionate age-related declines in memory precision was not always observed, and indeed significant age-related decreases in the probability of successful memory retrieval were also evident in some task conditions. It is thus possible that changes in these two memory components may reflect age-related declines on a single factor, to which memory precision may be more sensitive to. For instance, greater noise in memory representations in older age may impact both the probability of successfully retrieving a

memory as well as the precision with which it can be recalled. Similarly, age-related attentional limitations at encoding (reviewed in Zanto & Gazzaley, 2016) could potentially decrease both the precision with which memory representations are acquired and the probability of them being retained (see Chun & Turk-Browne, 2007; Liu, Shen, Olsen, & Ryan, 2017; Pertzov, Avidan, & Zohary, 2009). Further research is thus needed to fully characterize the extent to which changes in the success and precision of episodic memory in older age may reflect shared neurocognitive underpinnings.

The observation that age-related reductions in memory precision were evident in the current experiments, even when no such age differences in the probability of successful memory retrieval were detected, nevertheless highlights the sensitivity of this measure to memory changes associated with healthy ageing (see also Nilakantan et al., 2018). A valuable question for future research to explore is whether this measure may prove beneficial not only for detection of memory impairments associated with healthy ageing, but also for early identification of memory changes predicting later pathological cognitive decline. Indeed, some preliminary evidence suggests that continuous measures of memory retrieval may be sensitive for the identification of individuals at risk, or in prodromal stages of neurodegenerative disease (Hampstead, Towler, Stringer, & Sathian, 2018; Zokaei et al., 2019). In particular, continuous measures of object location retrieval have been found to be sensitive for the identification of older individuals with high genetic risk of developing Alzheimer's disease (Zokaei et al., 2019), as well as to differentiate between healthy older individuals and older adults diagnosed with mild cognitive impairment (Hampstead et al., 2018). Furthermore, Zokaei and colleagues (2015) found working memory precision to detect pre-medication short-term memory impairments in patients with Parkinson's disease, as well as to be sensitive to working memory improvements after the initiation of dopaminergic medication, while traditional neuropsychological tests of working memory span failed to detect both the pre-medication deficits and post-medication improvements. Thus, continuous measures of memory retrieval may be useful for not only the early identification of individuals at risk of developing clinical memory impairments but also for assessment of treatment efficacy after the disease onset.

In addition to providing a sensitive measure of memory quality, continuous measures of retrieval performance may also be advantageous for distinguishing the specific components underlying memory impairments in distinct populations. For instance, both

older adults and high-functioning individuals with autism have been observed to exhibit decreased episodic recollection performance (Cooper & Simons, 2019; Koen & Yonelinas, 2016). However, while reductions in memory performance exhibited by autistic individuals are characterized by decreased probability of successfully retrieving information from memory (Cooper et al., 2017), the current results suggest that more pronounced declines in memory precision may underlie deficits in episodic memory in older age (see also Nilakantan et al., 2018). Thus, seemingly similar memory impairments may reflect decreases in distinct subcomponents of memory retrieval, revealed by the decomposition of memory performance into its constituent parts with continuous retrieval measures and mixture modelling. This approach is likely to enhance the understanding of the neurocognitive basis of memory deficits beyond age-associated decline, as well as to aid in evaluation of the effects of treatments or interventions designed to enhance memory function on specific aspects of retrieval performance. Indeed, different approaches may be suitable for targeting declines in the probability of successful retrieval and memory fidelity (see Nilakantan et al., 2017).

The current findings of reduced fidelity of memory representations in older age parallel findings from neuroimaging studies demonstrating age-related reductions in the fidelity of neural representations during both visual perception and mnemonic processing (Bowman et al., 2019; Carp et al., 2011; St-Laurent et al., 2014; Trelle et al., 2019; Zheng et al., 2018). The specificity of brain activity to different stimulus categories, such as faces or objects, has been demonstrated to decrease in older age in the ventral visual stream (Berron et al., 2018; Carp et al., 2011; Park et al., 2004; Park et al., 2010; Park et al., 2012). In addition to reduced category-specificity, the sensitivity of neural responses to more fine-grained differences between individual items also appears to exhibit age-related degradation (Bowman et al., 2019; Goh et al., 2010). For instance, older adults display repetition suppression to not only identical, but also perceptually similar faces (Goh et al., 2010), as well as reduced distinctiveness of neural representations corresponding to perceptually highly similar exemplars of the same object (e.g., two similar pairs of glasses) (Bowman et al., 2019). Furthermore, the similarity of neural representations corresponding to the same stimulus exemplar across repetitions has been observed to be reduced in older age during memory encoding (Trelle et al., 2019; Zheng et al., 2018). Thus, in addition to greater variability in memory representations observed

on the behavioural level in the current experiments, the neural representations of mnemonic content appear to exhibit greater variability in older age.

This age-related dedifferentiation, or loss of specificity of neural function has been linked to changes in neurochemical properties of the brain, in particular to age-related reductions in dopamine and gamma-aminobutyric acid (GABA) (Koen & Rugg, 2019). Computational accounts have proposed age-related declines in dopaminergic neuromodulation to lead to increased neural noise and less precise neural representations in older age (Li et al., 2001; Li & Rieckmann, 2014). In line with this proposal, dopamine has been shown to modulate the specificity of hippocampal representations during memory retrieval (Abdulrahman et al., 2017), as well as to alleviate deficits in working memory precision observed on the behavioural level in patients with Parkinson's disease (Zokaei et al., 2015). Furthermore, both single-cell recordings in animals and human neuroimaging has provided evidence for a role of decreases in GABAergic neurotransmission in the age-related neural dedifferentiation (Lalwani et al., 2019; Leventhal, Wang, Pu, Zhou, & Ma, 2003). In particular, GABA has been observed to increase the selectivity of visual cortical neurons to stimulus orientations and directions in senescent monkeys (Leventhal et al., 2003). Moreover, individual differences in the levels of auditory cortex GABA have been linked to the specificity of neural representations for auditory stimuli in older age (Lalwani et al., 2019). An interesting question for future studies to address is whether the age-related dedifferentiation of neural representations might underlie the deficits in mnemonic precision observed in older age, as well as the contribution of dopamine and GABA to declines in representational fidelity.

An important caveat to note regarding the current findings is the cross-sectional design employed across the experiments presented in the current thesis. Although research on memory and ageing has predominantly relied on cross-sectional comparisons between age groups, age differences observed in such designs can be influenced by generational differences between cohorts in factors such as socio-economic conditions or educational attainment (Nilsson, Sternäng, Rönnlund, & Nyberg, 2009). Indeed, cross-sectional studies have been shown to occasionally lead to different conclusions about the nature of age-related differences in cognitive or neural function, in comparison to changes estimated from longitudinal studies measuring the same individuals across multiple time points. Whereas in cross-sectional studies a linear reduction in episodic memory from

younger adulthood is often observed, longitudinal studies have provided evidence for a much later onset of age-related declines (Nyberg, Pudas & Lundquist, 2016). Cross-sectional and longitudinal designs have yielded opposing findings regarding the nature of age-related changes in prefrontal function, with cross-sectional estimates providing evidence for an age-related increase, but longitudinal findings suggesting decreased activity with advancing age (Nyberg et al., 2010). In addition to the cross-sectional design, participants in the current studies were recruited via volunteer sampling, potentially biasing the recruitment of high-functioning older adults. Thus, future longitudinal studies with population sampling would be valuable for gaining insight into the onset and trajectory of age-related changes in the success and precision of episodic memory retrieval, as well as for addressing whether they may be differentially vulnerable to age-related decline. Interestingly, two year developmental increases in working memory performance have been observed to result primarily from increased precision of working memory retrieval (Burnett Heyes, Zokaei, & Husain, 2016). It remains to be seen whether longitudinal declines in memory performance in older age might similarly be driven by decreased fidelity of mnemonic representations.

Conclusion

The research presented in this thesis sought to elucidate the nature of age-related changes in episodic memory using continuous measures of retrieval performance. Findings across the experiments provided consistent evidence for a contribution of reduced precision of memory representations to the age-related episodic memory deficits. Age-related decreases in mnemonic precision were observed even when no significant differences in the probability of successful memory retrieval were detected, highlighting the sensitivity of this measure to memory changes accompanying healthy ageing. The findings further highlight the possibility that both common and distinct cognitive and neural factors may play a role in age-related changes in the success and precision of episodic memory retrieval. However, the exact extent to which age-related impairments in these two aspects of episodic memory reflect a dissociable neurocognitive basis remains to be clarified in future studies.

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