Age-related shifts in episodic memory for complex events: From behaviour to brain

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Abstract

Cognitive aging is marked by changes in episodic memory, our ability to remember past events, specific in time and place. Recent evidence challenges a purely decline-oriented view of cognitive aging to suggest that older adults shift how they represent past experiences. Neuroimaging studies show that during episodic memory tasks, older adults increasingly rely on anterior hippocampal and prefrontal brain regions, which support encoding and retrieving gist-based representations. Additionally, behavioural evidence indicates that older adults favor the gist of an event rather than its precise, specific details. The behavioural and functional brain shifts apparent in older age occur against a backdrop of psycho-social changes, which increasingly motivate older adults to recall past events for socially oriented goals rather than goals that prioritize a memory's accuracy and precision. Together, these observations suggest that episodic memory ability in older age is likely a multifactorial outcome, shaped by behavioural, neural, and psycho-social factors, which intersect to create differences in how younger and older adults form and recall memories.

My dissertation examined age-related shifts in how complex events are encoded and recalled, capturing memory use in the real world, at three levels of analyses: in the brain (Chapter 1), behaviourally (Chapter 2), and in the context of psycho-social changes that accompany aging (Chapter 3).

In Chapter 1, I examined how aging affects the brain regions involved in encoding, with a focus on the hippocampus, which is the bedrock of episodic memory and a primary target of cognitive aging. Specifically, I examined how the functionally distinct subregions of the hippocampus shift their connectivity patterns across the lifespan during movie watching —a proxy for naturalistic episodic memory encoding. I found patterns aligning with the well-

reported phenomenon of neural dedifferentiation characteristic of older age, suggesting that functionally specialized hippocampal subregions increasingly show integrated connectivity patterns in older age. These age-related functional shifts were especially apparent as increased connectivity between the anterior hippocampus and prefrontal regions, which are implicated in processing and forming coarse, gist-based representations of an event. Critically, relating the brain patterns to episodic memory measures collected outside the scanner revealed that the age-related shifts were negatively associated with task performance.

In Chapter 2, I behaviourally tested whether aging was associated with distinctions in how a movie was recalled by younger and older adults. To examine recall, I focused on three key features of how we remember complex past experiences: accuracy (whether the details were remembered correctly), content (what kinds of details were remembered) and organization (what order they were remembered in). Here, in two independent samples ($N_{\text{Original}} = 45$; $N_{\text{Replication}} = 60$), young and older adults encoded and recalled a movie. I developed and applied a novel scoring system on the recollections to quantify recall accuracy, temporal organization (temporal contiguity, forward asymmetry), and biases in memory content (perceptual, conceptual details). In both samples, despite no age effects on recall accuracy nor on metrics of temporal organization, older adults' recall was more biased towards conceptual and non-episodic content, whereas younger adults biased their recall towards a higher proportion of event-specific information.

Chapter 3 was motivated by psychosocial frameworks suggesting that age-related changes in how events are recalled, such as those observed in Chapter 2, might be due in part to changes in *why* younger and older adults remember past experiences (i.e., retrieval goals). To test this hypothesis, I conducted a between-group experiment in which younger and older participants (N = 120) recalled a movie with either an accuracy or a social retrieval goal. Following a 24-hour delay, participants completed two recognition memory tasks—one assessing memory for narrative aspects of the movie (i.e., story structure) and another for the perceptual aspects. Using a Natural Language Processing model, I compared the similarity in free recall content between the encoded movie and recollections. Overall, I found that shifting the retrieval goals for recalling an event affects the content similarly for younger and older adults, but older age impacts both the ability to tune recollections towards these goals and the precision of the underlying memory trace (as measured via the recognition memory tasks).

In summary, the results of my thesis indicate that there are age-related shifts in hippocampal connectivity during complex event encoding (Chapter 1), as well as age differences in what details are assembled together from memory (Chapter 2), which are in part influenced by retreival goals (Chapter 3). These results underscore the nuanced nature of episodic memory changes in older age. While traditionally, these changes have been viewed as deficits, the present work adds to a growing body of studies that suggest that for complex events, age-related episodic memory changes are better characterized as a shift towards forming more integrated, gist-based memory representations, which in turn emphasize different kinds of details than younger adults. The current work suggests that these changes emerge from brain changes and are to some extent shaped by motivational shifts that accompany older age. Thus, this dissertation comprehensively characterizes age-related neural and behavioural changes in episodic memory for complex events, akin to our experiences in the real world. This understanding is critical to a well-rounded understanding of how episodic memory changes in older age, beyond just its decline.

Résumé

Le vieillissement cognitif est marqué par des changements dans la mémoire épisodique, notre capacité à nous souvenir d'événements passés situés dans le temps et l'espace. Des données récentes remettent en question une vision uniquement déclinante du vieillissement cognitif et suggèrent que les adultes âgés modifient leur manière de représenter les expériences passées. Les études de neuroimagerie indiquent que lors de tâches de mémoire épisodique, les adultes âgés s'appuient de plus en plus sur les régions antérieures de l'hippocampe et du cortex préfrontal, qui soutiennent l'encodage et la récupération de représentations générales et globales. De plus, les preuves comportementales montrent que les adultes âgés privilégient les aspects généraux d'un événement plutôt que ses détails précis et spécifiques. Les changements comportementaux et fonctionnels dans le cerveau chez les personnes âgées se produisent également dans un contexte de transformations psychosociales, qui motivent de plus en plus les adultes âgés à se rappeler des événements passés pour des raisons sociales, plutôt que pour des objectifs qui privilégient la précision et l'exactitude. Ensemble, ces observations suggèrent que la mémoire épisodique à un âge avancé est vraisemblablement le résultat de multiples facteurs qui s'entrecroisent, y compris des aspects comportementaux, neuronaux et psychosociaux, qui influencent la manière dont les jeunes et les adultes âgés forment et rappellent des souvenirs.

Ma dissertation a examiné les changements liés à l'âge dans l'encodage et le rappel d'événements complexes, en capturant l'usage de la mémoire dans le monde réel, à trois niveaux d'analyse : dans le cerveau (chapitre 1), sur le plan comportemental (chapitre 2) et dans le contexte des changements psychosociaux qui accompagnent le vieillissement (chapitre 3).

Dans le chapitre 1, j'ai examiné comment le vieillissement affecte les régions cérébrales impliquées dans l'encodage, en mettant l'accent sur l'hippocampe, qui est la pierre angulaire de

la mémoire épisodique et une cible principale du vieillissement cognitif. J'ai spécifiquement analysé comment les sous-régions fonctionnellement distinctes de l'hippocampe modifient leurs schémas de connectivité tout au long de la vie lors du visionnage de films — un substitut pour l'encodage de la mémoire épisodique dans un cadre naturaliste. J'ai observé des schémas alignés avec le phénomène bien documenté de dédifférenciation neuronale caractéristique du vieillissement, suggérant que les sous-régions hippocampiques spécialisées montrent de plus en plus des schémas de connectivité intégrés avec l'âge. Ces changements fonctionnels liés à l'âge se manifestaient notamment par une connectivité accrue entre l'hippocampe antérieur et les régions préfrontales, impliquées dans le traitement et la formation de représentations globales et générales d'un événement. De manière critique, le lien entre ces schémas cérébraux et les mesures de mémoire épisodique collectées en dehors de l'IRM a révélé que ces changements liés à l'âge étaient négativement associés à la performance.

Dans le chapitre 2, j'ai testé comportementalement si le vieillissement était associé à des distinctions dans la manière dont les jeunes et les adultes âgés se rappellent un film. Pour examiner le rappel, je me suis concentré sur trois caractéristiques clés de la manière dont nous nous souvenons des expériences complexes passées : l'exactitude (si les détails sont correctement rappelés), le contenu (quels types de détails sont rappelés) et l'organisation (dans quel ordre ils sont rappelés). Dans deux échantillons indépendants (NTotal=45; NValidation = 60), des jeunes et des adultes âgés ont encodé et rappelé un film. J'ai développé et appliqué un système de notation innovant sur les récits pour quantifier l'exactitude du rappel, l'organisation temporelle (contiguïté temporelle, asymétrie avant-arrière) et les biais dans le contenu du souvenir (détails perceptuels, conceptuels). Dans les deux échantillons, bien qu'il n'y ait pas d'effets de l'âge sur l'exactitude du rappel ni sur les mesures d'organisation temporelle, le rappel des adultes âgés était davantage biaisé vers des contenus conceptuels et non épisodiques, tandis que les jeunes adultes avaient un rappel plus orienté vers des informations spécifiques à l'événement.

Le chapitre 3 s'inspire de cadres psychosociaux suggérant que les changements liés à l'âge dans la manière dont les événements sont rappelés, tels qu'observés dans le chapitre 2, pourraient être en partie dus aux changements dans les raisons pour lesquelles les jeunes et les adultes âgés se souviennent des expériences passées (c.-à-d., les objectifs de récupération). Pour tester cette hypothèse, j'ai mené une expérience intergroupe dans laquelle de jeunes et des adultes âgés (N = 120) rappelaient un film avec un objectif de rappel axé soit sur l'exactitude, soit sur un objectif social. Après un délai de 24 heures, les participants ont complété deux tâches de mémoire de reconnaissance — une évaluant la mémoire des aspects narratifs du film (c.-à-d., la structure de l'histoire) et l'autre des aspects perceptuels. À l'aide d'un modèle de traitement du langage naturel, j'ai comparé la similarité dans le contenu de rappel libre entre le film encodé et les récits. Globalement, j'ai trouvé que le changement d'objectif de récupération d'un événement affectait le contenu de manière similaire pour les jeunes et les adultes âgés, mais l'âge influençait à la fois la capacité à ajuster les souvenirs vers ces objectifs et la précision de la trace mnésique sous-jacente (mesurée par les tâches de reconnaissance).

En résumé, les résultats de ma thèse indiquent qu'il existe des changements de connectivité hippocampique lors de l'encodage d'événements complexes (chapitre 1), ainsi que des différences liées à l'âge dans les détails assemblés en mémoire (chapitre 2), qui sont en partie influencées par les objectifs de récupération (chapitre 3). Ces résultats mettent en évidence la nature nuancée des changements de la mémoire épisodique à un âge avancé. Bien que ces changements aient traditionnellement été vus comme des déficits, les travaux présents ajoutent à

un nombre croissant d'études suggérant que pour les événements complexes, les changements de mémoire épisodique liés à l'âge sont mieux caractérisés comme une tendance à former des représentations mnésiques plus intégrées et basées sur l'essentiel, qui mettent en avant différents types de détails par rapport aux jeunes adultes. Ce travail suggère que ces changements émanent de modifications cérébrales et sont en partie influencés par des changements de motivation qui accompagnent le vieillissement. Ainsi, cette dissertation caractérise de manière exhaustive les changements neuronaux et comportementaux de la mémoire épisodique pour les événements complexes, semblables à nos expériences dans le monde réel. Cette compréhension est cruciale pour une vision complète des changements de la mémoire épisodique avec l'âge, au-delà de son déclin.

Acknowledgements

"*We're not liars or self-deceivers-OK, we are all liars and self-deceivers, but it's a fact that our memories change as we do.*" Jeannette Winters

I have been incredibly lucky to be surrounded by wonderful people in and out of graduate school. I consider myself to be gifted –maybe not so much academically, but through the support of these incredible people for whom I am grateful.

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Contributions to Original Knowledge

No two people remember the same, albeit experiencing the same event. This is because our experiences are complex, involving various types of details (sensory-perceptual, attributed thoughts and emotions), which can be selected and assembled in different ways. Regarding aging, research has predominantly focused on describing age-related changes as deficits in the accuracy and quantity of information recalled from simple stimuli sets (e.g., list of words), leaving open questions about shifts in how complex events are represented by younger and older adults. As well, age-related changes in episodic memory coincide with shifts in the brain regions that support remembering, and motivations for why younger and older adults remember the past. This suggests that episodic memory in older age is a multifactorial outcome, shaped by neural, behavioural, and motivational changes. The overarching aim of my dissertation was to examine how these age-associated neural, behavioural, and motivational shifts shape episodic memory for complex events in older age.

In Chapter 1, I present original findings on how aging affects the connectivity patterns of the hippocampus during naturalistic encoding of complex events, using an audiovisual movie as a proxy for real-life episodic memory. Methodologically, a key contribution of this chapter is that it is the first to explore hippocampal patterns —and age-related changes to these patterns — during movie watching, which approximates the complexity of our experiences in the real world. These patterns have been traditionally examined via resting state scans, with no explicit external task or stimulation (Blum et al., 2014; Damoiseaux et al., 2016; Panitz et al., 2021; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022) and as result, it remained unclear to what extent the hippocampus shifted its connectivity patterns under conditions that mimic the complexity and dynamicity of our experiences. In addition, this study used the largest sample size reported to date (N=643), covering subjects across the adult lifespan (18-88 years), enabling a well-powered examination of hippocampal connectivity as it relates to episodic memory in older age. Theoretically, a notable finding from this chapter is that advanced age is associated with greater reliance on the anterior hippocampus and regions in the prefrontal cortex, which have been associated with gist-based processing. While such neural shifts have been predicted by recent theoretical frameworks for complex events (Grilli & Sheldon, 2022), this study provides empirical evidence for these frameworks. As well, the posterior to anterior shift in neural activity in older age has been previously reported as a broad functional pattern in the aging brain, whereas findings from this chapter suggests that these shifts are also expressed within the hippocampus. Together, these results critically implicate hippocampal subregions —and their connectivity patterns —in age-related episodic memory changes.

In Chapter 2, I extended these findings of neural changes in hippocampal connectivity to an examination of age-related shifts in remembering complex events behaviorally, examining the content, organization, and accuracy of recall. Key findings from this chapter are that aging is associated with selective shifts in the content but not the organization or accuracy of recall for complex events. This study makes important methodological and theoretical contributions to cognitive aging research. First, I developed and applied a novel scoring system to analyze participants' recall, teasing apart different aspects of episodic memory in a single, extended episode. This scoring protocol paired methods from the autobiographical memory and list-learning literatures to quantify the different kinds of content participants remembered and derive measures of temporal organization (e.g., temporal contiguity, forward-bias) for complex events. An important theoretical contribution of this work is that age-related shifts in memory content emerged in the absence of episodic memory deficits, as younger and older adults had comparable memory accuracy and temporal organization, albeit differing in the kinds of content they remembered. In this way, results from Chapter 2 suggest that younger and older adults form different memory representations, despite experiencing the same event, which can emerge in the absence of episodic memory deficits.

Chapter 3 expands on these behavioral findings by experimentally manipulating retrieval goals, revealing that older adults' memory recall is influenced not only by age-related neural changes but also in part, by shifts in retrieval goals. In Chapter 3, I applied a Natural Language Processing (NLP) model to examine the overlap between the encoded and recalled content for each participant as well as the free recall content between the participants. This novel application of NLP to recall data adds on to a burgeoning movement in the cognitive neuroscience research, which is starting to use these automated, computational tools to probe memory content. An important finding from this chapter is that older adults, just as well as younger adults, aligned the content they recalled with their on-line retrieval goals. Thus, the results from this chapter provides empirical data for recent theoretical frameworks that propose that age-related episodic memory changes are in part, motivated —such that younger and older adults form different kinds of representations due to age-related shifts in priorities and goals (Grilli & Sheldon, 2022).

Overall, this dissertation breaks new ground in understanding how aging shifts episodic memory for complex, real world events by using theoretically motivated, robust, and ecologically valid methodologies. Together, the presented studies advance the field by challenging the deficit-focused narrative of cognitive aging, providing evidence that episodic memory in older age is not simply a matter of decline, but a multifactorial outcome that shifts how memories are encoded and retrieved. This integrated approach provides a comprehensive understanding of episodic memory in healthy aging, which is critically informative for distinguishing between healthy and pathological aging, as well as for developing clinical interventions that capitalize on the preserved aspects of older adults' memory.

Contributions of Authors

This dissertation is comprised of three manuscripts that represent a portion of the doctoral work I conducted under the supervision of Dr. Signy Sheldon. All manuscripts were taken verbatim from published or submitted versions.

Chapter 1 "Lifespan Differences in Hippocampal Subregion Connectivity Patterns During Movie Watching" was co-authored by myself, Roni Setton, Giulia Baracchini, Jamie Snytte, R. Nathan Spreng, and Signy Sheldon. This manuscript was published in June 2024 in *Neurobiology of Aging*. For this manuscript, I submitted the application to obtain the data from the Cambridge Centre for Ageing Neuroscience. Following, I preprocessed the data and conducted statistical analyses with guidance and feedback from Roni Setton and Giulia Baracchini. I wrote the original draft of the manuscript with Signy Sheldon and received feedback from all co-authors.

Chapter 2 "Shift happens: aging alters the content but not the organization of memory for complex events" was co-authored by me, Emily E. Davis, Sarah E. Henderson, Karen Campbell, and Signy Sheldon. This manuscript was published in *Aging, Neuropsychology, and Cognition* in May 2024. Emily E. Davis and Karen L. Campbell developed and designed the experiment and Emily Chemnitz collected the data for the Original sample. Sarah E. Henderson and Karen L. Campbell designed the experiment and Sarah E. Henderson and Luke Atack collected the data for the Replication sample. The free recall data were scored by undergraduate students under my supervision (Bianca Adjei, Kayla Williams, Nameera Siddque, and Calourin Shehata). All statistical analyses and data visualizations were conducted by me with feedback and input from all co-authors. I wrote the original draft of the manuscript with Signy Sheldon and revised it with guidance and feedback from all authors.

Chapter 3 “The Impact of Retrieval Goals on Memory for Complex Events in Younger and Older Adults” was co-authored by me, Samantha O’Toole, Emma Ranalli, Kailin Summers, and Signy Sheldon. This manuscript was submitted to *Cognition* in May 2024 and a revised and resubmit decision was received in August 2024. A pre-print of the submitted manuscript was published on Social Science Research Network (SSRN). For this manuscript, I conceptualized and developed the experiments with Signy Sheldon’s guidance and supervision. I collected the data in this project with the help of undergraduate research assistants (Samantha O’Toole and Emma Ranalli). I analyzed the data with input from Kailin Summers and Signy Sheldon. I wrote the original draft of the manuscript with Signy Sheldon with feedback from all co-authors.

General Introduction

Our experiences are complex. We are continuously exposed to a stream of events brimming with multimodal, rich array of details. Most of us, to some degree, can mentally travel back in time and relive a particular moment by reassembling its details. This ability —our episodic memory —shows marked changes in healthy aging, even in the absence of pathology (Craik & Salthouse, 2011; Grady, 2012; Grady, 2008; Nyberg et al., 1996). Older adults can remember the general aspects or "gist" of their past experiences, yet their memory for precise, specific details decline (Castel, 2005; Grilli & Sheldon, 2022; Levine et al., 2002). Age-related episodic memory changes coincide with broad shifts in motivation (e.g., why younger and older adults remember their past), as well as functional shifts in key brain regions that support episodic memory (e.g., the hippocampus; Gorbach et al., 2017; Persson et al., 2006).

In this dissertation, I examined how these age-associated neural, behavioural, and motivational changes intersect to shape episodic memory in older age for complex events akin to our experiences in the real world. The dissertation is prepared according to a manuscript-based format in which each chapter contains a single manuscript. In the sections to follow, I will first review converging evidence from laboratory-based studies that seminally characterize episodic memory changes —both behavioural and neural —in aging. I will then ground these findings in neurocognitive models of aging, which will formulate hypotheses about how these changes might manifest for complex events. I will conclude this section with a broad overview of the behavioural and neuroimaging experiments that are part of my dissertation. I will describe how each experiment addresses the goal of understanding age-related changes to the brain-behaviour basis of episodic memory for complex events.

Literature Review

Episodic Memory: From Behaviour to Brain

We experience events once, yet our minds can bend the arrow of time and revisit these moments long after they have passed. This ability to mentally time travel to slices in time from minutes, days, or decades ago is attributed to episodic memory, our ability to encode, store, and retrieve past events that are specific in time and place (Tulving, 2002). Traditional frameworks conceptualize episodic memory processing to take place over three functionally distinct stages: encoding, consolidation, and retrieval (Tulving, 1983). During encoding, various details from an experienced event are processed into a cohesive memory representation (Gluck & Myers, 1998; Polster et al., 1991). Following encoding, the memory representation is consolidated for later retrieval. When needed, various details of the episode (e.g., the what, when, and where) are recombined to reconstruct the encoded representation and to piece together a coherent mental representation of the experienced event (Schacter & Addis, 2007a, 2007b). In this way, rather than a veridical reproduction of our past, episodic memory retrieval is a flexible, reconstructive process (Addis & Schacter, 2008).

The flexible, reconstructive nature of episodic memory retrieval allows for different ways to remember our past experiences, which is highly adaptive as it serves various goals of retrieval (Schacter, 2012; Sheldon et al., 2019). For example, while sharing a recently watched movie with a friend, recalling and describing what the movie was about (i.e., the gist) is more important for their comprehension and socially efficient sharing of the movie than the movie's minute details (e.g., the main actors' clothing). In other instances, however, focusing on these gist details and failing to remember specific details can lead to memory errors. For example, in eyewitness testimony, retrieving specific details of the event is crucial as, exclusively relying on gist-based details can lead to false recollections of who committed the crime. Thus, the detail content we use to reconstruct our experiences can be selectively emphasized by our current behavioural goals (Sheldon et al., 2019; Sheldon & Levine, 2016).

Contemporary memory theories propose that episodic memories can be reconstructed and represented on a continuum of specificity (Brainerd & Reyna, 1990; Craik, 2002; Craik & Lockhart, 1972; Greene & Naveh-Benjamin, 2020; Moscovitch et al., 2016; Reyna & Brainerd, 1998; Robin & Moscovitch, 2017; Sheldon et al., 2019; Surprenant & Neath, 2009). On one hand, an episode can be remembered at a highly specific level by focusing on the precise, sensory perceptual, contextual details about the event (e.g., "The leaves were a vibrant green at Gaspesie National Park"). On the other hand, the same experience can be remembered at a less specific, more general, gist-level by prioritizing the central features as well as the meaning and conceptual details of that episode (e.g., "I had a great time outdoors."). According to this line of work, gist representations capture the essence of an experience, retaining its basic details (e.g., who, what, and where) in addition to the interpretive aspects of that experience including but not limited to its general storyline and emotion, and convey the core meaning of the episode.

The distinction between verbatim (i.e., specific) and gist-based representations forms the backbone of Fuzzy-trace theory, which suggests these representations can co-exist independently and expressed depending on the context or the goals of the rememberer (Brainerd & Reyna, 1990). A similar proposal has been made by Robin and Moscovitch (2017), suggesting specific and gist representations can both exist independently but given particular task demands, one type of representation may be retrieved in preference to the other (Robin & Moscovitch, 2017). Finally, aligning with these frameworks, Sheldon, Gurguryan & Fenerci (2019) took a content-based view of this distinction, proposing that autobiographical memories can be remembered with predominantly conceptual or perceptual information and these different forms of remembering are specifically useful for open and close-ended tasks (Sheldon et al., 2019). To sum, episodic memories can be reconstructed as either specific or gist-based representations, which serve distinct functions or goals for remembering.

In the brain, how a memory is constructed relies on the hippocampus (Moscovitch et al., 2016; Scoville & Milner, 1957). A wealth of human (Bohbot et al., 2000; Dobbins et al., 1998; Jones-Gotman et al., 1997; Rempel-Clower et al., 1996; Rosenbaum et al., 2005; Scoville & Milner, 1957; Warrington & Weiskrantz, 1982) and animal studies (Bussey et al., 1999; Malkova & Mishkin, 2003; Meunier et al., 1993; Murray & Mishkin, 1998) have shown that selective damage to the hippocampus results in deficits in encoding and retrieving new experiences. These neuropsychological findings are supported by neuroimaging evidence, which show selective recruitment of hippocampus during episodic memory encoding and retrieval (Davachi, 2006; Diana et al., 2007; Eichenbaum, 2001; Eichenbaum et al., 2007; Grady et al., 1998; Kim, 2015; Kirwan & Stark, 2004; Lepage et al., 1998; Nyberg et al., 1996; Ranganath et al., 2004).

Even though, there is long-standing agreement that the hippocampus is essential for encoding and retrieving episodic memories (Milner & Scoville, 1957), it is increasingly clear that there is functional specialization along the hippocampal longitudinal axis —with anterior and posterior subregions playing distinct functional roles for memory (Brunec et al., 2018; Evensmoen et al., 2015; Moscovitch et al., 2016; Poppenk et al., 2013; Sheldon et al., 2019; Sheldon & Levine, 2016; Strange et al., 2014). Speaking to their functional specialization, evidence suggests that anterior and posterior hippocampus differ in terms of cell organization (Fanselow & Dong, 2010), gene expression (Bienkowski et al., 2018), place field activity (Jung, Wiener, & McNaughton, 1994; Kjelstrup et al., 2008), and molecular properties (Vogel et al., 2020). Recent models have proposed a gradient of processing resolution along the anterior-posterior axis (Brunec et al., 2018; Robin & Moscovitch, 2017; Sheldon et al., 2019; Sheldon & Levine, 2016). Specifically, the anterior hippocampus is suggested to represent, coarse-grained, gist-level information and posterior hippocampus fine-grained, specific contextual information. Support for these models come from rodent and human studies showing a representational granularity along the anterior-posterior axis during spatial navigation and episodic memory tasks (Brunec et al., 2018; Collin et al., 2015; Evensmoen et al., 2015; Milivojevic et al., 2016; Morton et al., 2017; Nadel et al., 2013; Ryan et al., 2010; Strange et al., 2014). For example, the size of place fields increase along the dorsal-ventral axis of the rodent hippocampus —corresponding to posterior-anterior axis in humans (Keinath et al., 2014; Kjelstrup et al., 2008; Maurer et al., 2005). The smaller place fields in the dorsal hippocampus code for detailed context (e.g., precise spatial position), and the increasingly larger place fields in ventral hippocampus code for global context information (e.g., larger portion of the environment; Keinath et al., 2014). Consistent with the place field organization in rodents, Brunec et al., (2018) showed greater similarity in anterior hippocampal activity over the course of a spatial navigation task compared to the posterior hippocampus (Brunec et al., 2018). The greater neural similarity (i.e., slower signal change) in the anterior hippocampus is attributed to its integrating information that occur closer together in time, allowing it to represent more global features of an event, such as its gist, spread across time and space. In agreement, Collin et al., (2015) reported that multi-event narratives are represented hierarchically along the anterior-posterior axis —such that the posterior hippocampus represents directly related event-pairs, whereas the anterior hippocampus represents inferred, indirect relationships among multiple events (Collin et al., 2015). Together, cross-species evidence indicates that gist and detailed representations are mediated by anterior and posterior hippocampus respectively.

When engaging in episodic memory, hippocampal subregions do not function in isolation. Several studies have shown that episodic memory emerges from the dynamic interactions between hippocampal subregions, as well as between the subregions and a distributed network of regions in the brain (Ranganath et al., 2005; Rugg & Vilberg, 2013). To begin, the functional specialization of the subregions requires close communication between the anterior and posterior hippocampus (Booker & Vida, 2018; Cossart & Khazipov, 2022; Fanselow & Dong, 2010; Modo et al., 2023). The connectivity among the subregions (i.e., intrahippocampal connectivity) is thought to be vital for the integration and coordination of information, separately processed by each subregion as well as across hemispheres (Banich & Belger, 1990; Reuter-Lorenz & Stanczak, 2000; Wang et al., 2014). As well, anterior and posterior subregions are embedded and operate within cortical regions distributed across the whole brain (Rugg & Vilberg, 2013). For example, structurally, in vivo fibre tracking studies have shown that anterior and posterior hippocampus are part of different functional pathways (Dalton et al., 2022). Posterior hippocampus, via the cingulum bundle, connects to regions in the medial parietal, medial prefrontal as well as the occipital cortices. Anterior hippocampus on the other hand, is connected to the amygdala, perirhinal cortex, temporal poles and the lateral temporal cortex via the uncinate fasciculus. These differences in structural connectivity are paralleled in subregions' functional connections. Meta-analytic (Grady, 2020) and neuroimaging evidence (Adnan et al., 2016; Barnett et al., 2021; Libby et al., 2012; Monk et al., 2021; Ranganath & Ritchey, 2012) suggests that hippocampal connectivity with cortical regions varies along its long axis. This body of work has shown preferential connectivity of the anterior hippocampus with regions implicated in semantic and gist-based processing located in the anterior temporal and ventro-medial prefrontal cortices, while the posterior hippocampus has been shown to preferentially connect with regions involved in contextual and visual processing including the parahippocampal, medial parietal and occipital cortices (Blessing et al., 2016; Kahn et al., 2008; Robinson et al., 2016). In sum, the distinct representations mediated by anterior and posterior hippocampus likely stem from their dissociable connectivity patterns.

In the sections to follow, I will begin by reviewing the key behavioural findings on age-related episodic memory changes as well as the theoretical frameworks that emerged from these findings. Next, I will detail how these age-associated behavioural changes manifest in the brain, with a particular focus on the hippocampus and its functionally distinct, anterior and posterior subregions. I will conclude by leveraging these behavioural and neural findings and associated frameworks to formulate hypotheses and predictions about age effects on how complex events akin to our experiences in the real world are represented.

Episodic Memory in Healthy Aging

Behavioural Findings

Not all our long-term memories are “episodic”, bound to a specific time and place. Semantic memory captures the storage and retrieval of general knowledge about the world (e.g., “Paris is the capital of France”) or the self (e.g., “I am an introvert”), including facts, concepts, and information, not tied to specific personal experiences (Renoult et al., 2019; Tulving, 1972). A large body of work has shown that episodic and semantic memory follow distinct trajectories in older age —such that aging selectively targets episodic but not semantic memory (Allen et al., 2002; Levine et al., 2002; Nyberg, Backman, et al., 1996; Spaniol et al., 2006). For example, older adults show intact or even enhanced semantic priming (Laver & Burke, 1993) and accrued vocabulary and world knowledge (Park & Reuter-Lorenz, 2009) but remember less information than younger adults in episodic memory tasks (Craik & Bialystok, 2006; Park et al., 2002).

The episodic memory deficits in aging are well-captured in standard laboratory tests. This body of work compares memory performance between younger and older adults for a series of discrete stimuli, features of which are carefully controlled (e.g., list of words, pictures of objects, etc.; Craik & Schloerscheidt, 2011; Fraundorf et al., 2019). In recognition memory paradigms, memory is tested by exposing participants to the same stimuli they encoded, along with unseen stimuli (i.e., lures), and deciding if they recognize the stimuli as previously encountered or new (i.e., old/new; Chalfonte & Johnson, 1996; Dennis et al., 2008; Howard et al., 2006). In free recall paradigms, participants remember and report as many of these stimuli as they can without explicit cues. This work converged on the finding that older adults show reduced ability to learn and retrieve both verbal and non-verbal material (Naveh-Benjamin et al., 2003; Nyberg, 1996; Nyberg, Backman, et al., 1996; Nyberg et al., 2003). For example, older adults recognize fewer words than younger adults (Craik & Schloerscheidt, 2011) and are less effective at discriminating new and old items in recognition memory paradigms (Fraundorf et al., 2019). As well, older adults recall fewer correct items from lists (Kahana et al., 2005) and they produce more errors in the form of intrusions of items that were not part of the list than younger adults (Devitt & Schacter, 2016; Norman & Schacter, 1997).

Age-related reductions in memory specificity have also been observed in tasks that examine memory for real-world, past personal events (i.e., autobiographical memories; Levine et al., 2002a; Piolino et al., 2009, 2010; St. Jacques et al., 2012). A popular approach to studying autobiographical memory in the laboratory is the Autobiographical Interview (AI; Levine et al., 2002). Here, participants complete a semi-structured interview, in which they self-select and freely recall past personal experiences in response to generic cues provided by the experimenter (e.g., flower). Participants' recollections are then transcribed and scored by segmenting them into discrete details, which are classified as either specific to the recalled event (i.e., internal) or non-specific, tangential (i.e., external). A well-reported finding from studies using this approach is an attenuation in episodic richness in older age, whereby older adults remember and describe their autobiographical memories with fewer event-specific details and with more non-episodic, general knowledge statements than younger adults (Addis et al., 2008, 2011; Levine et al., 2002; Simpson et al., 2023).

Even when younger and older adults have comparable memory for the studied items, older adults show deficits in recalling specific details about what they had studied. However, they recall, as well as younger adults, the general, gist-level information about those items (Castel, 2005; Flores et al., 2017; Gallo et al., 2019; Greene & Naveh-Benjamin, 2023). For example, when participants study fictitious facts (e.g., "Bob Hope's father was a fireman") presented by either a male or a female presenter, older adults fail to remember the gender of the presenter, while showing similar memory performance for the studied facts (Schacter et al., 1991). Similarly, older adults remember just as well as younger adults whether a grocery item was fairly priced or was too expensive (Castel, 2005) or which of the two grocery items was the "better" buy (Flores et al., 2017), yet younger but not older adults additionally remember specific details about that item, such as the item's exact cost. Furthermore, when learning a 7-day weather forecast, older but not younger adults are impaired in remembering the exact temperatures on certain days but remember as well as younger adults the best days for carrying an umbrella (i.e., gist-level information; Gallo et al., 2019). Further, when both younger and older adults remember the gist of where they previously encountered a person (e.g., the young man was in the park), older adults are less likely to remember the specific location this person was encountered (e.g., park A or park B; Greene & Naveh-Benjamin, 2020). Finally, speaking to age-related reductions in the specificity of information retained in memory, studies have shown that older adults successfully retrieve information from memory yet show decreased precision of the retrieved memory representations (Korkki et al., 2020; Nilakantan et al., 2018; Rhodes et al., 2020; Stark et al., 2013). For instance, in Korkki et al., (2020), younger and older adults encoded everyday objects overlaid on different locations on a scene background and recreated the locations of these objects during retrieval by moving the object back to its original location as closely as possible (Korkki et al., 2020). The results showed that both younger and older adults successfully recalled the objects, yet the angular difference between the encoded and recalled locations were greater for older adults, indexing the reduced precision with which these objects were recalled by older adults. Together, these studies demonstrate that older adults exhibit declines in the specificity of recollected details even when their response is accompanied by successful recognition or gist-memory.

Age-related retention of gist and loss of specific details have also been observed in studies that use narratives as memoranda (Morrow et al., 1992, 1997; Radvansky, 1999; Radvansky & Dijkstra, 2007; Reder et al., 1986; Stine-Morrow et al., 2002, 2004). The general result is that older adults have superior memory than younger adults for the meaning of what a narrative was about despite much poorer memory for specifically what was said or shown in a narrative. For example, after reading a text, older adults can accurately identify sentences with altered meanings as false, but they often mistakenly recognize paraphrased sentences as having been part of the original text (Radvansky et al., 2003). Similarly, in Radvansky et al., (2001), younger adults outperformed older adults in their ability to identify information that was presented verbatim in the text, whereas older adults did just as well as younger adults in discriminating information concerning what the text was about (Radvansky et al., 2001). Moreover, Adams et al., (1997) showed that when younger and older adults freely recalled a previously read text, younger adults were more likely to recall propositions and information that was actually present in the text, whereas older adults remembered more summary statements and interpreted aspects of the text (Adams et al., 1997). Finally, healthy younger and older participants in Delarazan et al., (2023) encoded a television sitcom and after a delay completed an old/new recognition task, which tested episodic memory for both the narrative gist, as well as more fine-grained sensory perceptual details of the sitcom (Delarazan et al., 2023). Their data showed that when older adults effectively retained the narrative details, they selectively showed episodic memory deficits for the specific, perceptual details of the sitcom. To sum, standard laboratory studies using both recognition and free recall paradigms have converged on the finding that decreases in memory specificity and intact memory for gist information is a consistent feature of age-related memory decline. As reviewed below, these changes are thought to arise from older adults' increased reliance on gist-based processing or motivational changes that accompany older age.

Behavioural Accounts

Increased Reliance on Gist-based Representations

One class of theories note that age-related decreases in memory specificity results from older adults' increased reliance on gist-based representations (Brainerd & Reyna, 2015; Craik & Bialystok, 2006; Grilli & Sheldon, 2022). For example, Craik's (2006) hierarchical framework proposes that knowledge representations are hierarchically organized: with general, context-free knowledge at higher levels and specific, contextualized information at lower levels (Craik &

Bialystok, 2006). This framework argues that older adults progressively have difficulties in encoding and subsequently accessing information at the lower, specific ends of the continuum but retain access to higher conceptual levels. In line, as reviewed above, Fuzzy-trace theory distinguishes between verbatim traces, which retain the specific details of an episode and gist traces, which capture the qualitative interpretations and the central aspects of that episode (Brainerd & Reyna, 2002, 2002). According to this theory, aging is associated with a significant decline in verbatim but not gist memory (Brainerd & Reyna, 2015). To sum, both theories share the idea that older adults' greater reliance on gist-representations is a necessity, driven by neurocognitive limitations or declines that prevent older adults from retaining detailed, specific representations of past experiences.

These theories were recently extended to complex event memories to suggest that aging is associated with shifts in how past experiences are represented and remembered. According to this framework older adults form gist-based representations of autobiographical memories, capturing the general aspects of their experiences, whereas younger adults tether their recollections on event-specific information, resulting in specific-representations (Grilli & Sheldon, 2022). Differently from the above work, this framework proposes that the specific-to-gist shift in older age is not exclusively driven by older adults' declining memory but rather partly motivated. That is, older adults may prefer to rely on gist representations because of normative, motivational changes that accompany aging. Below, I review the body of work that "motivated" this proposal.

Socio-emotional & Motivational Changes

Older adults may preferentially use gist representations due to motivational changes that come with cognitive aging. Notably, Socio-emotional Selectivity Theory (SST) attributes these motivational changes to the perceived constraints on older adults’ time horizons (Carstensen et al., 2003, 1999; Carstensen & Turk-Charles, 1994; Mather & Carstensen, 2005; Samanez-Larkin & Carstensen, 2011). Younger adults perceive time as expansive and they are more likely to be motivated by goals that are preparatory such as gathering information and experiencing novelty (Charles & Carstensen, 2010). However, as people get older and time horizons shorten, goals associated with emotional meaning and well-being override those associated with acquiring new knowledge and experiences. In support of SST, studies have shown that informational value of forming or fostering new relationships declines across the life span, yet emotional value of closeness with familiar others increase (Carstensen, 1992). When younger adults choose to spend time with social partners that offer new information (e.g., a book author), older adults are more likely to choose those that satisfy emotional goals (e.g., close friends or family members; Fung et al., 1999; Fredrickson et al., 1990).

These global, age-related motivational changes have been extended to shifts in why younger and older adults remember (Grilli & Sheldon, 2022). For example, a large body of research has shown that younger and older adults are motivated by different goals when recalling autobiographical memories (Bluck & Alea, 2009). This work is motivated by the functional approaches to memory, which propose that remembering autobiographical memories serves different adaptive functions (Alea & Bluck, 2003; Bluck, 2003; Bluck et al., 2005; Bluck & Alea, 2008, 2009, 2011). Chief among these approaches is the tripartite theory, which posits that autobiographical memory serves at least three functions: self, social, and directive (Bluck & Alea, 2011). The self-function emphasizes the role of autobiographical remembering in the continuity and the development of the self (Bluck & Levine, 1998). That is, remembering past personal events critically informs on who the self is, which is used to understand, develop, and maintain a sense of self in the present. The social function involves retrieving memories to develop, maintain and enhance social bonds (Alea & Bluck, 2003). For example, memories commonly provide the ingredients of our conversations and these memories can be shared to create intimacy in relationships or to show and incite empathy (Pillemer, 1992). Finally, the directive function involves retrieving past experiences accurately to guide present problem solving and to direct future thoughts and behaviours. When applied to aging, this body of work has shown that older adults tend to remember past events predominantly for social goals, which stress a more integrative lens, prioritizing forming social bonds and reflect on the past, sharing past experiences to teach/inform as well as entertain others, more than younger adults (Demiray et al., 2019; Grilli & Verfaellie, 2015; Hess, 2005).

If shifts in retrieval goals underlie age-related memory changes, then memories retrieved for different goals should have different content. In fact, several studies have shown that memory content (i.e., what we remember) shifts as a function of our retrieval goals (Elward & Rugg, 2015; Rugg, 2004; Rugg et al., 2000; Srokova et al., 2021). Many of these studies compared two critical functions of retrieval —to be accurate (akin to directive functions) or for social goals. A common finding is that recollections made for accuracy goals result in greater emphasis on reproducing precise, event-specific details, whereas remembering for socially oriented goals lead to more elaborative, reconstructed recollections, and those that deviate from the originally encoded event (Dudukovic et al., 2004; Dutemple & Sheldon, 2022). For example, in one study, two groups of younger adults encoded a story and after a delay remembered it with either an accuracy goal, stressing the precise and veridical recall of the story or a social goal, describing the story from memory as if they were socializing with their friend group (Dutemple & Sheldon, 2022). Compared to those remembered with an accuracy goal, social retrieval goals reduced the number of event-specific details recalled and increased the number of elaborative, additional details. Similarly, in another study, participants encoded a story and later, retold it from memory to entertain (i.e., socially oriented) or to be accurate (Wade & Clark, 1993). Participants showed better alignment with the story when instructed to be accurate than entertaining. Thus, this line of work suggests that age differences in memory might be driven not by older adults' ability to perform episodic memory tasks per se but rather by differences in *why* younger and older adults remember the past.

Neural Findings

Age effects on episodic memory are commonly attributed to structural and functional changes to the hippocampus (Gorbach et al., 2017; Persson et al., 2006). Structurally, older age is associated with reduced macro and micro-structural integrity of the hippocampus (Barnes et al., 2009) such as reduced hippocampal volume (Raz 2005; Raz et al. 2005; Fjell et al. 2009; Walhovd et al. 2011; Jäncke et al. 2020), which relates to reduced memory performance cross-sectionally (Driscoll et. Al., 2003; Jack et al., 1997; Fjell et al., 2014; Lemaitre et al., 2005) and longitudinally (Persson et. al., 2012; Raz et al., 2005; 2010; Resnick et al., 2003). Functionally, both cross sectional (Cabeza et al., 2004; Dennis, Kim, et al., 2007, 2008) and longitudinal (Persson et al., 2012) evidence suggest that even though older adults activate the hippocampus during episodic memory tasks, they often show decreased activity coupled with worse memory performance compared to younger adults.

Research has delved deeper into how age-related alterations to hippocampal subregions relate to memory (Gorbach et al., 2017; Langnes et al., 2019, 2020; Raz et al., 2004). Given the proposed involvement of anterior hippocampus in forming gist-based representations (Robin & Moscovitch, 2017; Sheldon et al., 2019) and older adults' bias towards these representations

(Grilli & Sheldon, 2022), one would expect greater reliance of older adults on anterior over posterior hippocampus during episodic memory tasks. Consistent with this proposal, there is a growing body of evidence, which indicates that older adults show relatively intact or greater use of the anterior compared to posterior hippocampus during memory tasks (Dalton et al., 2019; Damoiseaux et al., 2016; Langnes et al., 2020; Snytte et al., 2022; Viard et al., 2012). For example, a recent study by Snytte et al., (2022) showed that age-related declines in spatial context memory, our ability to encode and retrieve spatial details about past events (e.g., where on the screen an item was encoded) was mediated by the posterior but not anterior hippocampal volumes (Snytte et al., 2022). In a meta-analysis of studies on autobiographical memory in younger and older adults Viard et al., (2012) showed that older adults tend to recruit anterior hippocampus more so than younger adults when remembering autobiographical memories (Viard et al., 2012). Similarly, Reagh et al., (2020) showed that the hippocampus and posterior brain regions, display increased activity during salient changes in the movie (i.e., event boundaries), but these responses, especially in the posterior hippocampus, decrease with age, and relate to measures of episodic memory performance, collected outside the scanner (Reagh et al., 2020). Finally, lifespan studies reported that the posterior hippocampal preference in younger age during episodic memory tasks is replaced by gradually higher anterior relative to posterior hippocampal activity in older age (Langnes et al., 2019). Collectively, these studies point to the conclusion that older adults tend to rely more on the anterior hippocampus than the posterior hippocampus.

As reviewed above, hippocampal subregions are embedded within distinct functional networks, which means that older adults’ greater reliance on the anterior compared to posterior hippocampus likely extends to its functional connectivity patterns. However, the evidence on how aging influences these connectivity patterns has been mixed (Blum et al., 2014; Dalton, McCormick, De Luca, et al., 2019; Damoiseaux et al., 2016; Damoiseaux, 2017; Panitz et al., 2021; Salami et al., 2014; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022; Stark et al., 2021). The majority of extant work has examined subregions' connectivity during resting state scans, which measure low frequency oscillations in the Blood Oxygen Level Dependent (BOLD) signal, indexing intrinsic functional connectivity between a given set of brain regions or networks. For example, a subset of these studies have reported reduced resting state functional connectivity with age in both ipsilateral (anterior vs. posterior) and contralateral (e.g., right vs. left anterior) subregions (Panitz et al., 2021; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022), whereas others have observed this reduction only contralaterally (Damoiseaux et al., 2016) or even as increased connectivity between the subregions (Salami et al., 2014). Similarly, with regards to cortico-subregion connectivity, some studies have found that aging disproportionately reduces posterior compared to anterior cortico-hippocampal connectivity, especially with regions in the posterior cortex (Damoiseaux et al., 2016; Panitz et al., 2021; Salami et al., 2016). Other work has found global reductions in cortico-hippocampal connectivity (Blum et al., 2014; Salami et al., 2014) or increases in posterior but not anterior hippocampal connectivity with the cortex (Blum et al., 2014). Thus, precisely how the hippocampal subregions shift their connectivity patterns, especially when engaging episodic memory, remains to be characterized.

The hippocampus is not the only brain region that shows age-related changes. Chief among these regions is the prefrontal cortex, which also shows marked atrophy in older age (Buckner, 2004; Raz et al., 2005). Functionally, a commonly reported pattern of brain change in older adulthood is the greater recruitment of prefrontal cortical regions during episodic memory tasks (Cabeza et al., 2002; Dennis, Daselaar, et al., 2007; Grady, 2008). This effect is most pronounced in regions implicated in extracting generalities within a single episode or commonalities across several episodes such as the medial (Reagh et al., 2020) and dorsolateral prefrontal cortex (de Chastelaine et al., 2011; Düzel et al., 2011; Gutchess et al., 2005; Kapur et al., 1994; Nyberg et al., 1996). Another consistently reported finding is the bilateral recruitment of frontal regions in older adulthood (i.e., symmetrical activity), for which younger adults typically show unilateral activity (i.e., asymmetrical activity; Bäckman et al., 1997; Cabeza, 2001; Cabeza et al., 1997; Stebbins et al., 2002). This work is motivated by the observation that in younger adults, encoding and retrieval show lateral asymmetry in prefrontal cortex activity — with encoding being left and retrieval, right lateralized (Nyberg, Cabeza, et al., 1996). In older adults however, this asymmetry is reduced, such that older adults recruit both left and right prefrontal cortices during encoding (Stebbins et al., 2002) and retrieval tasks (Cabeza et al., 1997). For example, during episodic memory encoding, both younger and older adults activate left ventrolateral prefrontal cortex (vlPFC), whereas older adults additionally activate right vlPFC (Duverne et al., 2009; Morcom et al., 2003). In alignment with the behavioural evidence, these findings suggest that older adults rely on anterior, prefrontal regions, and do so bilaterally, especially those involved in encoding and retrieving the gist and general aspects of our experiences.

Earlier frameworks have viewed age-related functional brain changes as a form of compensation by older adults (Cabeza, 2001; Cabeza et al., 1997; Reuter-Lorenz & Cappell, 2008). These “compensation by reorganization” views argue that older adults overrecruit brain regions or recruit additional regions (e.g., bilaterally) to compensate for impaired function elsewhere in the brain (Grady, 2012; Grady, 2008; Reuter-Lorenz & Cappell, 2008). For example, this view is central to the Hemispheric Asymmetry Reduction in Older Adults framework (HAROLD; Cabeza, 2002). HAROLD is based on the above-reviewed finding that older adults show a significant reduction in the hemispheric lateralization during episodic memory tasks, especially in the prefrontal cortex. Importantly, the reduced asymmetry is considered to be compensatory (Reuter-Lorenz et al., 1999, 2000)—such that to overcome neurocognitive deficits, older adults engage both hemispheres for tasks that require one hemisphere in younger adults (Berlingeri et al., 2010; Cabeza, 2001). Another framework that favors the compensatory view is the Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH; Reuter-Lorenz & Cappell, 2008). According to this view, due to their declining neural efficiency, older adults engage more neural resources than younger adults to meet the task demands. When these demands are low, the over-activation is effective, aiding in older adults' task performance. As task demands increase however, older adults reach a resource ceiling and the neural compensation is insufficient to over-come their processing deficits, resulting in under-activation of prefrontal regions and downstream impairments in performance. Finally, compensation by reorganization forms the back bone of Posterior-Anterior Shift with Age account (PASA; Davis et al., 2008). This view rests on the above-reviewed finding of increased activity in the anterior prefrontal regions, coupled with reduced activation in posterior brain regions, especially in the occipito-temporal regions during episodic memory tasks (Grady et al., 1994). The increased activity in anterior regions is thought to compensate for deficits in sensory processing in occipito-temporal regions, which is commonly observed in older adults (Lindenberger, 2014; Lindenberger & Baltes, 1994), and is positively correlated with performance (Davis et al., 2008).

Another class of theories argue that age-related functional brain changes are best characterized as a loss of functional specialization in the aging brain (Koen et al., 2020; Koen & Rugg, 2019). These “dedifferentiation” accounts are based on the observation that younger adults have activation patterns typically quite selective for the particular stimulus features (e.g., places versus faces) or task demands involved (e.g., explicit versus implicit memory), whereas in older adults these patterns are much less distinct, or “differentiated”. Earlier evidence for this view comes from work showing that in younger adults, functionally distinct subregions of the ventral visual cortex respond selectively to categories or domains of visual input (e.g., faces, places, numbers, etc.) —yet in older adults, this region shows declining specificity such that subregions that normally respond to faces are also more responsive to places compared to younger adults (Park et al., 2004; Reuter-Lorenz & Park, 2010). Dedifferentiation at the neural level is also studied by comparing patterns of brain activity across different tasks to examine whether these patterns are idiosyncratic to each task. For example, Dennis & Cabeza (2011) contrasted implicit and explicit memory for word lists and found that younger adults showed selective recruitment of the hippocampus for explicit and the striatum for implicit learning, whereas older adults showed similar activity in these regions during the two tasks (Dennis & Cabeza, 2011). In a similar vein, when younger adults show unique patterns of activity during episodic, autobiographical, and semantic memory, these patterns tend to be less distinct for older adults (St-Laurent et al., 2011). Finally, graph theoretical approaches have shown that the younger brain is characterized by well-segregated networks—with strong connectivity between the regions belonging to the same network (i.e., higher within network connectivity), and weaker connectivity between those belonging to different networks (i.e., low between network connectivity; Schaefer et al., 2018; Yeo et al., 2011). In support of age-related neural dedifferentiation, several studies have shown reduced segregation of brain networks —such that increased age favors reduced within network connectivity and increased between network connectivity (Chan et al., 2014; Koen & Rugg, 2019; Setton, Mwilambwe-Tshilobo, Girn, et al., 2022). This view is used to explain the above-reviewed age-related asymmetry reductions as a difficulty of older adults' to recruit specialized neural mechanisms. That is, when younger adults selectively engage either the right or left hemisphere depending on the task demands (e.g., left prefrontal cortex for encoding), older adults recruit both hemispheres. Differently from compensation focused views however, dedifferentation accounts consider the loss of functional specialization as maladaptive to cognition (Li et al., 2001; Li & Rieckmann, 2014), with the extent to which older adults show dedifferentiation predicting poor performance (Chan et al., 2014; Varangis et al., 2019).

These frameworks help formulate hypotheses about how intra and cortico hippocampal connectivity patterns might change across the lifespan and relate to episodic memory. For example, if a posterior-to-anterior shift is apparent in subregion connectivity patterns, then increased age should result in more dominant anterior hippocampal connectivity, especially with anterior, prefrontal regions. As well, if dedifferentiation is a global feature of the aging brain, then older age should be associated with loss of functional specialization of the hippocampal subregions, with anterior and posterior hippocampus increasingly showing converging, non-specific changes to their intra and cortical connectivity patterns. Finally, if these age-related shifts are compensatory then, older adults who display these changes should show episodic memory benefits.

Studying aging with complex events.

Contemporary research has emerged to understand episodic memory for more complex stimuli, reflective of how memories are encoded and retrieved in daily life. Many of these studies use audiovisual movies as a proxy for real world experiences (Barnett et al., 2024; Ben-Yakov & Dudai, 2011; Ben-Yakov & Henson, 2018; Bonasia et al., 2018; Brandman et al., 2021; Chadwick et al., 2010; Chen et al., 2016, 2017; Frisoni et al., 2023; Furman et al., 2007; Hasson et al., 2008; Kauttonen et al., 2018; Kubit & Janata, 2022; Lee & Chen, 2022; Milivojevic et al., 2015, 2016; Nau et al., 2023). These stimuli are thought to offer more naturalistic encoding and retrieval conditions than traditional, lab-based stimuli (Sonkusare et al., 2019). Differently from the brief, discrete, and static stimuli, movies are experienced in their continuous form, presenting temporally unfolding sequence of events that are chronologically (e.g., Event B happened after Event A), causally (e.g., Event A led to Event B), logically (e.g., Event B can't happen without Event A) and thematically (e.g., Event A & B are about travelling) inter-related, imbuing them with an underlying narrative structure. As well, movies, much like our experiences in the real-world, are highly complex, as they expose the viewer to a continuous stream of multimodal information, involving rich spatiotemporal, semantic, and emotional details (Grall & Finn, 2022).

This dynamic, detail-rich content, combined with the flexibility in how they can be recalled, situate movies as powerful tools to study age differences in how events are represented. Even though the cognitive neuroscience literature is increasingly adopting them to study the cognitive and neural basis of episodic memory in younger adults, the use of movies as stimuli has yet to gain traction in cognitive aging research. Much of the extant work has focused on age differences in extracting the event structure from continuous episodes by identifying event boundaries (i.e., salient changes during an episode; DuBrow & Davachi, 2016; Ezzyat &

Davachi, 2011). A common finding is that older adults tend to segment events more idiosyncratically than younger adults, hinting at age differences in how these stimuli are processed by the age groups (Kurby et al., 2014; Kurby & Zacks, 2018; Zacks et al., 2006). In parallel, neuroimaging work has shown age-associated distinctions in brain responses to these stimuli. For example, in younger adults, movie watching drive reliable synchronous neural responses across different subjects and more synchronous responding has been linked to better subsequent memory for the movie (Hasson et al., 2008). In contrast, this neural synchrony declines with age and that it is most pronounced in regions implicated in top-down attentional control (i.e., frontoparietal control network) as well as memory (i.e., medial prefrontal cortex, hippocampus; Campbell et al., 2015; Geerligs et al., 2018).

Using movies as memoranda can introduce new perspectives to an age-old question: How does aging affect episodic memory for complex events? Specifically, these stimuli can allow us to examine age effects on the neural and behavioural correlates of how complex events are represented by younger and older adults, beyond its decline. For example, the dynamic and multimodal content of movies can put viewers under conditions in which functional patterns relevant to episodic memory encoding are likely to emerge. As a result, the coordinated engagement of key episodic memory regions (e.g., hippocampal subregions) and age effects to this system can be examined under conditions that approximate the complexity and dynamicity of our real world experiences. As well, if available, these patterns can be related to performance on episodic memory measures to understand whether the observed functional shifts in older age are compensatory (i.e., benefiting performance) or maladaptive—as proposed by the above-reviewed compensation and dedifferentiation accounts. By extension, examining how younger and older adults recall movies can help us distinguish between different representations these age groups form. As mentioned, movies expose viewers to a rich, diverse array of details, ranging in specificity from sensory perceptual (e.g., the color and type of objects in a scene) to more abtsracted content (e.g., emotions or mental state of characters). In turn, these details can be selectively encoded or retrieved by the age groups, resulting in different kinds of representations. Given the above-reviewed distinctions between forming specific and gist-based representations and an older adult bias towards the latter, younger and older adults will likely remember different kinds of details from these stimuli. Finally, memory differences can be examined in the context of broader, motivational changes in older age to further elucidate the role of retrieval goals in shaping episodic memory in older age. Thus, by using movies as memoranda, we can examine shifts in the representational quality of older adults' memories, beyond just deficits, allowing for a more complete picture of age effects on episodic memory.

Overview of dissertation experiments

Healthy aging is marked by both gains and losses in episodic memory. Memory for specific, precise details decreases, while memory for the gist, or general aspects of experiences is retained. These age-related episodic memory changes coincide with changes in motivation for why younger and older adults remember their past, as well as functional shifts in key brain regions that support episodic memory. A recent trend in cognitive neuroscience is to assess cognitive processes using naturalistic stimuli (e.g., audiovisual movies) to approximate the complexity of how we experience and remember events in the real world. However, these attempts are yet to penetrate cognitive aging research. As a result, what remains poorly understood is how behavioural, psycho-social and neural changes intersect in older age to encode and retrieve complex events akin to our experiences in the real world.

To address this gap in the literature, I conducted a series of neuroimaging and behavioural experiments. Based on a recent trend in the cognitive neuroscience research (Grall & Finn, 2022), I operationalized complex events by using an audiovisual movie, describing a series of unfolding events (Bang! You're Dead; Hitchcock, 1961), which was used in all three manuscripts presented here. In Manuscript 1, I examine the underlying neural processes that are recruited to encode the movie in a large-scale lifespan sample. Based on above-reviewed work, I focus this investigation on the hippocampal subregions and examine how they shift their connectivity patterns with each other and rest of the cortex across the lifespan. In Manuscript 2, I examine behaviourally, whether these neural changes manifest as differences in how younger and older adults represent and remember the movie, focusing on three key features of episodic memory: accuracy, temporal organization and content. Finally, In Manuscript 3, I test the notion that age differences in recall are due to changes in retrieval goals in older age (i.e., *why* we remember). Specifically, I examine whether shifting younger and older adults' retrieval goals will influence how they recall the movie.

Chapter 1: Lifespan differences in hippocampal subregion connectivity patterns during movie watching

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Abstract

Age-related episodic memory decline is attributed to functional alterations in the hippocampus. Less clear is how aging affects the functional connections of the hippocampus to the rest of the brain during episodic memory processing. We examined fMRI data from the CamCAN dataset, in which a large cohort of participants watched a movie (N=643; 18-88 years), a proxy for naturalistic episodic memory encoding. We examined connectivity profiles across the lifespan both within the hippocampus (anterior, posterior), and between the hippocampal subregions and cortical networks. Aging was associated with reductions in contralateral (left, right) but not ipsilateral (anterior, posterior) hippocampal subregion connectivity. Aging was primarily associated with increased coupling between the anterior hippocampus and regions affiliated with Control, Dorsal Attention and Default Mode networks, yet decreased coupling between the posterior hippocampus and a selection of these regions. Differences in age-related hippocampal-cortical, but not within-hippocampus circuitry selectively predicted worse memory performance. Our findings comprehensively characterize hippocampal functional topography in relation to cognition in older age, suggesting that shifts in cortico-hippocampal connectivity may be sensitive markers of age-related episodic memory decline.

Keywords: *aging*, *episodic memory*, *hippocampus; functional connectivity*

Introduction

Episodic memory entails the ability to encode, store, and retrieve past events, and is known to decline throughout the lifespan (Cabeza et al., 1997; Grady, 1999; Grady et al., 1998; Naveh-Benjamin et al., 2003; Nyberg et al., 2003, 2012). Studies have attributed age-related episodic memory decline to structural and functional changes to the hippocampus (Raz et al., 2005), the key brain region for encoding and retrieving episodic memories (Eichenbaum, 2001; Konkel & Cohen, 2009; Moscovitch et al., 2016; Scoville & Milner, 1957). The hippocampus is not a homogenous structure but shows hemispheric and long-axis functional specialization (Poppenk et al., 2013). Hippocampal subregions run anterior to posterior along the long-axis of the hippocampus and are functionally connected to one another as well as a distributed set of regions including but not limited to the anterior temporal, frontal, posterior medial, and parietal cortices (Libby et al., 2012). Due to their differential connectivity with these areas, anterior and posterior subregions contribute to different aspects of episodic memory formation (Diana et al., 2007; Horner et al., 2015; Ranganath, 2010). However, little is known about how the subregions' connectivity profiles differ cross-sectionally and relate to individual differences in cognition and especially, episodic memory functioning.

Naturalistic paradigms, such as movie watching, offer a unique window into understanding age-related shifts in how we process and encode our experiences in everyday life (Campbell & Schacter, 2017; Finn & Bandettini, 2021; Grall & Finn, 2022; Hasson, Landesman, et al., 2008; Meer et al., 2020). Movie watching, much like the encoding of everyday events, involves continuous exposure to chronologically related, temporally unfolding events rich in spatiotemporal, emotional, social, and narrative details (Kringelbach et al., 2023; Sonkusare et al., 2019). While we cannot predict the information we will need to encode and subsequently remember when watching a movie, our perception is tuned towards, and attention enhanced by, affective and salient information. In this way, movie watching puts viewers under conditions in which functional patterns relevant to episodic memory encoding are likely to emerge. Indeed, previous work has shown that viewers spontaneously and continuously engage episodic memory processes during movie watching —with individuals recollecting a considerable amount of movie specific details following passive, incidental viewing instructions (Fenerci et al., 2024; Hasson, Furman, et al., 2008; Shin et al., 2015). As well, studies have shown that hippocampus is highly engaged during movie watching, and the extent of this engagement predicts subsequent memory for the movie content (Hasson, Furman, et al., 2008). In the current study, we leveraged movie watching as a proxy for episodic memory encoding to study how hippocampal functional connectivity during this task differs across the lifespan and relate to individual differences in cognition.

When examining hippocampal functional connectivity, especially with respect to episodic memory processing, it is important to consider its functionally specialized subregions along the longitudinal axis and across the two hemispheres. First, evidence points to a gradient of processing resolution, such that the anterior hippocampus represents coarse-grained, conceptual information and posterior hippocampus, fine-grained, sensory-perceptual information (Brunec et al., 2018; Robin & Moscovitch, 2017b; Sheldon et al., 2019; Sheldon & Levine, 2016). Second, in addition to its long-axis specialization, hippocampal memory functions are also highly lateralized (Persson & Söderlund, 2015). A large body of work has shown that the left hippocampus is preferentially involved in processing and encoding verbal information, whereas the right hippocampus is particularly tuned to processing pictorial or spatially oriented details (Gabrieli et al., 1997; Golby et al., 2001; Kelley et al., 1998; Stern et al., 1996). The distinct roles played by the subregions emerge from their functional connectivity with one another (Banich & Belger, 1990; Reuter-Lorenz & Mikels, 2005; Reuter-Lorenz & Stanczak, 2000; Wang et al., 2014). That is, the subregions respond to and process different kinds of information and communicate with one another to bind together the processed details and form coherent episodic memories (N. J. Cohen et al., 1997, 1999; Konkel & Cohen, 2009).

Hippocampal subregions are embedded within larger cortical networks distributed across the whole brain (Blessing, Beissner, Schumann, Brünner, & Bär, 2016; Robinson, Salibi, & Deshpande, 2016; Wang, Ritchey, Libby, & Ranganath, 2016; Frankland & Bontempi, 2005). During episodic memory tasks, the distinct component processes of hippocampal subregions are bolstered by large-scale cortical networks (Rugg & Vilberg, 2013) including the Default, Dorsal Attention, and Control networks (DN, DAN, CN). The DN forms internal representations of experiences by carrying information about narrative content (Andrews-Hanna et al., 2014; Baldassano et al., 2017; Buckner et al., 2008; Buckner & DiNicola, 2019; Chen et al., 2017; Lee & Chen, 2022; Spreng & Andrews-Hanna, 2015). The DAN supports top-down attentional control, particularly when processing and encoding external stimuli (Corbetta et al., 2002; Corbetta & Shulman, 2002). The CN supports effortful cognitive control processes (Corbetta & Shulman, 2002; Niendam et al., 2012; Spreng et al., 2010). Evidence suggests that hippocampal connectivity with each of these networks varies along its long axis (Grady, 2020). In younger adults, meta-analytic and functional imaging studies have shown that the anterior hippocampus shows preferential connectivity with the DN, as well as Limbic, and Somatomotor networks, whereas posterior hippocampus is particularly tuned to the Visual Network and the DAN (Blessing et al., 2016; Kahn et al., 2008; Robinson et al., 2016).

Together, these studies indicate that episodic memory encoding involves the concerted interplay between hippocampal subregions and cortical networks (Ranganath & Ritchey, 2012), which likely show age-related alterations. Indeed, aging is associated with functional connectivity alterations in large-scale brain networks, which points to parallel changes in the subregions' connectivity patterns (Campbell et al., 2015; Geerligs et al., 2015; Geerligs & Campbell, 2018; Grady et al., 2016). Compared to younger adults, older adults demonstrate weaker within-network connectivity and stronger between-network connectivity (Andrews-Hanna et al., 2007, 2014; Betzel et al., 2014; Chan et al., 2014; Damoiseaux et al., 2008). This pattern of network dedifferentiation, linked to age-related episodic memory decline, has become a hallmark of functional reorganization in healthy aging (Koen et al., 2020; Koen & Rugg, 2019). It remains to be determined whether hippocampal subregions follow a similar trajectory with age, where connectivity profiles demonstrate less selectivity and hemispheric specificity in favor of more integration.

Current Study

Functional interactions within the hippocampus as well as between the hippocampal subregions and the rest of the brain are central for episodic memory, which suggests that shifts in subregion connectivity profiles may underlie age related episodic memory decline. In the current study, we examined differences in hippocampal functional connectivity across the lifespan and how these differences relate to cognitive functioning. Specifically, we probed hippocampal connectivity patterns at two levels, both within the hippocampus and between the hippocampus and cortical networks. We then assessed whether these patterns vary with cognitive functioning and episodic memory ability, specifically standard measures of story recall. Given the known functional and hemispheric specialization in the hippocampus, we considered subregion connectivity patterns in the context of laterality differences. To this end, we leveraged functional magnetic resonance imaging (fMRI) and neuropsychological data from a large-scale, healthy, population-based cohort of healthy adults. Based on previous work, we reasoned that if subregion connectivity patterns parallel age-related network dedifferentiation, then the subregions should show a more integrated (less distinct) pattern of connectivity in older age. Finally, if shifts in hippocampal connectivity underlie cognitive and episodic memory decline, then any age-related connectivity differences will be associated with lower cognitive and episodic memory performance.

Materials & Methods

Participants

The data were acquired from the Stage II of Cambridge Centre for Aging and Neuroscience (Cam-CAN) data repository. This is a large-scale, population-based study of the healthy adult lifespan. All participants included in the study were cognitively healthy (Mini Mental State Examination > 24), had normal or corrected-to-normal vision and hearing, were free of any medical, neurological or psychiatric conditions, and had English as their dominant language. Written, informed consent was collected from all participants and all study procedures were conducted in accordance with the ethical guidelines of Cambridge 2 Research Ethics Committee.

After data quality checks (outlined in section **Image Processing**), a sample of 520 participants (M = 263, $M_{age} = 52.58$, $SD_{age} = 18.24$) were included in the main analyses of this article. The demographic information for the final sample is provided, broken down by each age decade, in Table 1.

Table 1. Summary of participant demographics across age decades

Age Decade	**N**	**Sex (F/M)**	**M_{age} (SD)**	**Handedness (L/R/A)**
18-20	12	5/7	18.75 (0.87)	2/10/0
20-30	62	34/28	26.45 (2.34)	5/57/0
30-40	88	39/49	35.83 (2.90)	8/77/2
40-50	84	50/34	45.75 (2.77)	5/77/2
50-60	78	33/45	55.64 (3.05)	7/70/1
60-70	93	43/50	65.72 (2.74)	9/83/1
70-80	77	40/37	76.03 (3.08)	6/70/0
>80	26	13/13	83.58 (2.08)	1/24/1

Note: Handedness information was not available for 2 participants. L = left, R = right, A = ambidextrous, F = female, M = male, M_{age} = Mean, SD = standard deviation

Stimuli

Participants watched an 8-minute, shortened version of the “Bang! You’re Dead” episode from the television show Alfred Hitchcock Presents (1961). The full 25-minute episode was cut due to time constraints but retained the central plot of the original narrative. The instructions were to watch, listen, and pay attention to the movie. None of the participants reported having seen the movie before.

Additional measures of interest included performance indices on select neuropsychological tests from the full battery included in the CamCAN protocol. Of particular interest to us were the attentional orientation, composite memory, fluency, language, visuospatial performance, and total scores from the Addenbrooke’s Cognitive Examination (ACE-A; ACE-M; ACE-F; ACE-L; ACE-VS; ACE-R, respectively) as well as the Logical Memory Test (LMT) immediate and delayed recall tests from the Wechsler Memory Scale. In Wechsler LMT, participants read two short stories and freely recalled as many story details as they could immediately after reading the story and after a 20-minute delay. Participants’ free recall data were scored for the number of correctly recalled story details for each time point. The scores for each cognitive test are provided, broken down by each age decade, in Supplementary Table 1.

MRI data acquisition

The data were collected using a Siemens 3T TIM Trio scanner with a 32-channel head coil at the MRC Cognition and Brain Sciences Unit, Cambridge, UK. Functional data during movie watching were acquired with a multi-echo T2* EPI sequence over 193 volumes [32 axial slices, 3.7 mm thick, 0.74 mm gap, TR = 2470 ms, TE = [9.4, 21.2, 33, 45, 57] ms, flip angle = 78°, FOV =192 × 192 mm, voxel size = 3 × 3 × 4.44 mm]. T1-weighted images were acquired with a 3D MPRAGE sequence [TR = 2250 ms, TE = 2.99 ms, TI = 900 ms, flip angle = 9°, FOV = 256 × 240 × 192 m, 1 mm isotropic voxels, GRAPPA acceleration factor = 2].

Image Processing

The data were preprocessed with a combination of fMRIPrep 21.0.1 (Esteban, Markiewicz, et al. 2019), which is based on Nipype 1.6.1 (Gorgolewski et al. 2011), and *tedana* (DuPre et al., 2021).

Anatomical

The T1-weighted (T1w) images were corrected for intensity non-uniformity, then skull-stripped. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w.

Hippocampal subregions, including the anterior and posterior hippocampus were automatically segmented using the Automatic Segmentation of Hippocampal Subfields (ASHS; Yushkevich et al., 2015; atlas: ashsT1_atlas_upennpmc_07202018). ASHS employs multi-atlas label fusion to automatically label hippocampal subregions in individual participants (Wang et al., 2013). This segmentation method was chosen based on recent work validating its rigor among manual and automated segmentation approaches (Bussy et al., 2021). Quality control was performed on these data, which involved three researchers (CF, RS & JS) visually inspecting the outputs for gross errors in segmentation. Specifically, the quality control criteria included (1) correct labelling of the hippocampus as a whole, (2) whether regions other than the hippocampus were labeled as such, and (3) presence of the uncal apex in the anterior hippocampus. Gross errors were observed in 41 participants, who were excluded from analyses. The resulting outputs of interest were four hippocampal segments: anterior and posterior subregions for each hemisphere (i.e., right/left). Intracranial volume (ICV) as well as gray matter volumes from each subregion were extracted as part of the ASHS protocol and volumes were summed to obtain the whole hippocampal volume.

Functional

Data were minimally preprocessed using fMRIPrep, which is amenable to multi-echo functional images. Head-motion parameters with respect to the BOLD reference (i.e., transformation matrices, and six corresponding rotation and translation parameters) were estimated. BOLD runs were slice-time corrected to 1.2s (0.5 of slice acquisition range 0s-2.4s) using 3dTshift from AFNI (Cox & Hyde, 1997). The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying the transforms to correct for head-motion.

The minimally pre-processed outputs of fMRIPrep were then submitted to *tedana* (DuPre et al., 2021). Multi-echo data were optimally combined, after which principal component analysis and the 'stabilized' Kundu component selection decision tree (Kundu et al., 2013) was applied for dimensionality reduction. Independent component analysis was then used to decompose the dimensionally reduced dataset. Component selection was performed to identify BOLD (TE-dependent), non-BOLD (TE-independent), and uncertain (low-variance) components using the Kundu decision tree (v2.5; Kundu et al., 2013). Output of *tedana* contains the denoised ICA coefficients, which were used to compute functional connectivity in the subsequent steps.

Additional steps were taken to reduce the effects of motion on the functional connectivity results. Wavelet despiking was applied to remove residual motion artefacts following *tedana* (Patel et al., 2014). Wavelet despiking identifies irregular events at different frequencies by detecting sequences of wavelet coefficients that are outliers. Outlying wavelet coefficients are then projected out of the denoised coefficient set. This approach has been previously applied to the CamCAN data (Caldinelli & Cusack, 2022; Geerligs et al., 2016, 2017; Henson et al., 2016; Lehmann et al., 2021) and has been shown to remove a variety of motion artefacts, including spin-history effects and higher frequency events such as spikes (Geerligs et al., 2017; Patel et al., 2014).

Denoised and wavelet despiked data were quality checked by three researchers (CF & RS & GB). The quality check criteria were (1) successful co-registration between the anatomical and functional scans, (2) a framewise displacement value less than 0.50, (3) DVARS less than 2, (4) sufficiently high temporal signal to noise ratio (calculated as the mean signal intensity of a voxel divided by its standard deviation across the timeseries with a cutoff of > 50), (5) greater than 10 retained BOLD-like components, and finally, (6) average spike percentage 2 SDs below the mean. As a result of these quality check steps, 86 participants were excluded from the analyses.

Next, a 400-region, 17 network, Schaefer parcellation (Schaefer et al., 2018) was projected to each participant's native surface space and the BOLD coefficient sets were extracted from each parcel, as well as from the left and right anterior/posterior hippocampal regions of interest.

Functional Connectivity

To assess functional connectivity, we computed the product-moment (r) correlation coefficients between our four regions of interest—left/right & anterior/posterior hippocampus—as well as between these regions and the 400 cortical parcels from the Schaefer atlas. A canonical Fisher's r-to-z transformation was applied to these correlation matrices to normalize the correlation values, which included a term to account for varying degrees of freedom (Kundu et al., 2013). This step resulted in a 4x4 square matrix for intra-hippocampal connectivity and a 4x400 rectangular matrix for cortico-hippocampal subregion connectivity for each participant.

Statistical Analysis

Age effects on within-hippocampal connectivity and relationships to episodic memory

Prior to analyses, all continuous behavioural variables were mean centered.

Our first aim was to examine age effects on the connectivity between hippocampal subregions in relation to episodic memory. We used a linear mixed effects model (LMM) with the connectivity values as the dependent variable, and the connectivity type (contralateral vs. ipsilateral), chronological age, their interaction, ICV, gender, and the total hippocampal volume as fixed effects. We also included a connectivity type per participant random slope in the model to account for intra and inter-individual variability in subregion connectivity.

We conducted follow-up analyses across separate models to examine whether any observed changes in the contralateral or ipsilateral connectivity were driven by the anterior vs. posterior subregions or left vs. right hemisphere, respectively. In the model examining contralateral connectivity differences between the anterior and posterior hippocampus, we included hippocampal subregion, age, their interaction as well as ICV, gender and total hippocampal volume as fixed effects. The model examining ipsilateral connectivity differences between left and right hemispheres had a similar model structure, except with hemisphere (left vs. right) instead of hippocampal subregion as a fixed factor.

To examine whether within hippocampal connectivity related to behavioural measures, we used behavioural Partial Least Squares Correlation (bPLS; Krishnan et al., 2011; McIntosh & Lobaugh, 2004). bPLS is a multivariate method that captures latent patterns of maximal covariance between two sets of variables. The brain connectivity and behavioural matrices are cross-correlated, yielding a covariance matrix, which is then submitted to singular value decomposition to extract latent variables (LVs). LVs are orthogonal to one another and maximally capture relationships between the two matrices. For this analysis, the brain connectivity matrix was comprised of the contralateral (left anterior & right anterior; left posterior & right posterior) and ipsilateral (left anterior & left posterior; right anterior and right posterior) subregion connectivity (N = 4). The behavioural measures were those from the neuropsychological tests (N = 8). We conducted two hypothesis-driven bPLS analyses, one of which examined the association between within hippocampal connectivity and cognition due to age, and the other examined this association independently of age. For the latter, prior to the bPLS, we regressed out chronological age from all cognitive measures to assess whether within hippocampal connectivity related to cognition above and beyond age.

Age effects on cortico-hippocampal subregion connectivity and relationships to episodic memory

To examine cortico-hippocampal subregion connectivity across the lifespan we used the bPLS analysis. To run the bPLS, we first created separate data matrices storing each of the brain connectivity and the behavioural variables. Each row of the brain connectivity matrix corresponded to a vector of a participant's subregion connectivity with the 400 parcels, which was then ordered by the hippocampal subregion. The behavioural matrix consisted of participants' chronological age in the same order as the brain connectivity matrix.

As described above, we submitted the brain connectivity and behavioural matrices to bPLS. We extracted three measures of interest for each LV from bPLS: (1) a left singular value, representing the brain connectivity patterns that best characterizes the covariance, (2) a scalar singular value, containing covariance strength between the chronological age and connectivity, and (3) a right singular vector representing the weighted behavioural variable. The amount of variance each LV accounted for was calculated by dividing the square of each LV's singular value by the sum of squares of all singular values (hereon referred to as percent cross-block covariance). The bPLS additionally assigns each individual participant a brain connectivity score by calculating the dot product of the left singular value and each participant's connectivity matrix. Brain connectivity scores represent how strongly each participant expresses a given LV for each hippocampal subregion. For each LV, stronger positive values represent stronger expression of warmer colors, whereas stronger negative values represent stronger expression of cooler colors.

To determine the significance of the LVs, we used permutation testing (N = 1,000), in which the rows of the brain connectivity matrix were randomly reordered to create a new *permutation sample*. A new bPLS was then re-run for each of the resampled data set to obtain a set of singular values representing the sampling distribution under the null hypothesis. Statistical significance was determined as the probability that the permuted singular values are greater than the observed singular value for a given LV ($p < 0.05$; McIntosh & Lobaugh, 2004). Following permutation testing, we then used bootstrap resampling with replacement (N = 500) to assess the stability of the connectivity weights. For each resampling, a new bPLS was run and a bootstrap ratio (BSR) was calculated as the bootstrap estimated mean connectivity weight divided by the standard error. In this way, higher BSR values represent more stable connectivity weights for a given LV. We used a threshold of ±1.96, which represents the 95% confidence interval.

To examine the relationship between cortico-hippocampal connectivity and performance on the cognitive tasks, we derived brain connectivity scores for each of the observed patterns from the bPLS. We then calculated the correlation between participants' brain connectivity scores and performance on the neuropsychological tests.

Results

Aging reduces contralateral functional connectivity of the anterior and posterior hippocampus

We first examined age effects on contralateral (e.g., left vs. right anterior) and ipsilateral (e.g., anterior vs. posterior) within-hippocampal connectivity (i.e., 4x4 square matrix). The LMM with the within hippocampal functional connectivity as the outcome revealed a significant interaction between connectivity type (contralateral vs. ipsilateral) and age [$ß = 1.42$, $t(517) = 3.49$, $p < 0.001$], indicating that contralateral connectivity showed a greater decline across the lifespan compared to ipsilateral connectivity (see Figure 1A). We found significant main effects of both age [$ß = -0.70$, $t(537) = -4.11$, $p < 0.001$], indicating reduced functional connectivity regardless of connectivity type across the lifespan, and connectivity type [$ß = -1.58$, $t(518) = -14.88$, $p < 0.001$]. In other words, functional connectivity values decreased overall across the lifespan, and contralateral connectivity was greater than ipsilateral connectivity. No other significant main effects emerged (all $ps > 0.40$).

We next examined whether the reduced contralateral connectivity across the lifespan was most related to the anterior or posterior hippocampus. The LMM with the contralateral functional connectivity as the outcome variable and hippocampal subregions (anterior vs. posterior) collapsing across hemispheres, chronological age, as well as their interaction, ICV, gender, and total hippocampal volume revealed a significant main effect of chronological age [$ß = 1.42$, $t(517) = 3.49$, $p < 0.001$] as well as ICV [$ß = 1.42$, $t(517) = 3.49$, $p < 0.001$]. No other significant interaction or main effects were observed (See Figure 1B). This finding suggests that neither the anterior nor the posterior hippocampus differ in the extent to which they show reductions in contralateral connectivity across the lifespan (see Figure 1C).

Finally, we assessed whether the observed null effect on ipsilateral connectivity across the lifespan was stable across hemispheres (left vs. right). The LMM with the above model structure, except with ipsilateral connectivity as the outcome variable and hemisphere (left vs. right) as the fixed factor, revealed no significant interactions nor main effects (all *p*s > 0.07), indicating no hemispheric differences in the stable patterns of ipsilateral subregion connectivity.

Next, we examined whether within hippocampal connectivity (N=4) was related to cognition by conducting bPLS analyses. No significant associations between within hippocampal connectivity and cognition were found (all ps>0.3).

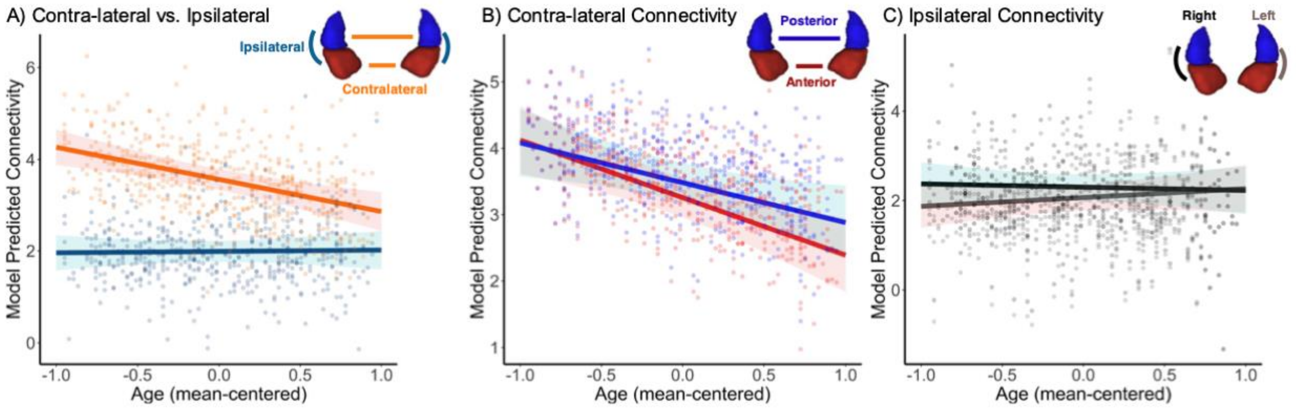

Figure 1. Model predicted, fisher-z-transformed, functional connectivity values for Linear Mixed Effects Models contrasting (A) contralateral vs. ipsilateral connectivity, (B) contralateral connectivity for the anterior vs. posterior hippocampus, and (C) ipsilateral connectivity for the right and left hemisphere across the lifespan.

Age differences in anterior and posterior hippocampal-cortical connectivity patterns

We computed a bPLS to investigate how cortico-hippocampal connectivity patterns differ across the lifespan. This analysis revealed two significant LVs.

The first LV (43% cross-block covariance, permuted $p < 0.001$) revealed a connectivity pattern that varied with chronological age and was shared among the bilateral anterior hippocampus and to a lesser extent, the right posterior hippocampus (see Figure 2A). BSR values for each significant parcel are presented in Supplementary Table 2. Regionally, these parcels were predominantly right lateralized (92%) and involved the lateral (Control A) and ventro-lateral prefrontal cortex, inferior parietal lobule (Control B), precuneus, posterior cingulate (Default A), ventral prefrontal cortex as well as the temporal lobe (Default B) and regions in the superior parietal (Dorsal Attention B) and post-central cortices (Dorsal Attention B). These regions showed increased connectivity with the bilateral anterior and posterior subregions. In contrast, these subregions showed decreased connectivity with parcels in the left hemisphere (66%) and included regions within the left medial prefrontal cortex (Default A). BSR values for these regions are projected on to a template brain surface in Figure 2B. Taken together, these age-related differences point to less specific connectivity patterns of the hippocampal subregions (i.e., reduced asymmetry), with increased coupling to regions in the right hemisphere.

The second LV (29% cross-block covariance, permuted $p < 0.05$) captured a distinct connectivity pattern that covaried with age for bilateral posterior hippocampus (see Figure 3A). BSR values for each significant parcel are presented in Supplementary Table 3. Increased age was associated with increased connectivity of the posterior hippocampus with the left intraparietal sulcus (Control A), left extrastriate superior (Visual Peripheral), right medial prefrontal cortex (Default A), as well as the left medial parietal and right ventro-lateral prefrontal cortices (Salience/Ventral Attention A & B). In contrast, increased age was associated with reduced connectivity of posterior hippocampus with parcels in the medial prefrontal cortex (Default A), temporal lobes in the left hemisphere (Default B), and precuneus/posterior cingulate, medial prefrontal (Default A) and dorsal prefrontal cortices (Default B) in the right hemisphere. Additionally, we observed reduced posterior hippocampal connectivity with the bilateral temporal pole (Limbic A), extrastriate (Visual Peripheral) and striate cortices (Visual Central) as well as the left superior parietal lobule (Dorsal Attention A) and right auditory cortex (Somatomotor B). BSR values for these regions are projected on to a template brain surface in Figure 3B.

Age related differences in cortico-hippocampal subregion connectivity are associated with episodic memory performance

Finally, we assessed whether the above reported patterns of cortico-hippocampal subregion connectivity changes in older age were related to cognitive and standardized measures of story recall (Figures 2C & 3C). In LV1, for both left and right anterior hippocampus, higher brain connectivity scores were negatively associated with delayed memory recall performance on the Wechsler LMT [LANT: $r(520) = -0.12$, $p < 0.01$; RANT: $r(520) = -0.16$, $p < 0.01$]. In addition, brain connectivity scores for the right anterior hippocampus were negatively associated with immediate recall [$r(520) = -0.14$, $p < 0.01$] as well as ACE-Memory and ACE-total scores [ACE-M: $r(520) = -0.12$, $p < 0.01$; ACE-R: $r(520) = -0.12$, $p < 0.01$; Figure 2C]. Overall, these findings indicate that greater connectivity between the anterior hippocampus and cortical networks such as the Control, Dorsal Attention as well as Default Networks is associated with worse episodic memory performance. Scatterplots relating brain connectivity scores to cognition are provided in Supplemental Figure 3.

In LV2, higher brain connectivity scores were significantly negatively associated with delayed memory recall performance for the left posterior hippocampus [$r(520) = -0.11$, $p < 0.01$; Figure 3C]. Thus, reduced connectivity between the posterior hippocampus and the Default, Visual, and Limbic Networks is associated with worse episodic memory performance. Scatterplots relating brain connectivity scores to cognition for each LV are provided in Supplemental Figures 3A & 3B.

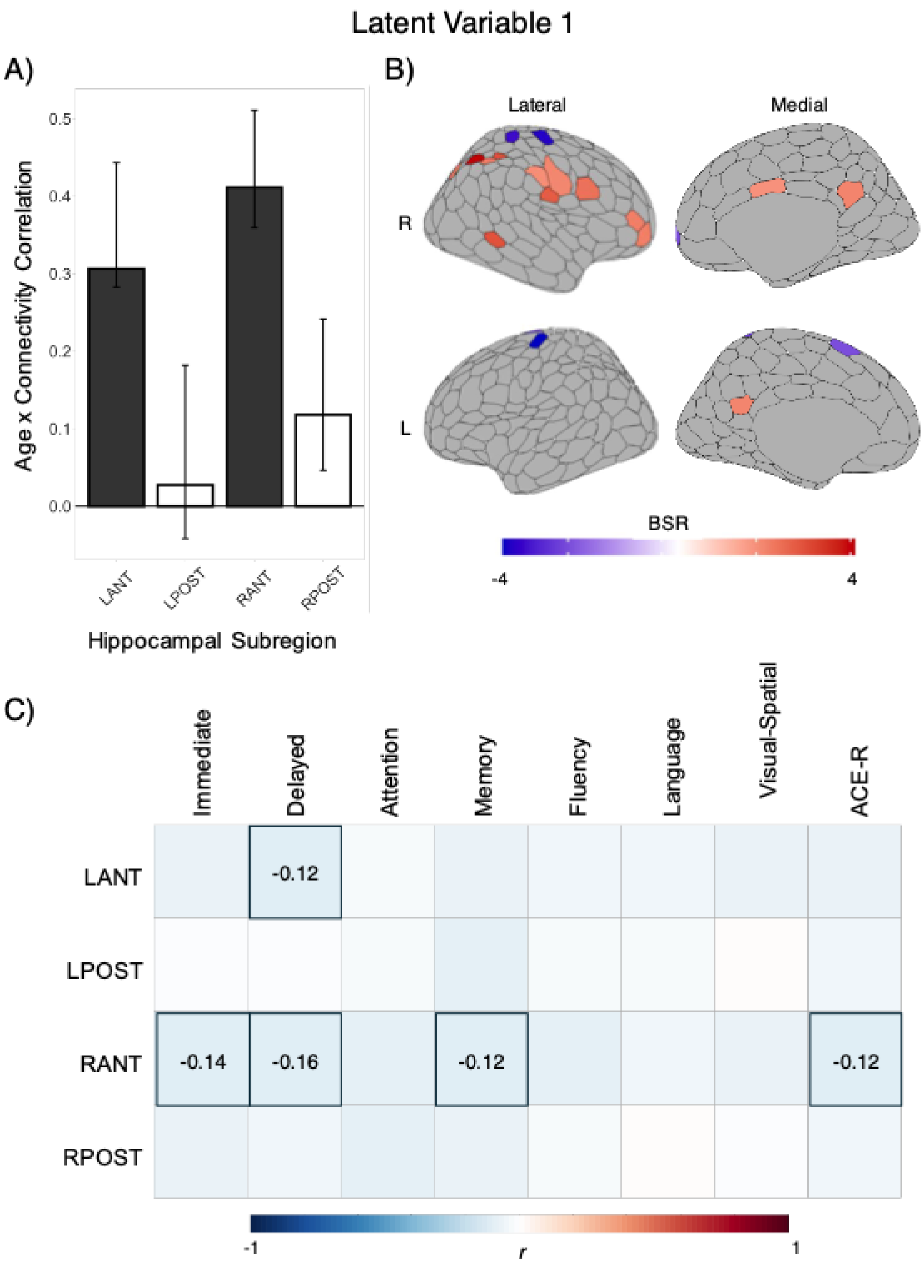

Figure 2. A) Age-connectivity correlation profile for Latent Variable (LV) 1. This LV explained 43% of the cross-block covariance (permuted $p < 0.001$) and captured a pattern expressed more by the bilateral anterior and to some extent right posterior hippocampus. Error bars represent 95% confidence intervals derived from bootstrap estimation. B) BSR values projected on the brain surface. Warm colors represent regions that show increased coupling with the anterior hippocampus in older age. Cool colors show the opposite of this pattern (*right panel*). C) Brain connectivity scores for each hippocampal subregion for LV1 correlated with the cognitive measures. LANT = left anterior, LPOST = left posterior, RANT = right anterior, RPOST = right posterior, BSR = bootstrap ratio, ACE-R = Addenbrooke's Cognitive Examination-Revised total score

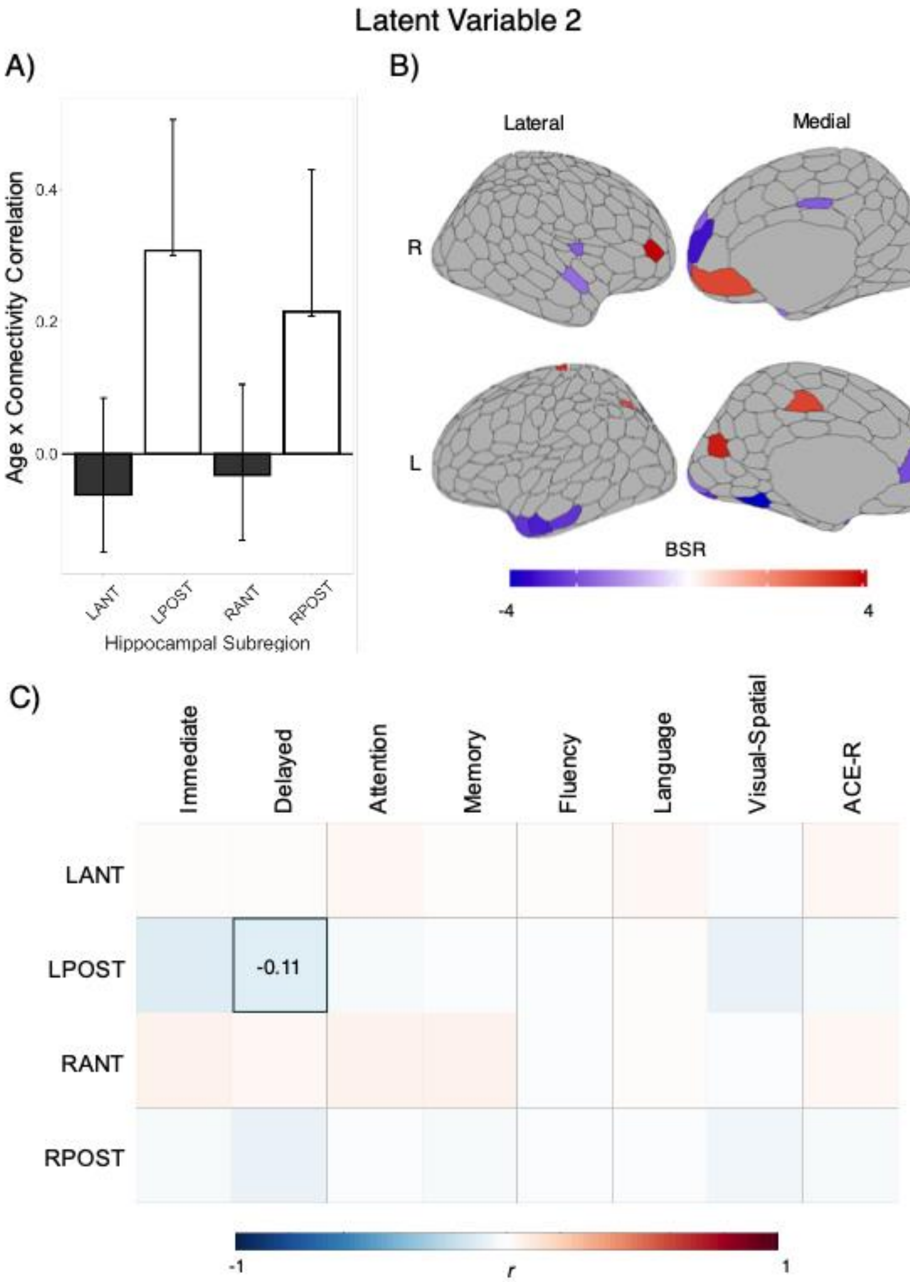

Figure 3. A) Age-connectivity correlation profile for Latent Variable (LV) 2. This LV explained 29% of the cross-block covariance (permuted $p < 0.05$) captured a pattern expressed only by the posterior hippocampus, bilaterally. Error bars represent 95% confidence intervals derived from bootstrap estimation. B) BSR values projected on the brain surface. Warm colors represent regions that show greater coupling with the bilateral posterior hippocampus with older age. Cool colors show the opposite of this pattern (*right panel*). C) Brain connectivity scores for each hippocampal subregion for LV2 correlated with the cognitive measures. LANT = left anterior, LPOST = left posterior, RANT = right anterior, RPOST = right posterior, BSR = bootstrap ratio, ACE-R = Addenbrooke's Cognitive Examination-Revised total score

Discussion

Episodic memory emerges from the functional interactions within the hippocampus and with the cortical mantle. Shifts in subregion connectivity patterns may be critical to age-related episodic memory decline. We tested this proposal by first examining hippocampal connectivity patterns during movie watching, then relating these patterns to performance on cognitive tests and standard measures of story recall. First, we observed reduced contralateral connectivity between the hippocampal subregions in older age. Examining cortico-subregion connectivity profiles revealed greater bilateral anterior hippocampal connectivity with regions predominantly located in the Control, Dorsal Attention, and Default Networks and reduced bilateral posterior hippocampal connectivity with regions in the Visual, Limbic, and Default Networks. Both patterns were related to lower performance on the standard story recall measures. Broadly, these results align with the well-reported pattern of neural dedifferentiation in older age, suggesting that functionally specialized hippocampal subregions become increasingly integrated in older age. Together, our findings establish a significant role for the hippocampal subregions in age-related episodic memory deficits, indicating that shifts in subregion connectivity profiles may be sensitive markers of how aging alters the ability to encode complex events.

Lifespan trajectory of within hippocampal connectivity patterns

When examining connectivity within the hippocampus, we found that advanced age was linked to reduced contralateral subregion connectivity (e.g., left anterior to right anterior), whereas ipsilateral subregion connectivity (e.g., left anterior to left posterior) remained stable across the lifespan. Prior work has typically examined age effects on hippocampal connectivity using extreme groups designs, comparing connectivity patterns between young and old adults (Eisenstein et al., 2021; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022; Stark et al., 2021), whereas we examined differences in subregion connectivity patterns across the adult lifespan, identifying connectivity patterns that continuously scale with increasing age. To our knowledge, only one other study has tested the effects of age on within hippocampal connectivity across the lifespan (6.80-80.80 years) during an associative memory task (Langnes et al., 2020). This study found that ipsilateral subregion connectivity remained stable, whereas contralateral subregion connectivity showed a monotonic reduction with increasing age, aligning with the connectivity shifts we found during a more naturalistic encoding condition (i.e., movie watching).

In considering the cognitive correlates of age-related reductions in contralateral hippocampal subregion connectivity, the evidence suggests that connectivity between contralateral hippocampal subregions is integral to bind and integrate information that is separately processed across the hemispheres into a coherent episodic memory representation (Gee et al., 2011; Stark et al., 2008). However, if this were the case, then one would expect a link between contralateral hippocampal subregion connectivity strength and episodic memory ability, which did not emerge in our study. Rather, a more plausible interpretation of our finding is that it speaks to the well-reported pattern of neural dedifferentiation in older age (Chan et al., 2014; Setton, Mwilambwe-Tshilobo, Girn, et al., 2022; Setton, et al., 2022). That is, given the well-reported functional specialization along the hippocampal long-axis, our finding of reduced contralateral functional connectivity in both the anterior and posterior hippocampus indicates that aging is associated with non-selective shifts in how subregions support episodic memory encoding and integrate information.

Lifespan trajectory of cortical-hippocampal subregion connectivity patterns

We assessed subregion connectivity at the whole brain level in relation to episodic memory ability. Two important findings emerged. First, we found that the left and right anterior, as well as to some degree, the right posterior hippocampus showed increased functional connectivity with a set of right lateralized regions in the Control, Dorsal Attention and Default Networks —with the greater proportion of these regions being in the Control Network. This finding parallels previous work showing that during episodic memory encoding, older adults exhibit greater connectivity with anterior brain regions, especially the prefrontal cortex (Dennis et al., 2008). Older adults' greater reliance on prefrontal, cognitive control regions during episodic memory tasks have been attributed to a multitude of aging phenomena. For example, a large body of work considers greater prefrontal recruitment in older age as a compensatory strategy employed by older adults during a given task to offset age-related cognitive decline (Grady, 2012). The additional recruitment of brain regions confers performance benefits for older adults, "compensating" for episodic memory deficits (Cabeza & Dennis, 2012; Reuter-Lorenz & Cappell, 2008). However, we found that the increased hippocampal, Control Network connectivity was related to lower episodic memory ability, which speaks against the compensation view of aging. Our results better align with accounts proposing age-related functional dedifferentiation (Goh, 2011; Koen et al., 2020). This view suggests that aging is associated with difficulty recruiting domain-specific neural mechanisms for a given task, which results in upregulated recruitment of a general cognitive control network (S.-C. Li & Lindenberger, 1999). In accord with this proposal, in our study, we observed greater connectivity with the prefrontal regions for both the anterior and posterior hippocampus, suggesting that these functionally specialized regions become less differentiated in older age and commonly synchronize with the Control Network. The greater connectivity between the anterior hippocampus and prefrontal cortex could also index age-related distinctions in the processing style (Castel, 2005b; Umanath & Marsh, 2014). Previous work has shown that anterior hippocampus —via its functional connections to prefrontal regions implicated in schema-based knowledge –supports the formation of coarse, gist-based representations of an event (Frank et al., 2019; Robin & Moscovitch, 2017b; Sheldon et al., 2019). Given that older adults increasingly rely on prior knowledge (Castel, 2005b; Umanath & Marsh, 2014) and more likely form more gist-based representations of events than younger adults (Fenerci et al., 2024; Grilli & Sheldon, 2022b; Koutstaal & Schacter, 1997), the increased coupling between anterior hippocampus and prefrontal cortex can underlie these behavioural shifts in information processing.

Second, we found that with increased age, both left and right posterior hippocampus showed reduced connectivity with regions located predominantly in the Default Network, as well as those in the Visual and Sensorimotor Networks. In addition, the subregions showed increased connectivity with Default, and Salience/Ventral Attention Networks. The finding of age-related reductions in posterior hippocampal connectivity parallels previous cross-sectional and longitudinal work showing that aging disproportionately reduces posterior cortico-hippocampal connectivity, especially with regions in the posterior Default Network (Damoiseaux et al., 2016; Panitz et al., 2021; Salami et al., 2016; see exception: Blum et al., 2014). These results are commonly interpreted in the context of age-related microstructural changes to the posterior hippocampus (Dalton, McCormick, De Luca, et al., 2019; Damoiseaux, 2017; Salami et al., 2016) and reduced volume of this subregion in older age (Langnes et al., 2020; Setton, Sheldon, Turner, et al., 2022), leading to changes in brain activity during episodic memory encoding (Cabeza et al., 2002; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008b; Snytte et al., 2022b). Expanding on this work, we found that the reduced posterior-DN connectivity in older age was specific to the dorsomedial subsystem of the DN (Default B), whereas regions in the core DN (Default A) showed both increased and decreased connectivity with this subregion.

The dorsomedial subsystem has been implicated in tasks that rely on semantic memory processes such as conceptual and abstract processing (Andrews-Hanna et al., 2019). One interpretation for this finding could be that aging is associated with a shift towards utilizing prior semantic knowledge during episodic memory tasks, which manifests as reduced connectivity between regions involved in processing fine-grained episodic information (i.e., posterior hippocampus) and semantic, schematic knowledge (i.e., temporal pole, medial prefrontal cortex). Broadly, the shared differences in the connectivity patterns of the left and right posterior hippocampus suggest that increased age is associated with a loss of hemispheric specialization in the hippocampus.

Even though our results closely align with the neural dedifferentiation accounts of aging, they extend several other neuro-cognitive frameworks (Davis et al., 2008; Koen et al., 2020; S.-C. Li & Lindenberger, 1999; Spreng et al., 2018). One of which is a framework suggesting that aging is associated with shifts in activation from more posterior to more anterior regions during episodic memory tasks (PASA; Davis et al., 2007). This account predominantly rests on the finding of reduced activation in posterior brain regions (e.g., visual cortex, occipitotemporal regions) coupled with age-related increases in prefrontal activity (Dennis et al., 2008; Grady et al., 1994). In accord with these activation patterns, we found a posterior to anterior shift in older age in cortico-hippocampal connectivity profiles —with anterior hippocampus primarily showing increases in connectivity with anterior cortical regions and posterior hippocampus showing decreased connectivity with posterior cortical regions. An earlier model, the Hemispheric Asymmetry Reduction in Older Adults (HAROLD; Cabeza, 2002), proposes that when younger adults primarily recruit left lateralized regions during episodic memory encoding, older adults additionally recruit right-lateralized regions during the same task (Stebbins et al., 2002). The greater reliance on right-lateralized regions by older adults was evident in our cortico-hippocampal connectivity results, where we found that most regions showing increased coupling with the anterior hippocampus were right lateralized.

Together, our results expand on the above-reviewed work in important ways. First, ours is the first study to examine age effects on hippocampal subregion connectivity patterns during movie watching, mimicking the complexity and the nature of our everyday experiences (Campbell et al., 2015b; Finn, 2021; Finn et al., 2020; Sonkusare et al., 2019). Given that functional connectivity during movie watching outperforms rest in predicting individual differences in cognition (Finn & Bandettini, 2021), this paradigm allowed us to draw a more complete picture of hippocampal functional topography as it relates to cognition in older age (Lacy & Stark, 2012). As well, we analyzed the largest sample reported to date to probe hippocampal connectivity patterns, which allowed for a well-powered examination of functional connectivity and its relation to episodic memory across the lifespan. We also employed a comprehensive approach to minimize age-related confounds and derive reliable measures of functional connectivity (e.g., motion artefacts, spatial normalization). We took advantage of the multi-echo data, which significantly mitigates motion artifacts after processing and denoising (Gotts et al., 2020), yielding a higher temporal signal-to-noise ratio (Kundu et al., 2013) and allowing reliable estimation of functional connectivity (Lynch et al., 2020). Second, we conducted our analyses in the participants' native space as well as with individualized hippocampal segmentation, circumventing issues with poor registration to standard, normalized templates, which are especially pervasive with older adult samples (Braga & Buckner, 2017; Wang et al., 2015).

However, our results deviate from other reports of age-related changes to functional brain connectivity at rest. For example, previous work reported that older adults have reduced resting state functional connectivity in both ipsilateral and contralateral hippocampal subregions (Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022; but see Salami et al., 2014 and Damoiseaux et al., 2016 for different results). Although this inconsistency could be due to analytical differences (e.g., modeling age as a continuous vs. cohort variable; controlling for hippocampal volume in statistical models), it could also be because our study estimated connectivity profiles during movie watching, which is a more constrained, and ecologically valid assessment of connectivity that is known to differ from resting state scans in important ways (Finn & Bandettini, 2021; Kringelbach et al., 2023; Lacy & Stark, 2012; Meer et al., 2020).

Despite these advantages, our study was not without limitations. For example, in the CamCAN dataset, participants' memory for the movie was not tested. For this reason, episodic memory ability was measured using tests from a standardized neuropsychological battery which are limited in how much they relate to encoding and remembering complex events. This limitation might explain why we did not find a significant association between contralateral subregion connectivity and episodic memory performance as previously reported in neuropsychological studies (McCormick et al., 2018). The lack of memory measures for the encoded movie also precludes determining whether the observed functional connectivity patterns are driven by younger and older adults attending to different features of the movie. To this point, several studies using movie watching paradigms have shown differences in how events are processed by younger and older adults (Kurby & Zacks, 2019; Magliano et al., 2012; Zacks et al., 2006). For example, older adults show less agreement in where they perceive salient changes in a movie (Kurby & Zacks, 2019; Stawarczyk et al., 2020) as well as less hippocampal activity at these time points (Reagh et al., 2020) than younger adults. To examine whether age-related differences in hippocampal connectivity patterns relate to differences in attended movie features, current data can be supplemented by recent advances in fMRI analysis tools, which can reconstruct viewing behaviour from the MR-signal of the eyeballs (Frey et al., 2021; Nau et al., 2023).

Moreover, without collecting behavioural data associated with the movie-watching, it remains unclear whether the observed shifts in hippocampal connectivity patterns lead to age differences in how memories are represented by younger and older adults. A hypothesis in light of patterns reported here is that aging will be associated with qualitative shifts in the way memories are represented by younger and older adults (Grilli & Sheldon, 2022b). In support of this hypothesis, emerging work finds differences in the recollected content from the same movie between younger and older adults (Davis et al., 2021; Fenerci et al., 2024; Henderson & Campbell, 2023). Future work can employ free recall paradigms in conjunction with in-scanner movie watching to map the observed patterns to the content younger and older adults use to remember the movie.

Last but not least, distinct from the subregions, the hippocampus is also composed of cytoarchitecturally distinct subfields, each of which playing an ascribed role in episodic memory processing (S. G. Mueller et al., 2011), showing dissociable cortical functional connectivity patterns (Chang et al., 2021; Dalton, McCormick, De Luca, et al., 2019; Dalton, McCormick, & Maguire, 2019; Vos de Wael et al., 2018) and selective age-related deterioration (de Flores et al., 2015; G. B. Frisoni et al., 2008; La Joie et al., 2010; Pereira et al., 2014). In the current study, it was not possible to assess age effects on hippocampal subfield connectivity given the high-resolution needed to reliably segment these subfields. Thus, an important future avenue is to characterize how aging affects hippocampal subfield connectivity in concert with changes in episodic memory (Dalton, McCormick, De Luca, et al., 2019). Future work should also examine age-related connectivity differences in extra-hippocampal, medial temporal lobe structures. Several studies have shown functional heterogeneity within the medial temporal lobes (Davachi, 2006; Eichenbaum et al., 2007; Graham et al., 2010; Wan et al., 1999). Content-based accounts have suggested that perirhinal cortex, as part of a broader anterior temporal network, supports item representations as well as related conceptual knowledge and parahippocampal cortex, embedded within a posterior medial network, supports context representations (Ranganath & Ritchey, 2012; Ritchey & Cooper, 2020). Since aging selectively impairs context, but not item memory (Naveh-Benjamin et al., 2003), this may be reflected in connectivity differences in these key medial temporal lobe regions, along with their associated networks.

Conclusions

To conclude, our study draws a comprehensive picture of hippocampal subregion connectivity patterns across the lifespan as they relate to episodic memory performance. We show that during movie watching —a proxy for naturalistic episodic memory encoding — age-related differences in subregion connectivity are apparent both within the hippocampus as well as between the hippocampus and the rest of the brain. These results suggest that advanced age is associated with a loss of hemispheric and to some extent, long-axis specialization of the hippocampal subregions, which might be a sensitive marker of age-related episodic memory decline.

Statements and Declarations / Compliance with Ethical Standards

Ethical Approval: All study procedures were conducted in accordance with the ethical guidelines of Cambridge 2 Research Ethics Committee.

Competing interests: The authors have no relevant financial or non-financial interests to disclose.

Author's contributions: C.F.: Conceptualization, Methodology, Formal Analysis, Visualization, Validation, Software, Writing-Reviewing and Editing. R.S.: Conceptualization, Formal Analysis, Validation, Software, Writing-Reviewing and Editing. G.B.: Writing-Reviewing and Editing, Validation, Methodology, Data Curation. J.S.: Writing-Reviewing and Editing, Validation, Data Curation. R.N.S.: Writing-Reviewing and Editing, Supervision. S.S.: Writing-Reviewing and Editing, Conceptualization, Supervision, Resources, Funding Acquisition

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Availability of data and materials: All analyses scripts will be made available upon request from the corresponding author. CamCAN data are available upon request here: https://camcan-archive.mrc-cbu.cam.ac.uk/dataaccess/datarequest.php

Clinical trial: This was not a clinical trial.

Trial Registration Number (TRN): N/A

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Supplementary Material

Supplemental Table 1. Summary of scores on the neuropsychological test battery across age decades.

Age Decade	**LMT Immediate**	**LMT Delayed**	**ACE-Attention**	**ACE-Memory**	**ACE-Fluency**	**ACE-Language**	**ACE-Visuospatial**	**ACE-Total**
18-20	16.08	14.75	16.92	23.67	12.17	24.67	15.17	92.58
(20,30]	16.86	15.44	17.64	24.81	12.98	25.59	15.77	96.80
(30,40]	16.03	14.61	17.63	24.76	13.31	25.65	15.76	97.10
(40,50]	15.84	14.35	17.52	24.62	13.18	25.43	15.75	96.51
(50,60]	14.76	13.29	17.62	24.41	13.05	25.17	15.56	95.80
(60,70]	14.13	12.43	17.38	23.85	12.51	25.25	15.48	94.47
(70,80]	13.05	10.87	17.07	23.01	11.94	24.85	15.07	91.94
>80	12.03	9.93	17.43	22.63	11.87	25.00	15.37	92.30

Note: ACE= Addenbrooke’s Cognitive Examination, LMT = Logical Memory Test

Supplemental Table 2. Network and parcel assignment, as well as their bootstrap ratios (BSR) for Latent Variable (LV) 1

Hemisphere	**Network Name**	**Parcel**	**BSR**
L	DefaultB	dorsal PFC	-1.97
L	DorsAttnB	post central	-2.25
L	SomMotA	9	-3.39
L	SomMotA	16	-2.61
R	DefaultA	medial PFC	-2.02
R	SomMotA	7	-3.17
R	SomMotA	8	-2.90
R	SomMotA	17	-2.11
L	DefaultA	precuneus/PCC	2.15
R	ContA	mid-cingulate	1.96
R	ContA	intraparietal sulcus	2.31
R	ContA	lateral PFC	2.47
R	ContB	lateral ventral PFC	2.24
R	ContB	inferior parietal lobule	4.09
R	DefaultA	precuneus/PCC	2.17
R	DefaultB	temporal	2.98
R	DorsAttnA	superior parietal lobule	2.30
R	DorsAttnB	post central	2.03
R	DorsAttnB	post central	3.02
R	SalVentAttnB	lateral ventral PFC	2.25
R	SomMotB	central	2.14
R	SomMotB	S2	2.83

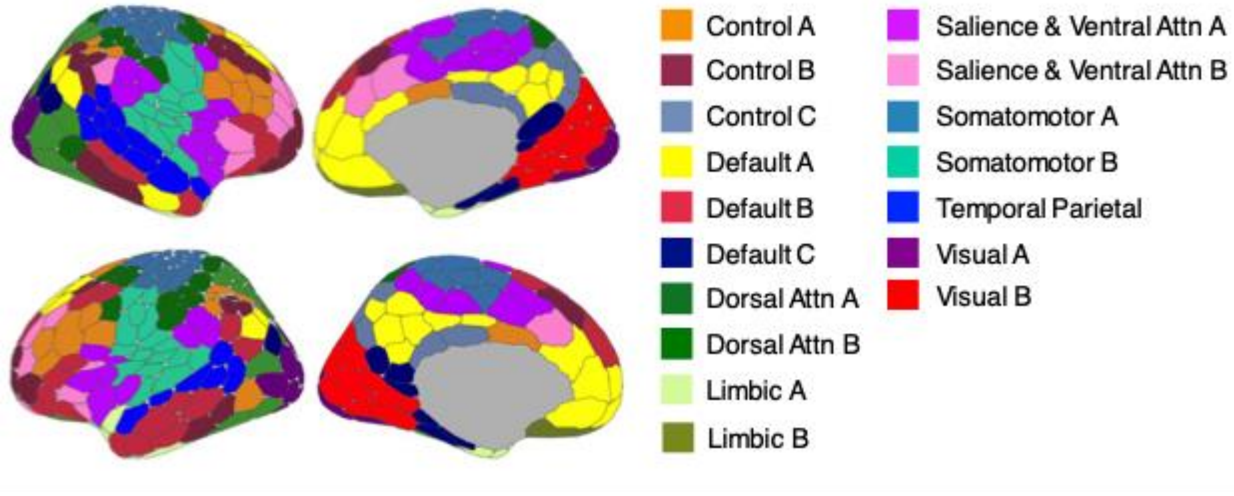
Note: L= left, R=right, PFC = prefrontal cortex, PCC = posterior cingulate cortex

Supplemental Table 3. Network and parcel assignment, as well as their bootstrap ratios (BSR) for Latent Variable (LV) 2

Hemisphere	**Network**	**Parcel**	**BSR**
L	DefaultA	medial PFC	-2.49
L	DefaultB	temporal	-3.11
L	DefaultB	temporal	-2.83
L	DefaultB	temporal	-2.82
L	DorsAttnA	Superior parietal lobule	-2.28
L	LimbicA	temporal pole	-2.64
L	LimbicA	temporal pole	-2.50
L	VisCent	extra-striate cortex	-2.91
L	VisCent	striate cortex	-2.22
L	VisPeri	extra-striate inferior	-3.73
R	DefaultA	medial PFC	-3.25
R	DefaultA	medial PFC	-2.48
R	DefaultA	precuneus/PCC	-2.26
R	DefaultB	dorsal PFC	-2.24
R	LimbicA	temporal pole	-2.04
R	SomMotB	S2	-2.28
R	SomMotB	auditory	-2.06
R	VisCent	extra-striate cortex	-2.28
L	ContA	intraparietal sulcus	2.05
L	SalVentAttnA	medial parietal	2.15
L	SomMotA	13	2.47
L	VisPeri	extra-striate superior	2.66
R	DefaultA	medial PFC	2.10
R	SalVentAttnB	lateral ventral PFC	2.95

Note: L= left, R=right, PFC = prefrontal cortex, PCC = posterior cingulate cortex

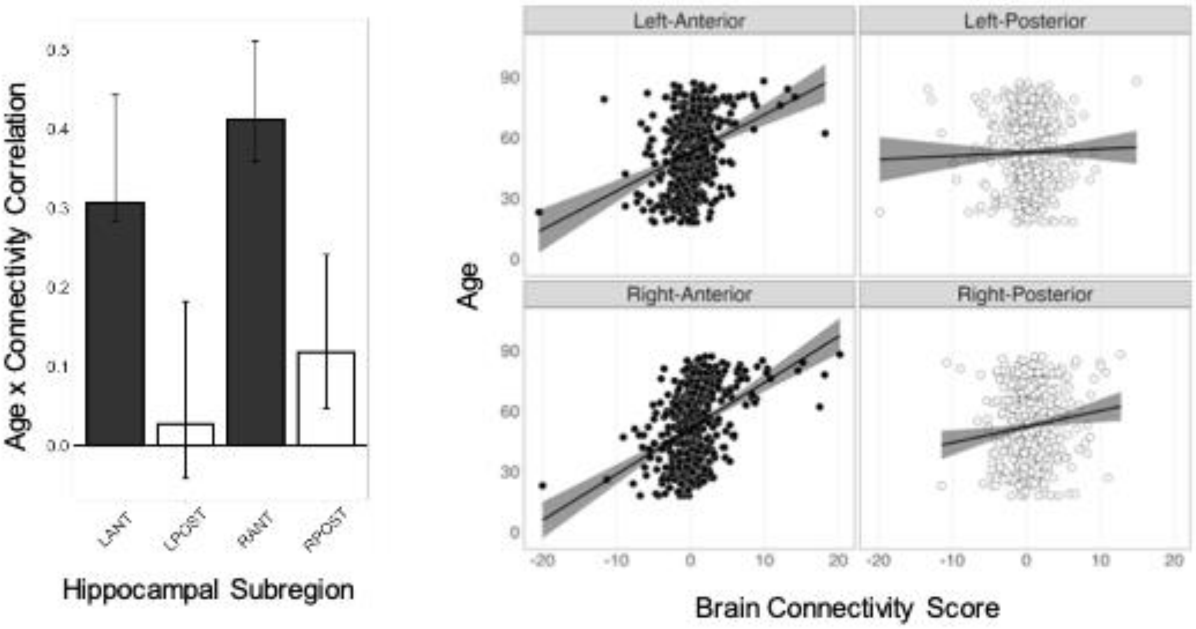
Supplemental Figure 1.
The 400-region, 17 network, Schaefer parcellation (Schaefer et al., 2018) that was projected onto each participant's native surface, shown here on a template brain.



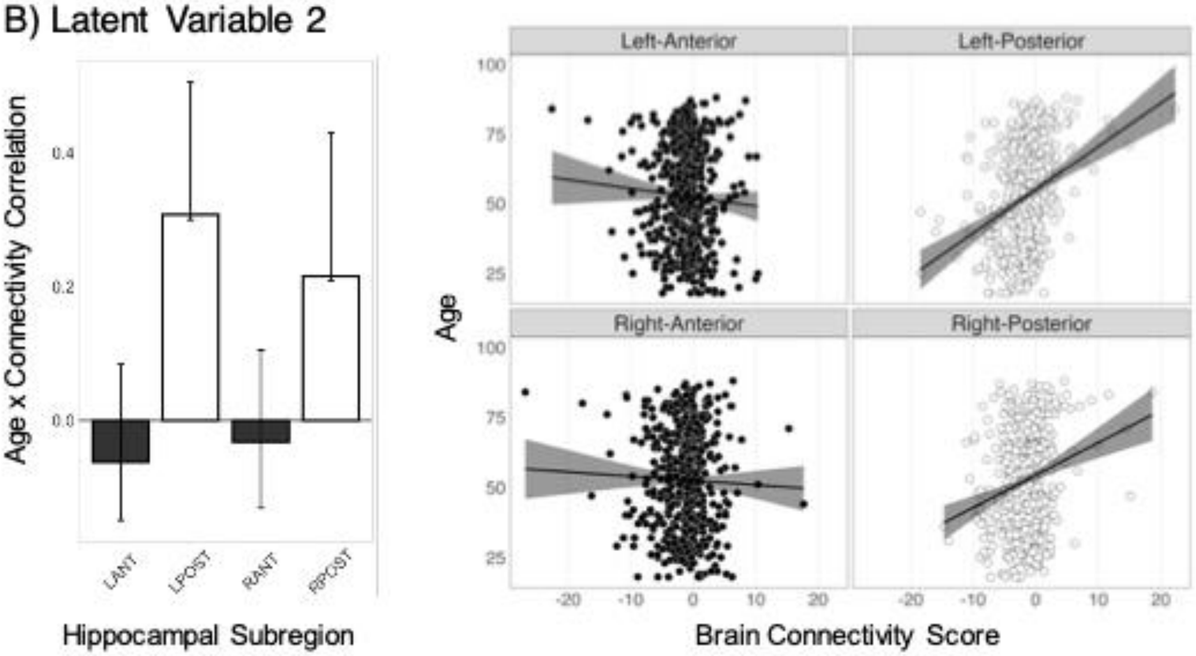
Supplemental Figure 2.

Associations between brain connectivity and chronological age. The scatterplots show associations between the brain connectivity scores from Figure 2 and participants' chronological age. A) Latent Variable 1 revealed a connectivity pattern varying with chronological age in the bilateral anterior hippocampus and the right posterior hippocampus. B) Latent Variable 2 revealed a connectivity pattern, varying with age, shared among the bilateral posterior hippocampus.

A) Latent Variable 1



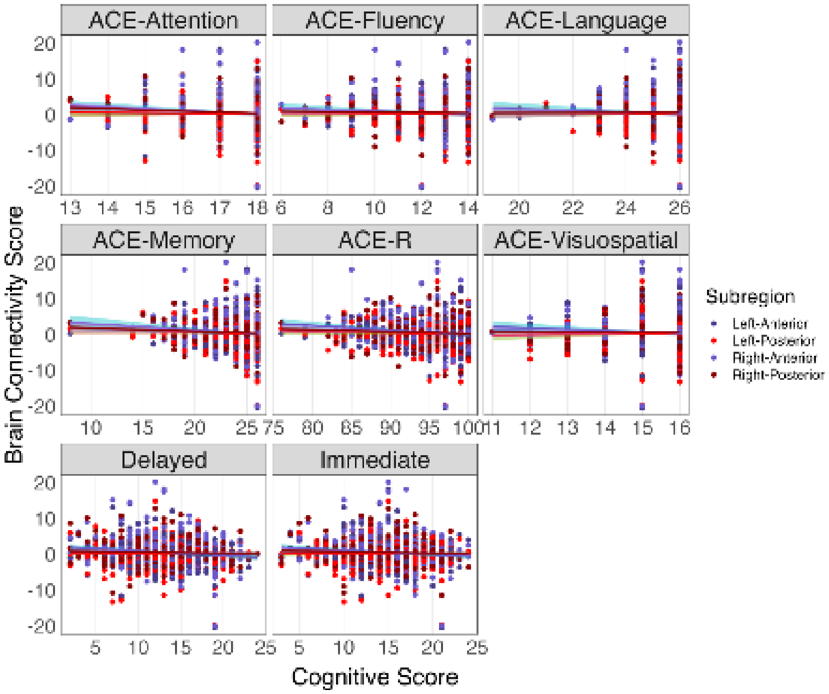
B) Latent Variable 2



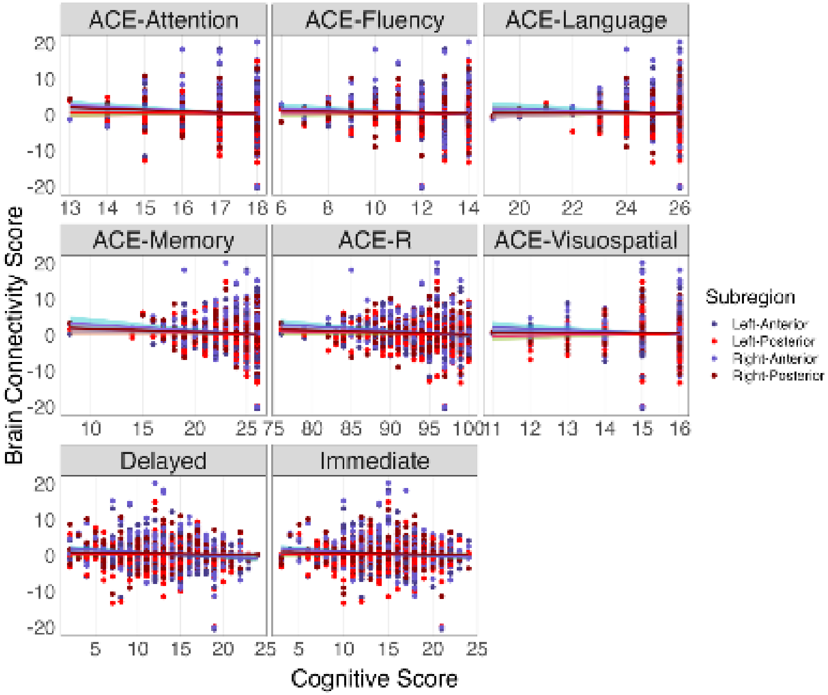
Supplemental Figure 3.

Associations between brain connectivity and cognitive measures for A) Latent Variable 1 and B) Latent Variable 2

A) Latent Variable 1



B) Latent Variable 2



Bridge to Chapter 2

Chapter 1 examined hippocampal subregion connectivity patterns during encoding, across the lifespan, and in relation to episodic memory performance. This chapter revealed three key insights. First, aging reduced contralateral (left vs. right anterior) but not ipsilateral (anterior vs. posterior) hippocampal connectivity. Older age was associated with greater bilateral recruitment of the anterior hippocampus, which showed increased connectivity with regions predominantly located in the prefrontal cortex, and reduced connectivity of the posterior hippocampus, primarily with posterior cortical regions. Finally, age-related cortico-hippocampal connectivity patterns were associated with lower performance on standard story recall measures. Together, these results critically implicate hippocampal subregions in age-related episodic memory changes, suggesting that advanced age is linked to greater reliance on brain regions implicated in forming coarse, gist-based representations of an event.

In Chapter 2, I examined whether these functional brain shifts observed in older age while encoding a complex event is reflected as distinctions in how younger and older adults recall the movie. Critically, I examined age-related shifts in different components of episodic memory: content, organization, and accuracy, which are thought to be core functions of the hippocampus (Moscovitch et al., 2016). I hypothesized that younger and older adults will represent the movie differently, which will be reflected in the content and organization of their recall. As well, if these age-related shifts are maladaptive, then these differences will present in the presence of reduced memory accuracy for older adults.

Chapter 2: Shift happens: Aging alters the content but not the organization of memory for complex events

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Abstract

Cognitive aging research has focused on comparing episodic memory accuracy between younger and older adults. Less work has described qualitative shifts in how episodic memories are encoded and recalled. This is especially relevant for memories of real-world experiences, since there is immense variability in which details can be accessed and organized into a coherent narrative. To address this knowledge gap, we investigated age effects on the organization and content of memory for complex events. In two independent samples (N=45; 60), young and older adults encoded and recalled the same short-movie, depicting a series of events, which allowed us to examine the organization and content dimensions of recall within a single, complex, and extended episode. We developed and applied a novel scoring on the recollections to quantify recall accuracy, temporal organization (temporal contiguity, forward asymmetry), and biases in memory content (perceptual, conceptual details). In both samples, despite no age-effects on recall accuracy nor on metrics of temporal organization, older adults' recall was more biased towards conceptual and non-episodic content, whereas younger adults biased their recall towards a higher proportion of event-specific information. Our results indicate that age-related differences in episodic recall reflect qualitative distinctions in what details younger and older adults assemble from the past events.

Keywords *episodic memory; aging; free recall; content; organization*

Introduction

Episodic memory, our ability to remember past events, specific in time and place (Tulving, 2002), shows marked changes in older age (Park & Reuter-Lorenz, 2009). A major focus of cognitive aging research has been to describe age-related deficits in encoding and recalling episodic memories (Naveh-Benjamin et al., 2003). Many studies have estimated these deficits as a reduction in accuracy (i.e., remembered or not) for items encoded from simple stimulus sets (e.g., words lists or images). However, memories formed in the real-world are much more complex, requiring an individual to bring together a diverse array of details into an organized description of the past (Schacter & Addis, 2007). The complexity inherent to our memories allows for numerous ways to represent and remember our past experiences (Sheldon et al., 2019), which raises important questions about how aging affects the way complex episodic memories are remembered.

Recent theories of cognitive aging propose that episodic memory differences between younger and older adults are better viewed as qualitative shifts in the way memories are represented (Grilli & Sheldon, 2022). When younger adults form specific representations, which reproduce precise, high-fidelity details of past events in their memories, older adults form gist-based representations, which capture the essential, core aspects of an experience including its meaning (Amer et al., 2022; Grilli & Sheldon, 2022). These theories rest on evidence from recognition memory paradigms showing that older adults retain gist-level information about individual items while forgetting their specific details (Castel, 2005), but are yet to be tested with more complex event memories. To address this gap, in the current study, we test whether age-related shifts towards forming gist-based memory representations affect the organization and content of complex memories, which are the building blocks of episodic memory (Tulving, 2002).

A critical feature of our experiences in the real-world is their multi-dimensionality, involving a diverse array of details, which are assembled during retrieval (Moscovitch et al., 2016). For complex memories, there is a distinction between representing an event's content by focusing on the specific, perceptual details (e.g., "I had a blue shirt on.") versus higher-order, conceptual details that capture one's evaluations and inferences about the event (e.g., "I was so happy to see all my friends together."; Sheldon et al., 2019; Gurguryan et al., 2019). It is proposed that focusing on perceptual details results in highly precise, specific memory representations, whereas focusing on conceptual details results in gist or meaning-based memory representations (Grilli & Sheldon, 2022). Thus, older adults' tendency to represent events at the gist-level should shift the content of their memory towards such higher-level, conceptual details.

According to retrieved-context models, memory organization emerges from effectively encoding and retrieving temporal associations between items (Howard & Kahana, 2002; Polyn & Cutler, 2017). While encoding a list of items, participants embed the items into a gradually changing context – with temporally proximal items sharing more contextual overlap (Kahana, 1996; Lohnas et al., 2015). Recalling an item from the list reinstates its associated context and cues other items from nearby positions. This results in participants successively recalling items presented close together during encoding (i.e., temporal contiguity) and remembering them with a forward-going bias. A large body of work has shown that older adults present with reduced temporal contiguity effects and forward-going biases when recalling items learned as part of a list (Kahana et al., 2002; Talamonti et al., 2021) or in a real-world setting (Diamond & Levine, 2020). These age-related differences have been attributed to younger and older adults' relying on different methods to associate items of a list in memory – with younger adults leveraging temporal associations between items/events, and older adults utilizing meaning-based, semantic associations (Golomb et al., 2008).

The above work leads to the prediction that older adults will show reduced temporal organization and retention of temporal associations between the elements of a complex memory. However, an important distinction between the items learned as part of a list and the events we experience in the real world is that the latter follow a narrative structure (Schank & Abelson, 1975; Conway and Rubin 2019; Cohn-Sheehy et al. 2022). Thus, beyond temporal associations (e.g., Event A happened before Event B), real-world events are linked together through causal, logical, and meaning-based associations (e.g., Event A caused Event B). Context Maintenance and Retrieval model (CMR) suggests that these non-temporal factors (i.e., higher-level, meaning-based relations) can be used to organize the items during recall (Polyn et al., 2009). Consequently, one possibility is that older adults' gist-based focus while remembering might mask their deficits in forming temporal associations and facilitate their organization of events that mimic everyday experiences (Howard and Kahana, 2002b, Polyn et al., 2011). In line with this possibility, previous work examining the organization of scripts for everyday events (i.e., causal sequences of events within specific contexts; Schank & Abelson, 1975), have found no age differences in the temporal organization of these scripts between younger and older adults (Rosen et al., 2003). An alternative prediction is that older adults' gist-based focus will scaffold the recall of complex events, resulting in comparable temporal organization to younger adults.

Finally, whether qualitative shifts in the content and organization of memory in older adults present alongside or reflect episodic memory deficits remains unknown. Traditionally, qualitative changes to episodic memory are viewed as a product of or compensation for deficits in aging (Naveh-Benjamin et al., 2003; Piolino et al., 2010). For example, older adults' reduced reliance on temporal associations while recalling word-lists has been linked to their recalling fewer items from the lists (Diamond & Levine, 2020) and autobiographical memory research has commonly reported that older adults remember and report more non-episodic, semantic content, and fewer event-specific details than younger adults, which is attributed to older adults' declining episodic memory (Levine et al., 2002). Yet, another explanation is that the qualitative differences in memory reflect other changes that accompany healthy aging (e.g., narrative style, motivational changes) that offer the opportunity to offset such declines and improve memory (Allison et al., 2006; Mair et al., 2019; 2021). Thus, open questions remain about whether the hypothesized qualitative distinctions in how complex events are represented and remembered will be accompanied by episodic memory deficits traditionally reported in older age.

Current study

Expanding beyond current research that focuses on quantifying age-related deficits in episodic memory, the goal of the present study was to understand how aging leads to qualitative shifts in the way complex events are represented and remembered. We tested the proposal that there is an age-related shift towards forming gist-based representations while remembering complex events (Grilli & Sheldon, 2022) that will present as age differences in the content and potentially, the underlying organization of an associated memory. We re-analyzed two independent, previously published data sets (Davis et al., 2021; Henderson & Campbell, 2023) in which younger and older participants encoded the same short-movie depicting a series of events, allowing us to test the organization and content dimensions of recall within the constraints of a single, complex, and extended episode. First, we developed and applied a novel scoring technique to identify the number of event details participants recalled, which allowed us to test for age differences in memory accuracy. Second, we assessed additional types of content in participants' recall, quantifying the perceptual, conceptual, and non-episodic details, which allowed us to estimate qualitative shifts in mnemonic content. Finally, we measured the extent to which younger and older adult's recall narratives were temporally organized by applying measures from list-learning paradigms to quantify the remembered events' temporal contiguity and forward asymmetry.

Based on the above reviewed evidence and theories proposing an age-related shift towards gist-based remembering, we predicted that younger and older adults would represent and remember the movie with different kinds of content – with older adults prioritizing conceptual, and younger adults, event-specific content. Furthermore, we predicted that compared to younger adults, older adults will be less likely to rely on temporal associations as an organizational tool while recalling the movie, which will be evident in the reduced retention of the temporal associations among the movie events, as indexed via the temporal contiguity and forward asymmetry effects. Finally, if these qualitative shifts in how older adults organize and represent the content of a complex event reflect an adaptive method to engage in memory, then these qualitative differences between younger and older adults should present alongside comparable memory accuracy.

Methods

Participants

Original Sample

Forty-nine younger and older participants were recruited to participate in the experiment. Older participants were recruited from the Niagara Region community and were compensated $10/hour for their participation. Younger participants were recruited from Brock University (located in St. Catherines, Ontario, Canada, which is a midsized city) and received 1 course credit for their participation. All participants had normal or corrected-to-normal vision, were free of any medical or neurological conditions, and had English as their dominant language. All experimental procedures were approved by the Brock University Office of Research Ethics and written informed consent was collected from all participants prior to testing. Data for the Original Sample were collected November 2017-August 2018.

After removing four participants for scoring less than 23 on the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), the final analyzed sample included 21 younger adults (M= 20.90, SD= 2.81; Range= 18-28 years; F = 16; self-identified ethnicity: 21 White) and 24 older adults (M= 70.33, SD= 5.28; Range= 61-82 years; F= 13; 20 White; two Latinx; one Black, one Asian). Notably, there were no significant differences in participants' scores on the MoCA, and as expected, older participants had more years of education [t(34.89)= -2.93, p = 0.01] as well as higher vocabulary scores on the Shipley Vocabulary Scale [t(36.72)= -4.10, p < 0.001] than younger adults (Shipley, 1946).

Replication Sample

Sixty-four younger and older participants were recruited to participate in the experiment. Recruitment strategy and criteria were identical to the original sample. As before, all participants were fluent English speakers and had normal or corrected-to-normal vision. None of the participants reported any medical or neurological conditions. Approval from Brock University Office of Research Ethics and written informed consent from all participants were obtained prior to testing. Data for the Replication Sample were collected September 2018 - July 2022.

After excluding 4 participants based on MoCA scores (< 23), the final analyzed sample was comprised of 31 younger (self-identified ethnicity: 18 White, two First Nations, four Asian, one West Asian, one Arab, one Filipino, four South Asian; M= 20.20, SD= 2.96; Range= 18-27 years; F = 20) and 29 older adults (M= 69.30, SD= 6.30; Range= 61-82 years; F= 18; 27 White; two unknown). As before we found no age differences in MoCA scores [t(53.50)= -1.63, p = 0.11] and that older adults had higher Shipley Vocabulary scores [MD = 6.10; t(53.70)= -5.60, p < 0.01] as well as a higher number of years of education than younger adults [MD = 4.10; t(38.90)= -3.45, p < 0.01]. Demographic information for the two participant groups (YA vs. OA) and samples (Original vs. Replication) are provided in Table 1.

Table 1.
Demographic Information

	Original Sample		Replication Sample	
	YA (N=21)	**OA** (N=24)	**YA** (N=31)	**OA** (N=29)
Sex				
Male	5 (23.80%)	11 (45.80%)	10 (32.30%)	11 (37.90%)
Female	16 (76.20%)	13 (54.20%)	21 (64.50%)	18 (62.10%)
Age				
Mean (SD)	20.90 (2.81)	70.30 (5.28)	20.20 (2.96)	69.30 (6.19)
Median	20.00	70.00	19.00	67.50
Min, Max	18, 28	61, 82	18, 27	61, 82
Education				
Mean (SD)	14.90 (2.27)	17.70 (4.51)	13.5 (2.82)	17.60 (5.39)
Median	15.00	17.00	13.00	17.00
Min, Max	11.00, 19.50	10.00, 29.00	15.00, 19.00	18.00, 30.00
Shipley				
Mean (SD)	30.4 (4.31)	35.1 (3.20)	29.00 (3.75)	35.10 (4.55)
Median	31.00	35.00	29.00	36.00
Min, Max	21.00, 38.00	27.00, 39.00	21.00, 36.00	15.00, 40.00
MoCA				
Mean (SD)	27.20 (2.20)	26.50 (2.08)	26.90 (1.79)	27.60 (1.57)
Median	27.00	26.50	27.00	28.00
Min, Max	23.00, 30.00	23.00, 30.00	23.00, 30.00	24.00, 30.00

Note: Group means for the original sample do not include 1 younger adult participant with missing age information. Group means for the replication sample do not include 3 participants (N_{YA} = 2) with missing age information, 3 younger adult participants with missing MoCA and Shipley scores as well as years of education.

Stimuli

The stimulus for both experiments was an 8-minute, shortened version of the black and white movie “Bang! You’re Dead” from the television series Alfred Hitchcock Presents (1961). This movie has been widely used by previous studies probing age differences in cognition (Campbell et al., 2015; Geerligs & Campbell, 2018). The movie was displayed on a 24-inch monitor in 960 x 720 pixels in the original sample and 768 x 576 in the replication sample.

Procedure

For both experiments, the study consisted of two phases: an encoding and a retrieval phase. During the encoding phase, participants were told that the current experiment was interested in individual differences in movie watching and that their job was to pay attention and watch the movie as they normally would. After watching the video, participants completed the retrieval phase in which they were first given a cued-recall task, in which they were presented with 24 short clips from the movie, and they were asked to report what happened in the movie immediately after the clip. All clips were presented in the same temporal order as the movie. Data from this task are not reported here (n.b. there were no age group differences in performance in either experiment; Davis et al., 2021; Henderson & Campbell, 2023). After, participants were asked to freely recall the movie. Here, participants were told to remember and report as many details as they could from the movie they watched and were given unlimited time. Participants’ responses were audio recorded. Only data from the free recall were analyzed in the current study. Data for our original sample were originally collected for a project interested in eye-movements during movie watching (Davis, et al., 2021), and for this reason participants watched the movie with their head in a chin rest to minimize head movement. Data for the replication sample were collected as part of an on-going project using electroencephalogram

(EEG) to measure brain activity, thus participants in this sample watched and remembered the movie wearing an EEG cap, with their head in a chin rest at encoding.

Scoring & Measures

Memory Accuracy and Detail Content

We scored the free recall narratives for different kinds of episodic content participants recalled using a novel scoring technique. Each detail segment was categorized as either a conceptual, perceptual, an event, external or incorrect detail. As noted above, event details describe the unfolding of the story and move the story further (i.e., the what) including actions or happenings in the movie. As these details reflect veridical occurrences from the movie, we counted and compared the number of movie events recalled by younger and older adults to estimate differences in memory accuracy. Specifically, memory accuracy was calculated by dividing the number of unique event details participants remembered by the total events in the movie (N = 101, as defined by the two researchers CF & ED, see Temporal Organization section for more detail on how these events were determined). The other detail types reflect additional inferences or details, and thus, were used to assess for differences in content across the age groups. First, conceptual details were those that can reasonably be inferred from the movie, including inferences about participant's own or the movie character's mental states. Perceptual details were those that described the spatial context in which the events in the movie unfolded, including details about the objects in these contexts. Semantic information as well as repetitions, meta-cognitive and editorial statements were all scored as External details. Finally, details that were incorrectly remembered were scored as Incorrect details. Table 2 summarizes each detail category with examples.

Two scorers blind to the participants' age scored all aspects of the transcriptions (i.e., order of events, detail content). Interrater reliability was calculated for eight randomly selected transcriptions (four younger and four older participants) scored by both scorers. An intraclass correlation (ICC) of 0.91 for total details in the original and 0.99 in the replication samples (k=2, ICC1; Shrout and Fleiss, 1979) demonstrated high agreement between the raters and verified the consistency and reliability of the segmentation as well as the scoring method used (for a breakdown of ICC for each detail subcategory and sample, see Table 2). Our main measure of interest was the proportion of details reported for each category, which was the number of details reported for a given category divided by the total number of details provided. In keeping with previous work, using proportion of details results in an estimate, unbiased by individual differences in verbosity (Levine et al., 2002b; Peters et al., 2019).

Temporal Organization

We scored participants' free recall narratives for the order in which the events in the movie were recalled (see Figure 1). To this aim, we identified the unique events that happened in the movie by taking on a similar approach to previous work by Chen et al. (2017). Each scene in the movie was manually annotated by two researchers (C.F. & E.D.), which included a brief narrative description of what was happening in the scene as well as descriptions of where the action took place, and the names of the characters on the screen (e.g., "In the bedroom, Jackie finds a real gun in a holster in the suitcase."). This procedure resulted in 101 unique annotations for event segments ranging from 1-16 seconds (M= 4.70, SD= 3.01). We also assigned a number to each event segment, denoting when (i.e., order) in the movie the event happened (Chen et al., 2017).

To derive a measure of participants' ability to encode and remember the temporal associations among movie events, we used the lag-conditional response probability (lag-CRP) analysis on each participant's vector of event numbers to measure temporal contiguity effects and a forward recall bias in recall transitions (Kahana, 1996). We measured the probability of transitioning from a recalled event *I* to the following event *I* + 1 given their lag and the events' original order at encoding. The lag refers to the distance between two successively recalled events, and the sign of the lag represents the direction of the transition – with positive lags representing forward and negative lags representing backward transitions. For each lag, the CRP is calculated as the number of transitions a participant made, divided by the number of transitions that were available for them for that event, yielding the probability values that are plotted to obtain the lag-CRP curves.

We additionally, extracted two characteristic features of recalling temporal associations from the lag-CRP curves. First is forward asymmetry, which is participants' tendency to recall events in the forward compared to backward direction (i.e., the conditional probability of recall is higher for positive than negative lags). Second is temporal contiguity, which refers to the fact that events that are viewed closer together in time in the movie have a higher probability of being recalled together – with the conditional probability of recall being higher for closer (e.g., -1 or +1) compared to more distal lags (e.g., -2 or +2).

To visualize the temporal contiguity effects, we used chance-adjusted temporal bias scores, which remove potential confounds from serial position effects that can produce spurious temporal organization (introduced by; Uitvlugt & Healey, 2019). For each participant and lag, temporal bias score is calculated by counting the total number of transitions for that lag (i.e., actual count) and the number of transitions that would have been made if participants were recalling the movie in a random order (i.e., expected count). The expected counts were determined via permutation tests, by randomly shuffling the recall order 100,000 times, calculating the number of expected transitions for each permutation, and calculating the permutation means (Polyn et al., 2011). The temporal bias scores are estimated by subtracting the expected counts from the actual count and dividing by the expected count. Here, scores that are greater than 0 for a given lag indicates that participants made these transitions more often than expected by chance, suggesting that there is a bias for this lag. On the other hand, a score less than 0 indicates transitions occurred less than expected by chance. Higher temporal contiguity effects are indexed by positive temporal bias scores for proximal (e.g., lags +/- 1), and negative temporal bias scores for farther lags (e.g., lags +/- 10). None of the experiments were preregistered.

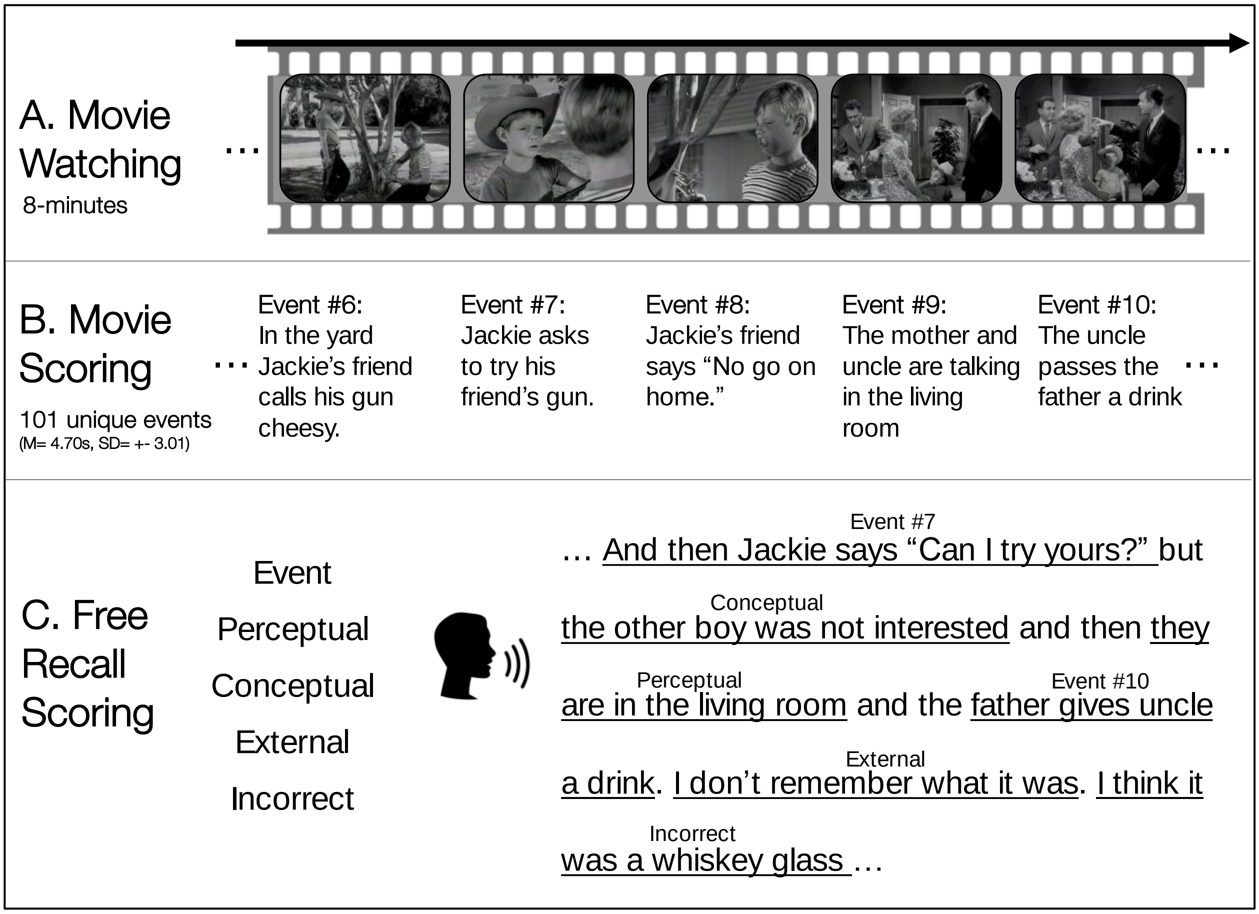


Figure 1. Schematic of how the movie's events were annotated for both experiments (A) participants watched an 8-minute movie. (B) we annotated the movie events using an approach similar to Chen et al., (2017). (C) participants' free recall data were scored for the movie events, noting the order in which they were remembered, other kinds of episodic (i.e., perceptual & conceptual) as well as non-episodic (i.e., external) and incorrectly remembered content.

Table 2.

Description of detail categories with examples and ICC between the raters for each detail category

Detail Category	Definition	Example	$ICC_{original}$	$ICC_{replication}$
Event	Details that describe the unfolding of the story. These move the story further (i.e. what) and are happenings/actions.	"The dad handed the uncle a drink."	0.96	0.99
Perceptual	Details that describe the spatial context in which the events in the movie unfold and sensory perceptual details about the objects in these contexts or the scene in general.	"There were a couple of bullets in the suitcase."	0.93	0.80
Concept	Details that can reasonably be inferred or implied from the movie, yet they were never directly mentioned or shown.	"The mother was worried about her son."	0.88	0.91
External	Non-episodic details that are general knowledge statements, repetitions, metacognitive or editorial statements.	"Drinking was very common in the 60s…"	0.86	0.99
Incorrect	Details in the movie that were remembered incorrectly.	"Jackie was in the kitchen."	0.84	0.80

Results

None of the participants reported having seen the movie. All statistical analyses were conducted using R (version 3.2.2; R Core Team, 2017); intraclass correlations using the ICC function in the *psych* package (version 1.9.12; Revelle, 2017); data visualization using the *ggplot2* package (version 3.1.0; Wickham, 2016); group comparisons using the *rstatix* and *afex* packages [t_test() function; version 0.6.0; Kassambara, 2020; aov_car(); version 0.16-1; Singmann et al., 2016]. For brevity, the results from the original and replication experiments are reported together. We present a summary of descriptives across age groups for measures of temporal organization and content in Table 3.

Memory Accuracy

First, we compared the number verifiable event details participants remembered out of all movie events (N=101) across the age groups. We found no significant group differences in accuracy between the age groups in the original [t(39.29) = 0.30, p = 0.77; M_{YA} = 0.44, SE_{YA} = 0.03; M_{OA} = 0.43, SE_{OA} = 0.02; Cohen's d = 0.09] nor the replication samples [t(57.48) = -0.25, p = 0.81; M_{YA} = 0.42, SE_{YA} = 0.02; M_{OA} = 0.43, SE_{OA} = 0.02; d = -0.06]. These results indicate that younger and older adults showed similar episodic memory performance during recall.

Biases in Episodic Content

We compared the proportion of details for each detail category between the age groups. All comparisons were corrected using the Bonferroni method (alpha/5). We found evidence that younger adults focused on recollecting event details from the movie, such that their recollections contained a higher proportion of event details compared to older adults [t(40.51) = 3.64; $p < 0.01$;]. Older adults were more likely to focus on recollecting conceptual [t(40.70) = -2.49; $p < 0.01$] as well as external details [t(42.61) = -4.65; $p < 0.01$] than younger adults, as both were proportionally higher in the older adult group (Figure 2). Mean differences, confidence intervals and the effect sizes associated with each comparison for the original and replication samples are reported in Table 5. We additionally present age-group comparisons between the raw numbers of details in Appendix Table 1 and mean number of details for each category for each age group and sample in Table 3.

We explored the relation between each episodic detail category (i.e., event, perceptual & conceptual) within each age group using product-moment correlations. A correlation among different detail categories would indicate that generating these details rely on similar cognitive processes and reflect a holistic, gist-based retrieval (Ngo et al., 2020). To increase power for this analysis, we pooled observations from both experiments. In the older adult group, we found significant correlations between all detail categories, namely perceptual and event details [$r = 0.77$, $p < 0.01$], conceptual and event details [$r = 0.55$, $p < 0.01$], and perceptual and conceptual details [$r = 0.29$, $p = 0.04$]. In the younger adult group, the only significant relation was between the perceptual and event details [$r = 0.71$, $p < 0.01$; see Figure 3], suggesting that there are weaker distinctions amongst the processes used to generate different types of details in older than younger adults.

Temporal Organization of Events in Episodic Memory

We explored participants' recall transitions to estimate two measures of temporal associations at retrieval: forward asymmetry bias and temporal contiguity effects. We first tested for potential age differences in forward asymmetry via a 2-way mixed ANOVA on the lag-CRP measures with age group as the between-subjects factor and direction of transition at the closest lags ±1 (forward vs. backward) as a within-subjects factor (for a similar analysis see Jayakumar et al., 2023). We found a significant main effect of direction in both the original [($F(1, 43) =$

220.69, $p < 0.001$] and replication samples [($F(1,58) = 329.81$, $p < 0.001$], suggesting a strong forward asymmetry for both younger and older adults (see Figure 4). No main effect of age group, nor an interaction between the age group and direction emerged [all *p*s > 0.06].

We then assessed potential age differences in the temporal contiguity by conducting a 2-way mixed ANOVA on the lag-CRP measures with age group as the between-subjects factor and closest lags (i.e., lags 1 & 2 or lags -1 & -2) as a within-subjects factor, separately in each direction. We found a significant main effect of lag in the original sample for both the positive [($F(1, 43) = 53.57$, $p < 0.01$] and negative transitions [($F(1,43) = 15.31$, $p < 0.01$], both of which replicated in our replication sample [*positive*: ($F(1,58) = 29.88$, $p < 0.01$; *negative*: ($F(1,58) = 4.49$, $p = 0.04$], indicating temporal contiguity effects in recall, regardless of age group (see Figure 4). In the replication sample, we additionally found a significant age by lag interaction for positive transitions [($F(1,58) = 5.25$, $p = 0.03$]. Post-hoc comparisons revealed that compared to younger adults, older adults had higher lag-CRP values for lag +2 [$t(58) = 2.14$, $p = 0.04$; Estimated $\text{difference}_{\text{OA-YA}} = 0.04$], indicative of weaker temporal contiguity effects in older adults.

Given that serial position effects can introduce spurious temporal contiguity effects and disguise true differences between the age groups, we calculated temporal bias scores, which determine whether the observed level of organization is greater than expected by chance (Mundorf et al., 2021). We present the temporal bias score curves for younger and older adults in Figure 5. In both samples, we found strong temporal contiguity effects for both younger and older adults. That is, temporal bias scores were above 0 for nearby lags and gradually approached 0 (no bias) for farther lags, suggesting that both age groups made transitions to near-lag events more frequently than expected by chance. In addition, the temporal bias scores showed a robust asymmetry for both age groups, with scores peaking at the +1 lag, suggesting that younger and older participants in both samples were more likely to make transitions forward in time than backward in time.

We refrained from performing an ANOVA on the temporal bias scores to compare the near vs. farther lags or positive vs. negative lags since the temporal bias scores in relation to different lags inherently violates the assumption of independence (Howard et al., 2009). In other words, when transitions between certain time lags occur more frequently than expected by chance, it leads to transitions between other time lags happening less frequently than expected by chance (Mundorf et al., 2022). For this reason, we limited our analyses to comparing temporal bias scores between the age groups but not across lags. Specifically, to examine whether the temporal contiguity effects differed between the age groups, we compared temporal bias scores at lag +1, which revealed no age group differences in the original [$t(43) = 0.48$, $p = 0.14$; Mean Difference = 0.15; Cohen's $d = 0.14$] nor the replication samples [$t(58) = -1.06$, $p = 0.29$; Mean Difference = -0.30; Cohen's $d = -0.27$].

Table 3.
Measures of Content and Temporal Organization for the Original and Replication samples.

	Original Sample		Replication Sample	
	YA	**OA**	**YA**	**OA**
Accuracy				
Memory Accuracy	0.44 (0.03)	0.43 (0.02)	0.42 (0.02)	0.43 (0.02)
Detail Content				
Event	53.00 (23.60)	50.10 (18.60)	54.90 (23.90)	55.50 (18.90)
Perceptual	10.70 (5.76)	13.80 (10.40)	10.30 (5.56)	13.10 (8.91)
Conceptual	8.24 (5.28)	15.50 (9.83)	5.97 (4.96)	10.80 (7.38)
External	5.00 (5.69)	11.30 (8.64)	5.32 (4.69)	9.72 (10.10)
Incorrect	8.62 (3.73)	8.42 (3.39)	4.65 (3.02)	5.10 (3.26)
Temporal Organization				
Lag-CRP				
+1	0.32 (0.13)	0.36 (0.11)	0.34 (0.13)	0.30 (0.12)
-1	0.09 (0.06)	0.05 (0.03)	0.04 (0.05)	0.05 (0.04)
+2	0.21 (0.07)	0.21 (0.06)	0.20 (0.08)	0.25 (0.08)
-2	0.04 (0.04)	0.03 (0.03)	0.02 (0.03)	0.03 (0.04)
Temporal Bias Score				
+1	2.96 (1.06)	3.11 (1.30)	3.26 (1.18)	2.97 (0.96)
-1	0.40 (0.34)	0.19 (0.23)	0.11 (0.27)	0.23 (0.29)

Note: Standard deviation is presented in parentheses. Forward asymmetry refers to lag-CRP differences for transitions at the closest lags +1 and -1 (forward vs. backward). Temporal contiguity refers to lag-CRP differences in closest lags for each direction separately (i.e., lags 1 & 2 or lags -1 & -2).

Table 4.
Independent samples t-tests comparing proportion of detail content types between the age groups.

Detail	MD	t	p	df	95% CI	Cohen's *d*
Original Sample						
Concept	-0.05	-2.49	<0.01*	40.70	[-0.09, -0.02]	-0.75
Perceptual	0.00	-0.32	0.75	42.65	[-0.03, 0.02]	-0.10
Event	0.10	3.64	<0.01*	40.51	[0.04, 0.15]	1.09
External	-0.05	-4.65	<0.01*	42.61	[-0.08, -0.03]	-1.40
Incorrect	0.01	0.93	0.36	42.87	[-0.01, 0.04]	0.28
Replication Sample						
Concept	-0.05	-2.82	<0.01*	54.11	[-0.09, -0.02]	-0.73
Perceptual	0.00	-0.04	0.97	55.68	[-0.03, 0.03]	-0.01
Event	0.09	3.00	<0.01*	53.52	[0.04, 0.14]	0.78
External	-0.04	-2.58	<0.01*	53.46	[-0.07, -0.01]	-0.67
Incorrect	0.00	0.94	0.35	55.73	[-0.01, 0.01]	0.24

Note: MD=Mean difference in group means (YA-OA); CI= Confidence Interval; * denotes significant comparisons after Bonferroni correction

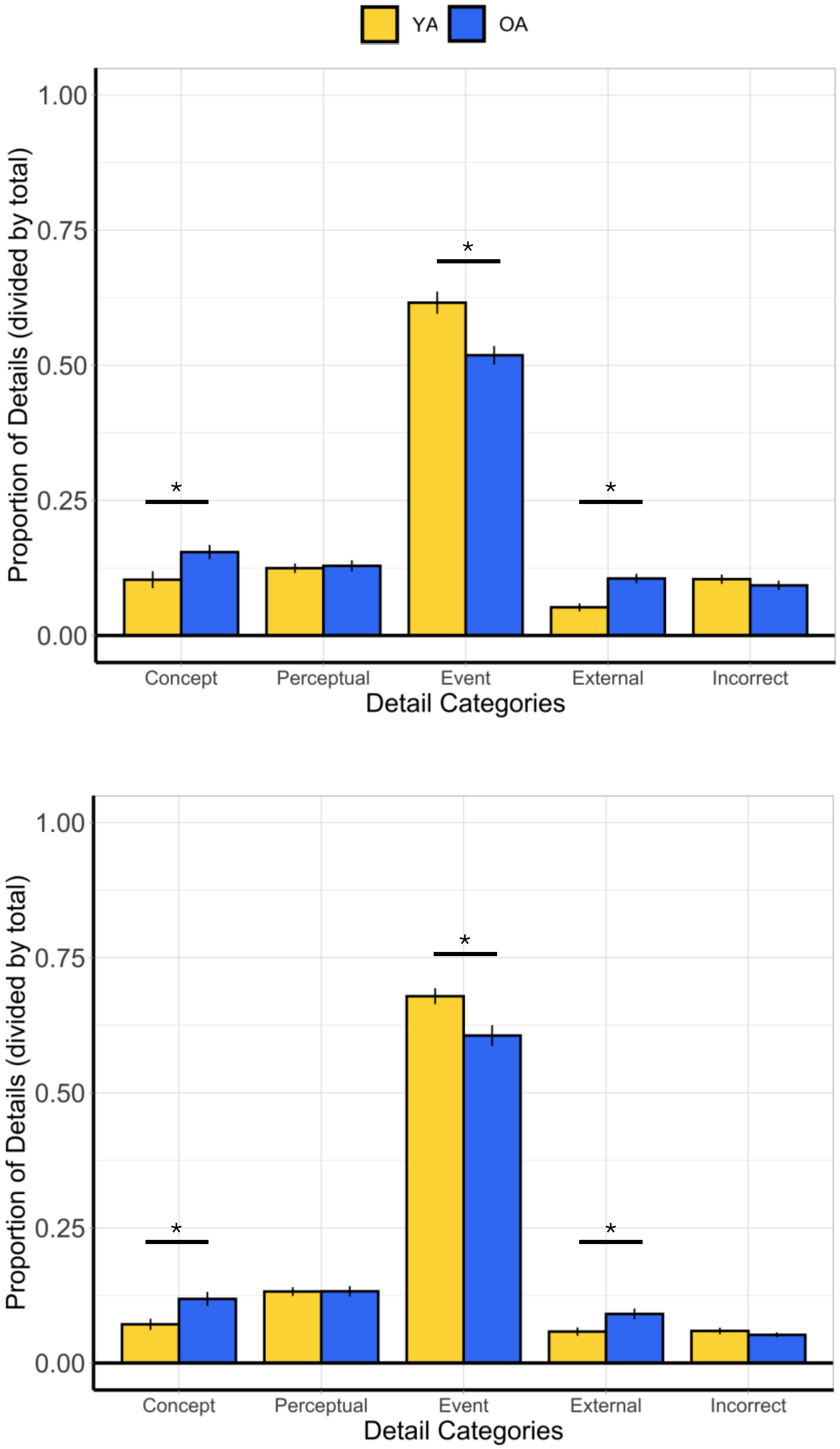


Figure 2. Age group differences in the proportion of details by detail type. Error bars represent standard error of the mean. *denotes significant comparisons after Bonferroni correction. YA = Younger Adults; OA = Older Adults

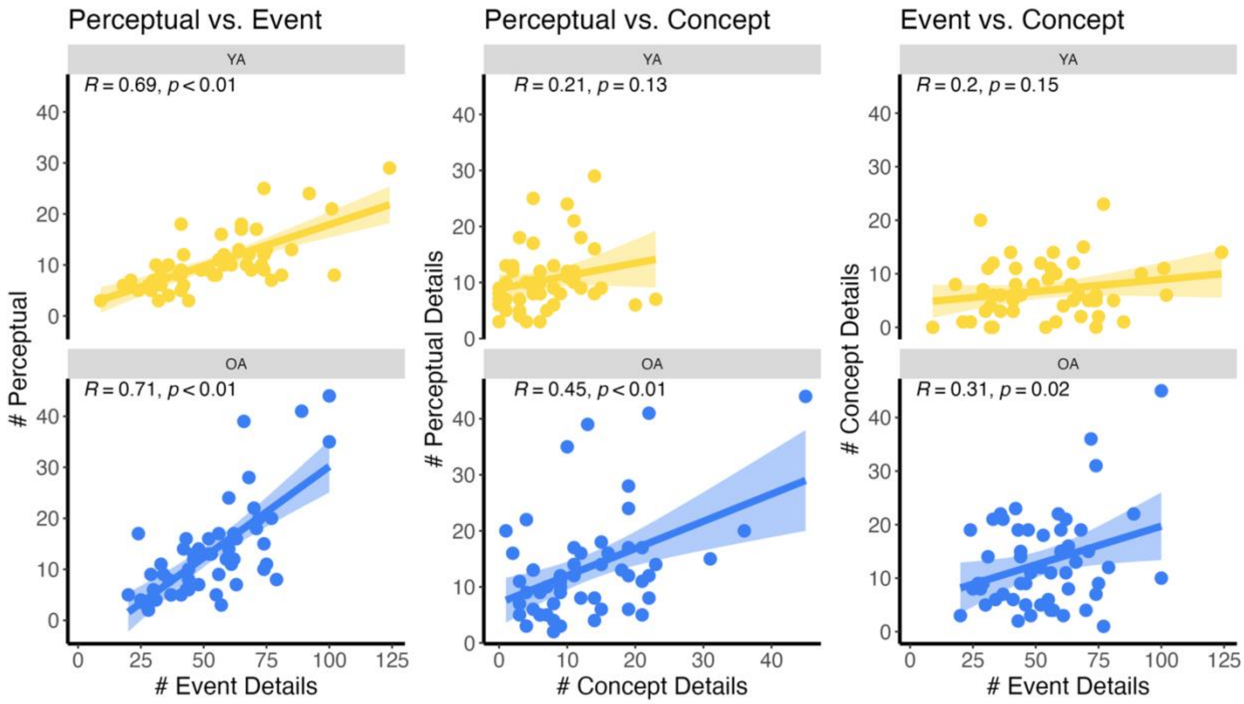
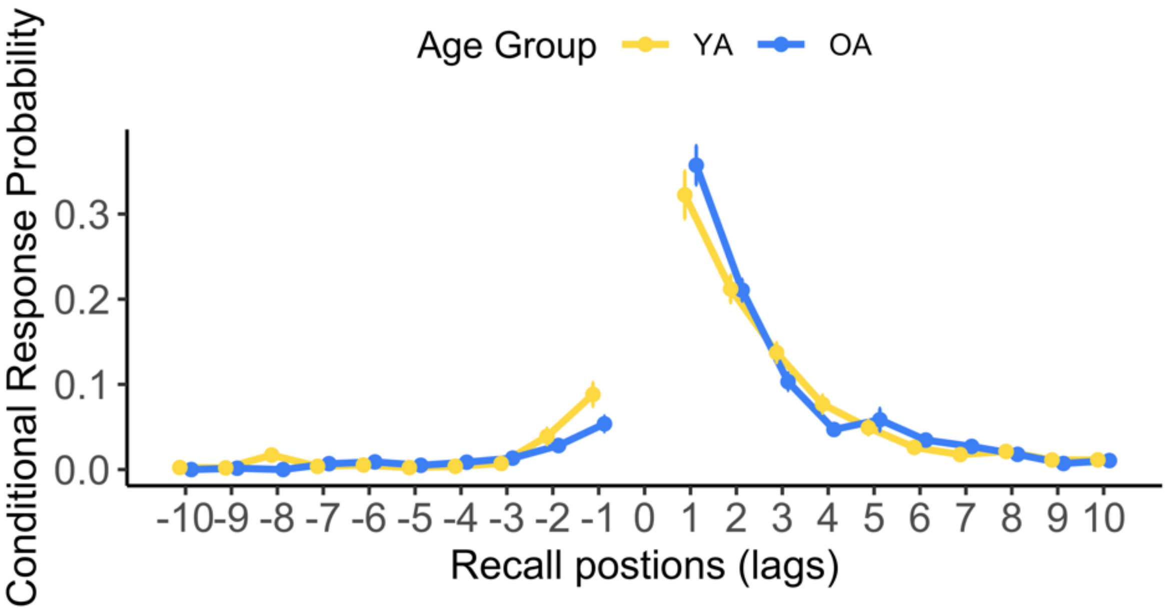


Figure 3. Relationship between episodic detail categories in each age group (younger adults, upper panel; older adults, lower panel). Data from the original and replication samples were combined to increase power.

Original Sample



Replication Sample

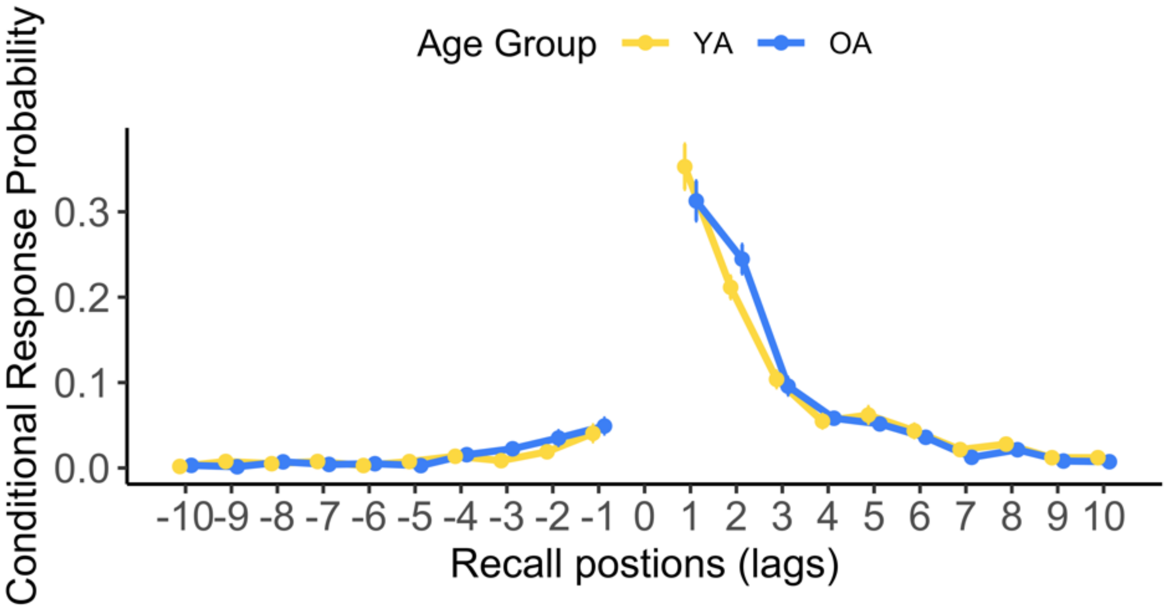


Figure 4. Lag-CRP curves by age group, plotted for the first 10 lags in each direction. No differences were found between the two groups in the forward asymmetry of recall (contrasting lags -1 and +1) nor temporal contiguity (contrasting lags 1 and 2 in each direction). Error bars represent the standard error. YA = Younger Adults; OA = Older Adults

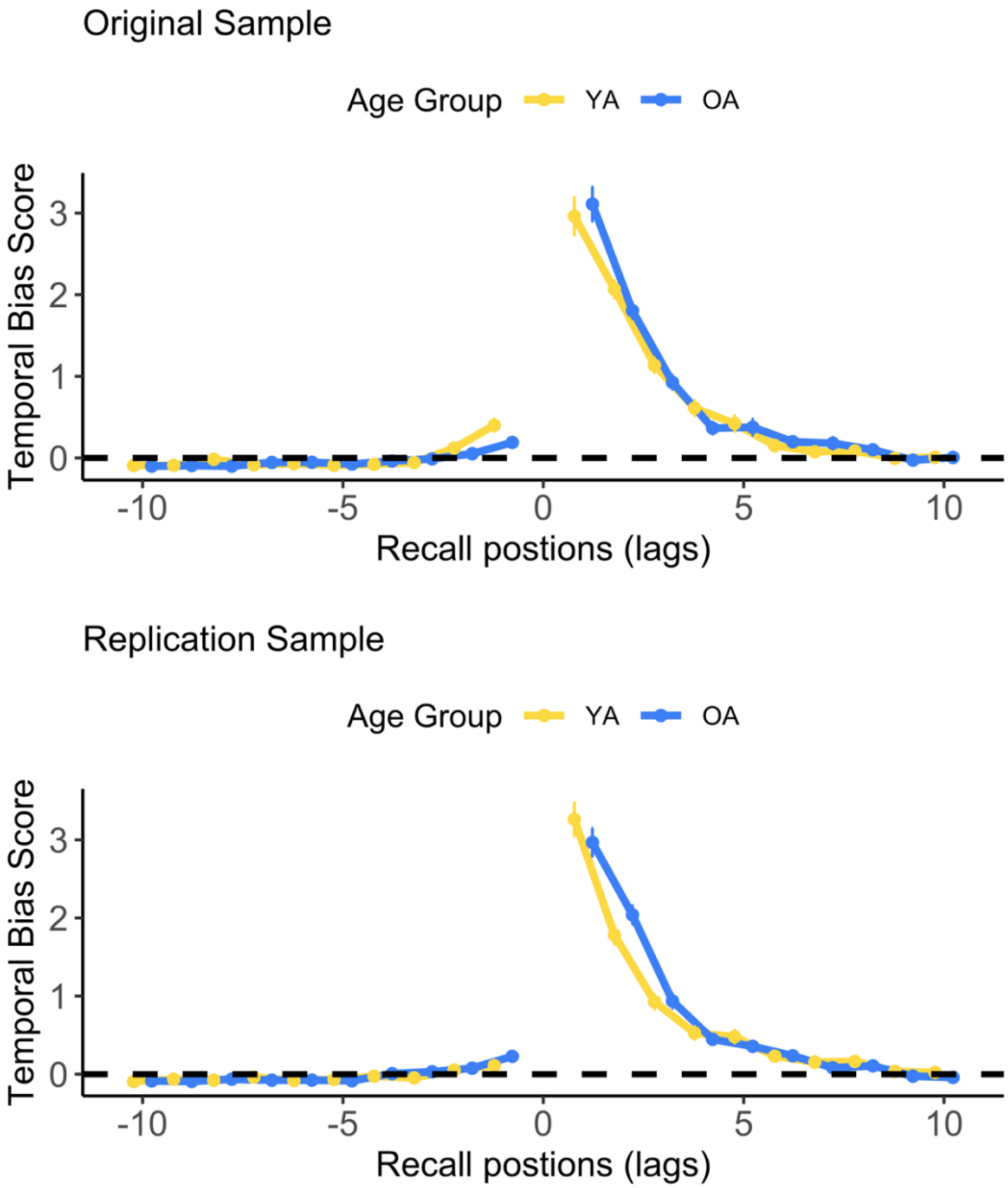


Figure 5. Temporal bias scores from lag = -10 to + 10. We calculated temporal bias scores for each lag by counting the number of times participants made a transition of that lag and the number of times that transition would be expected by chance (i.e., if the participants were recalling the events in a random order). We determined the expected counts by permuting recall order 100,000 times and counting the number of times each lag occurred for each permutation. Temporal bias scores are (actual count – expected count) / expected count. Dotted line represents no bias. Error bars represent the standard error. YA = Younger Adults; OA = Older Adults

Discussion

Real world experiences are complex, allowing the associated memories to be represented and remembered differently (Palombo et al., 2018; Sheldon et al., 2019). This raises an important question for cognitive aging research: Is aging associated with qualitative shifts in how past experiences are represented and remembered? To answer this question, we examined how aging affects the content and organization of memory for complex events, the two basic building blocks of episodic memory (Tulving, 2002). Specifically, we tested the proposal of an age-related shift towards forming gist-based representations of complex events and examined potential differences in the content and temporal organization of recall between younger and older adults. Across two independent datasets, we found that when younger and older participants freely recalled a recently encoded movie clip, younger adults biased their recall towards a higher proportion of event-specific information, whereas older adults' recall was more biased towards conceptual and non-episodic content (i.e., external details). This age-related shift in the content of memory was accompanied by intact memory accuracy and temporal associations among events as we found the groups recalled a similar proportion of event details out of all the details in the movie, our measure of accuracy, and showed patterns and principles of temporal contiguity and forward asymmetry effects for the movie events. Together, these results suggest that not all is lost in aging, but rather younger and older adults form qualitatively different memory representations albeit experiencing the same event.

First, we found that younger and older adults remembered similar proportions of event details out of all the events in the movie. However, we found evidence that each age group prioritized different kinds of content when remembering the movie. In support of older adults' tendency to represent past events at a gist-level, we found that younger adults prioritized specific, event-based information, whereas older adults prioritized conceptual details as well as non-episodic information (Grilli & Sheldon, 2022). In addition, based on recent investigations suggesting that remembering an event at the gist-level results in different event elements becoming dependent in memory (Cooper & Ritchey, 2022; Ngo et al., 2021), we also explored the relationship between the different detail content types for each age group. While we found significant correlations between the different content categories for older adults, for younger adults, significant correlations only emerged between the perceptual and event detail types. This finding supports our interpretation that older but not younger adults spontaneously take on a gist-based approach while remembering given that the generation of different content types become dependent in memory.

When examining participants' ability to encode and retain associations among the movie events, we found that both younger and older adults showed typical features of temporal organization. That is, both age groups showed a bias towards recalling movie events that occurred close together in time (temporal contiguity), with a forward going bias (forward asymmetry), which emerged robustly for all measures of temporal contiguity (e.g., lag-CRP, temporal bias scores) and both in our original and replication samples. This finding aligns with and extends retrieved context models in important ways. Specifically, the temporal contiguity effects in our study emerged in the absence of explicit instructions to encode and recall the sequence of movie events, which parallels the predictions of retrieved context models, considering contiguity effects to emerge from automatic encoding and retrieval processes (Burns, 1996; Healey, 2018; Nairne et al., 2007). In addition, retrieved context models primarily find support from list-learning paradigms, which is extended to the recall of movie events, closely mimicking our experiences in the real-world.

Notably, we did not find evidence for age differences in temporal contiguity effects for the movie events. This finding deviates from those reported in list-learning paradigms, in which forward asymmetry and temporal contiguity effects appear robustly for both age groups, but tend to be stronger for younger than older adults (Diamond & Levine, 2020; Howard et al., 2006; Kahana et al., 2002). We speculate that this deviation speaks to the important qualitative distinction between learning and recalling lists of largely arbitrary, unrelated words and complex events such as movies. Much like our experiences in the real-world, events in a movie are causally and logically linked to another, whereas items in a list are merely linked by their temporal associations. In this way, movies, and narrative stimuli in general, allow for enriched encoding and retrieval opportunities, whereby the constituent events become strongly linked to one another in addition to their chronological ties, and serve as better cues for proceeding events (Cohn-Sheehy et al., 2022; Uitvlugt & Healey, 2019). Thus, one possibility is that older adults' gist-based focus while remembering can supplement deficits in forming temporal associations among movie events with higher level, meaning-based associations and show comparable temporal organization for these events to younger adults.

Although our results point to age-related shifts in how events are assembled in memory, precisely why such shifts occur remains an open question. A popular way to view age-differences in recall is that they are due to episodic memory deficits in the older adult group (Naveh-Benjamin et al., 2007; Piolino et al., 2010). This interpretation is unlikely, given that we did not observe age-differences in the ability to accurately recall event details from the movie, and found comparable patterns of temporal contiguity and forward asymmetry between the age groups. In fact, our results more closely align with the idea that older adults form gist-based memories to offset for episodic memory deficits (Reuter-Lorenz & Cappell, 2008).

Another explanation for the qualitative shifts we observed is the motivational differences between younger and older adults (Carstensen & Turk-Charles, 1994; Grilli & Sheldon, 2022; Ryan & Campbell, 2021; Samanez-Larkin & Carstensen, 2011). To this point, previous work has noted that relative to younger adults, older adults are motivated more by socially oriented goals while remembering the past than younger adults and differences in retrieval goals have been linked to differences in retrieved content from episodic memories (Hess, 2005). For example, in recent study with young adults, taking on social retrieval goals resulted in reduced number of event-specific details compared to goals that stress accurate retrieval of the past (Dutemple & Sheldon, 2022). This finding aligns with the recall pattern we observed in the older adult group, suggesting that social retrieval goals adopted by older adults might lead to a bias towards meaning-based, evaluative content, akin to the conceptual detail category in our study. Future work can more directly examine whether shifting retrieval goals can shift the content of memories in older adults.

Finally, another possibility is that the reported age-differences are due to how a memory is encoded. Recent theories have suggested that age-related reductions in cognitive control and inhibitory mechanisms lead older adults to store too much information in memory (Arbuckle & Gold, 1993; Campbell et al., 2010) and these cluttered memory representations might force older adults to represent and retrieve events at the gist level (Amer et al., 2022). Whether age-related differences in memory emerge at recall or encoding are not mutually exclusive, however future work may disentangle what aspects of qualitative shifts towards gist-based representations (i.e., organization and content) are preferentially the result of encoding or retrieval changes.

Conclusion

To conclude, our findings provide critical insight into age effects on recalling complex events and show qualitative distinctions in how younger and older adults assemble the details of past experiences. We show that older adults’ tendency to form gist-based representations shifts content of their episodic memory and that these qualitative shifts emerge in the absence of episodic memory deficits (e.g., memory accuracy) or age differences in temporal organization. Overall, our findings align with recent theoretical frameworks to suggest that rather than a deficit, age-related focus on gist-based representations are better characterized as qualitative shifts in how an individual represents and remembers the past (Grilli & Sheldon, 2022).

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Declaration of Interest Statement

The authors report no conflict of interest.

Data Availability Statement

De-identified data, analytic code, and stimulus information for the Original and Replication samples are available at the Open Science Framework (OSF; https://osf.io/jq438/). The stimulus used is under copyright and cannot be shared. For this reason, we have included a document with event annotations, time stamps, and event numbers in the link above. Given that open ended responses contained potentially identifying information, we only provide the scored data. All statistical analyses were conducted using R (version 3.2.2; R Core Team, 2017) and required packages for each analysis are listed in the Results section, including each package's version number. Neither the study design nor the analytic plans were pre-registered.

Appendix

Appendix Table 1.

Independent samples t-tests comparing episodic detail type between the two groups.

Detail	MD	t	p	df	95% CI
			Original Sample		
Concept	-7.26	-3.14	0.00	36.15	[-11.96,-2.57]
Perceptual	-3.08	-1.25	0.22	36.77	[-8.08,1.91]
Event	2.88	0.45	0.66	37.94	[-10.09,15.84]
External	-6.29	-2.92	0.01	40.12	[-10.65,-1.93]
Incorrect	0.20	0.19	0.85	40.78	[-1.96,2.36]
			Replication Sample		
Concept	-6.05	-3.66	0.00	54.11	[-9.4,-2.7]
Perceptual	-3.10	-1.45	0.15	55.68	[-7.4,1.2]
Event	-1.30	-0.22	0.83	53.52	[-13.33,10.72]
External	-5.28	-2.38	0.02	53.46	[-9.78,-0.77]
Incorrect	-1.06	-1.26	0.21	55.73	[-2.74,0.63]

Note: MD=Mean difference in group means (YA-OA); CI= Confidence Interval; * denotes significant comparisons according to Bonferroni-corrected p-values

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Bridge to Chapter 3

In Chapter 2, I examined whether younger and older adults remember the movie differently, focusing on the content, organization, and accuracy of recall. In two independent datasets, I found that younger and older adults recalled different kinds of content from the movie, but older age did not affect the organization nor accuracy of their recall. Specifically, younger adults recalled a greater proportion of event-specific information, whereas older adults' recall contained more conceptual and non-episodic content than younger adults. The recall content shifts align with the age-related functional shifts observed in Chapter 1 and suggest that older adults' gist-based bias is reflected in the content they recollect from the movie.

Recent theoretical frameworks suggest that the specific-to-gist shift in older adults' memory, and the resulting changes in recall content, are partly due to motivational shifts that accompany aging (i.e., why younger and older adults remember). That is, older adults are increasingly motivated by retrieval goals that prioritize maintaining social relationships, to inform and entertain other more than younger adults. As a result, when remembering, older adults take on an integrated approach, which manifests as age differences in the content recollected from past experiences. In light of this framework, in Chapter 3, I examined whether the content differences I observed in Chapter 2 are in part driven by age-related retrieval goal shifts. Specifically, I examined whether and how different retrieval goals (accuracy vs. social) influence the content recalled by younger and older adults. I hypothesized that if retrieval goals drive age-related differences in content, then when younger and older adults recall information with the same goal in mind, their recalled content should be similar.

Chapter 3: The impact of retrieval goals on memory for complex events in younger and older adults

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Abstract

Retrieval goals influence what individuals remember from past experiences. Previous research has demonstrated that adopting accuracy and social goals modify the content of an associated episodic memory. Age-related episodic memory changes coincide with shifts in retrieval goals, leading to questions about how retrieval goals alter memory in the context of aging. To answer these questions, we conducted a between-group experiment in which younger and older participants (N = 120) encoded an audiovisual movie and later recalled it with either an accuracy or social retrieval goal. Following a 24-hour delay, participants completed two recognition memory tasks—one assessing memory for narrative (i.e., story structure) and another for the perceptual aspects of the movie. Using a Natural Language Processing model, we compared the similarity in content between the encoded movie and recollections. We found higher similarity for participants recalling the movie with an accuracy compared to a social goal, but no difference across younger and older adults. Examining content similarity between the memories retrieved for accuracy and social goals revealed that older adults showed higher recall similarity between these goals than younger adults. Finally, we found that younger adults outperformed older adults in both recognition tasks, but this effect was more robust for the perceptual than the narrative recognition memory task. These findings suggest that aligning retrieval goals removes age-related differences in recall, but age differences persist as a reduced ability to tune recall to retrieval goals and access precise details from a memory.

Key words: *episodic memory, aging, free recall, natural language processing*

Introduction

In our daily lives, we remember our past experiences for a number of different reasons (Bluck, 2003; Bluck et al., 2005; Bluck & Alea, 2009; Marsh & Tversky, 2004). For example, while chatting with a new acquaintance, you might remember and share a recently attended birthday party, in order to foster a social bond with that person (social goals; Alea & Bluck, 2003). On another occasion, you might remember the same experience but this time to inform and guide your planning of an upcoming birthday party (i.e., directive goals; Bluck et al., 2005; Pillemer, 2003). However, not all aspects of the birthday party will be relevant to these different retrieval goals. For example, recalling and sharing the emotional aspects of that birthday party (e.g., "I was very excited to enter my favorite restaurant.") may be effective to meet a social goal, but less so when using that memory to plan for your next party. On the other hand, recalling the numerous precise details from the party (e.g., "The restaurant had 5 tables in total.") may not be as useful to serve social goals but will be instrumental in guiding your planning.

This example illustrates an important feature of our episodic memory system, which is to prioritize the aspects of a past experience relevant for a given retrieval goal (Elward & Rugg, 2015; Rugg, 2004; Rugg et al., 2000; Srokova et al., 2021). In fact, several studies have shown that memory content shifts as a function of our retrieval goals, with many of these studies comparing two critical functions of retrieval —to be accurate or for social/entertainment purposes (Dudukovic et al., 2004; Dutemple & Sheldon, 2022; Marsh & Tversky, 2004; Pasupathi & Oldroyd, 2015; Tversky & Marsh, 2000). A common finding is that recollections made for accuracy goals result in greater emphasis on reproducing precise, event-specific details, whereas remembering for socially oriented goals lead to more elaborative, reconstructed recollections, and those that deviate from the originally encoded event (Dudukovic et al., 2004;

Dutemple & Sheldon, 2022). For example, in one study, two groups of younger adults encoded a story and after a delay remembered it with either an accuracy goal, stressing the precise and veridical recall of the story or a social goal, describing the story from memory as if they were socializing with their friend group (Dutemple & Sheldon, 2022). Compared to those remembered with an accuracy goal, social retrieval goals reduced the number of event-specific details recalled and increased the number of elaborative, additional details. Similarly, in another study, participants encoded a story and later, retold it from memory to entertain (i.e., socially oriented) or to be accurate (Wade & Clark, 1993). Participants showed better alignment with the story when instructed to be accurate than entertaining. Together, these studies indicate that accuracy and social retrieval goals shape the content of memory.

A less investigated consequence of retrieval goals is on the subsequent memory, particularly when these goals are implemented shortly after encoding (Hupbach et al., 2007; Dudai & Eisenberg, 2004). According to consolidation theory, episodic memories are labile during the post-encoding period, after which they are consolidated, becoming stable representations (Hupbach et al., 2007; McGaugh, 2000). During this period, recently learned memories are reactivated and replayed by hippocampally mediated episodic memory processes to stabilize the learned event (Axmacher et al., 2008; Carr et al., 2011). This suggests that recounting a recently encoded event for a particular goal (e.g., social or accuracy) may bias the consolidation of content relevant to the goal, potentially leading to “retroactive” forgetting of the goal irrelevant content (Lechner et al., 1999). In support of this possibility, Dutemple and Sheldon (2022) examined how narratives, initially recollected with accuracy and social goals, were recalled after a critical 24-hour consolidation period. They found that participants who initially remembered the narrative with social retrieval goals (i.e., with fewer specific details) showed a significant reduction in the ability to generate specific details when probed to recall the story with accuracy goal after 24-hours (Dutemple & Sheldon, 2022). In another study, when participants described a previously watched video to the police (i.e., stressing accuracy goals), they emphasized video-specific details during recall, whereas participants describing the video to their friends (i.e., stressing social goals) focused on their emotional reactions. After a short, 25-minute delay, those who recalled the video with socially oriented goals committed a greater number of memory errors (i.e., false alarms) when recalling the entire video (Marsh et al., 2005). These results and others (Dudukovic et al., 2004) suggest that accuracy and social retrieval goals pose distinct consequences for subsequent memory, particularly the precision with which these events are recollected. That is, accuracy goals result in more precise memory representations (i.e., fewer added details) than social goals.

Understanding the role of retrieval goals in shaping episodic memory is especially relevant to cognitive aging. This is because a large body of work has shown that episodic memory declines with age, presenting as impaired ability to encode and retrieve specific details from everyday events (Dennis, Kim, et al., 2008; Kensinger & Schacter, 1999; Naveh-Benjamin, 2000). However, some more recent views propose that age-related changes in how events are recollected might in part be due to changes in retrieval goals that accompany aging (Grilli & Sheldon, 2022b). This proposal emerges from a large body of work, which has pointed to shifts from accuracy-oriented goals in younger age to socially oriented, emotion regulation goals in older adulthood (Carstensen & Turk-Charles, 1994; Mather & Carstensen, 2005; Samanez-Larkin & Carstensen, 2011; Scheibe & Carstensen, 2010). For example, studies have shown that when younger adults remember past experiences to direct future behaviour and to create self-continuity, older adults predominantly remember autobiographical memories to forge and maintain social bonds (Bluck & Alea, 2009). In support, a parallel line of work has shown that older adults tend to remember past events through an integrative lens, sharing their past experiences to teach/inform as well as entertain others, more than younger adults (Demiray et al., 2019; Hess, 2005; Webster, 1995). Together, these studies suggest that older adults predominantly recall past experiences with socially oriented retrieval goals, which might manifest as age differences in the content recollected from past experiences.

Even if age differences in episodic memory content can be partly explained by a shift away from accuracy and towards socially oriented goals, it remains unclear if aging alters the ability to tune recollections to retrieval goals. While some work suggests that retrieval goals modulate episodic memory similarly for younger and older adults (Adams et al., 2002; Mair et al., 2024), other work has shown that older adults present with reduced distinctiveness in recollections across different retrieval goals compared to younger adults (Ford et al., 2014; Srokova et al., 2021). For example, in one study, younger and older participants remembered autobiographical memories under different instructions, requiring them to recall memories that were specific (single event that occurred over minutes or hours), general (events that extend beyond a single day), or without explicit instructions (Ford et al., 2014). Comparing the recall content between the age groups and instruction conditions revealed that younger adults modified how they recollected the memories depending on the task instructions, whereas older adults showed similar patterns of recall across the different instructions (also see Melega et al., 2024; Strikwerda-Brown et al., 2021).

As well, it remains unknown whether retrieval goals near the time of encoding an event affects subsequent memory similarly in these age groups. Evidence thus far suggests that accuracy and social goals pose distinct mnemonic consequences for younger and older adults.

For example, Barber and Mather (2014) instructed younger and older adults to recall a previously learned story either with an accuracy goal, remembering the story in a precise manner, or with an entertainment goal, suitable for a group of friends (Barber & Mather, 2014). In both age groups, stories recalled with entertainment goals contained fewer story-specific details. However, the impact of retrieval goals on subsequent recall performance was observed only among older adults. That is, older adults recalling the story with an entertainment goal had worse memory performance during a subsequent free recall task compared to the accuracy group (Barber & Mather, 2014), suggesting that when implemented shortly after encoding, retrieval goals affect older but not younger adults' subsequent memory.

Another open question is whether the potential effects of retrieval goals on younger and older adults' subsequent episodic memory is similar for different kinds of memory content. According to Fuzzy-Trace Theory, episodic memories can be based on verbatim and gist-based traces —with the latter including an event's general meaning and happenings, yet lacking perceptual details (Brainerd & Reyna, 1990, 2002, 2002). Given that older age is associated with loss of verbatim but relative preservation of gist-representations (Brainerd & Reyna, 1990; Castel, 2005a; Flores et al., 2017; Gallo et al., 2019; Grilli & Sheldon, 2022b; Koutstaal & Schacter, 1997), in the current study, we examined retrieval goal effects on younger and older adults' subsequent memory for narrative and perceptual details.

1.1. Current Study

In the current study, we conducted a two-day experiment in which younger and older adults encoded and then recalled a short movie for either an accuracy and social retrieval goal (Day 1) and then completed recognition memory tests (Day 2). This design tested the following questions: (1) Do different retrieval goals change the content of an encoded event for younger and older adults? and (2) How does aging affect the ability to access narrative and perceptual details from an encoded event, subsequently recalled for different goals?

With respect to retrieval goal effects, we predicted accuracy and social retrieval goals to prioritize different aspects of the encoded movie. First, memories retrieved for accuracy goals will include more event-specific details and be more similar to the encoded material than those recollected for social goals. Second, memories recollected for accuracy goals should be more similar to one another, compared to those recollected with social goals, given that social goals have been associated with the production of more "asides" or elaborative details than memories recalled for an accuracy goal (Barber & Mather, 2014; Dudukovic et al., 2004; Dutemple & Sheldon, 2022). With respect to age effects, we reasoned that if the previously reported shifts in memory content in older age are driven by the prioritization of distinct retrieval goals, then younger and older adults should perform similarly when recalling an event with the same retrieval goals. As well, if older adults are less able to orient their recollections as a function of retrieval goals, then the recall content between the different goals should be more similar for older than younger adults. Finally, if retrieval goals affect what is included in the memory trace for older but not younger adults' memories, then older adults in the social goal condition should perform worse in the recognition tests than those in the accuracy goal condition.

Methods

1.1. Participants

One hundred and thirty-two participants were recruited to participate in the experiment. Older adults were compensated 20$ for their participation. Younger adults were recruited from SONA Undergraduate Participant Pool. All participants had normal or corrected-to-normal vision, were free of any medical or neurological conditions, and had English as their dominant language. All experimental procedures were approved by the Office of Research Ethics and written informed consent was collected from all participants prior to testing.

After excluding participants who did not complete both days (N=2; N_{YA}=1), recording malfunction (N_{OA}=2), or scoring less than 23 on the Montreal Cognitive Assessment (N_{OA} = 1; MoCA; Nasreddine et al., 2005), the final sample included 64 younger (M= 20.50, SD= 2.33; Range= 18-28 years; F = 35) and 63 older adults (M= 72.40, SD= 6.55; Range= 65-87 years; F = 49). Notably, there were no significant differences in participants' scores on the MoCA [t(124)= -1.93, p = 0.06], and as expected, older participants had more years of education [t(124)= 2.30, p = 0.02] than younger adults. Participants in each age group were pseudo-randomly assigned to different retrieval goal groups, with odd-numbered participants being assigned to accuracy goal, even numbered participants to social goal group. Demographic information for the sample is provided in Table 1. De-identified data are available at the Open Science Framework (OSF: https://osf.io/2vmbd/?view_only=9803509736414c8ab85f3e67ffa40b4e).

Table 1.

Demographic Information

Sample	**Younger Adults**		**Older Adults**	
Retrieval Goal	**Accuracy** (N=32)	**Social** (N=31)	**Accuracy** (N=32)	**Social** (N=31)
Gender				
Male	18 (56.30%)	17 (53.10%)	29 (90.60%)	20 (64.50%)
Female	14 (43.80%)	13 (40.60%)	3 (9.40%)	11 (35.50%)
Other	0 (0%)	1 (3.10%)	0 (0%)	0 (0%)
Age				
Mean (SD)	20.30 (2.28)	20.60 (2.40)	70.60 (6.74)	74.30 (5.83)
Median	20.00	20.00	71.00	73.50
Min, Max	[18.00, 28.00]	[18.00, 26.00]	[55.00, 82.00]	[62.00, 87.00]
Education				
Mean (SD)	14.9 (2.22)	15.0 (2.62)	16.8 (3.72)	18.1 (11.3)
Median	15.0	15.0	16.0	17.0
Min, Max	[11.00, 23.00]	[7.00, 22.00]	[10.00, 23.00]	[11.00, 26.00]
MoCA				
Mean (SD)	26.50 (2.78)	27.50 (1.68)	26.30 (2.10)	26.10 (2.31)
Median	27.00	28.00	26.00	26.00
Min, Max	[25.00, 30.00]	[25.00, 30.00]	[23.00, 30.00]	[23.00, 30.00]

Note: Group means for younger adults do not include 1 participant with missing education and Gender information.

1.2. Materials

All participants watched an 8-minute, shortened version of “Bang! You’re Dead”, which is a black-and-white audiovisual movie from the television series Alfred Hitchcock Presents (1961). This movie clip is commonly used in previous studies examining age-related changes in cognition (Campbell et al., 2015; Fenerci et al., 2024; Henderson & Campbell, 2023; Shafto et al., 2014). The movie was displayed on a 24-inch monitor in 960 x 720 pixels. All participants were naïve to the movie.

Recognition memory tasks were programmed and administered using PsychoPy (v2021.1.4; Peirce et al., 2019). To create trials for the narrative recognition memory task, 75 true and 75 false statements were created about the narrative elements of the movie. The statements were brief descriptions of things that happened in the movie. The true statements depicted moments from the encoded movie (e.g., “Jackie’s dad tells him to unpack Uncle Rick’s suitcase), whereas false statements were created by altering the narrative elements (e.g., “Jackie’s uncle tells him to unpack his suitcase”). Trials for the perceptual recognition memory task included 36 screenshots from the 8-minute version of the movie (i.e., target images) and 36 screenshots from the full-length movie, not including the scenes from the 8-minute version, which served as lures. The lure images were perceptually similar to the target images and involved the same characters as well as spatial contexts from the full 27-minute version of the movie yet were not shown to the participants as part of the 8-minute, shortened version. Screenshots were extracted from the full-length movie with Python 3.7.4 using the OpenCV library.

1.3. Experimental Procedure

The experiment was conducted over two days, which were 24-hours apart. Day 1 involved an encoding and initial recall phase, while Day 2 involved two recognition memory tasks as well as an additional recall phase.

In Day 1, participants watched the movie clip. They were instructed to remain attentive and alert as they would be asked questions about the movie later. After a 5-minute filled delay, participants were asked to recall the movie according to their assigned retrieval goals. Instructions for the different retrieval goals were adapted from previous work examining retrieval goal differences in episodic memory content in younger adults (Dudukovic et al., 2004; Dutemple & Sheldon, 2022). Briefly, participants in the accuracy goal group were told to remember the movie in a precise manner, describing it exactly as they watched it and as close as possible to the original events. Instead, participants in the social goal group were told to imagine themselves surrounded by their friend group and describe the movie in this context, as if they were socializing with their friends (please see Appendix for the task instructions). Participants' responses were audio recorded.

In Day 2, all participants completed two recognition memory tasks based on narrative and perceptual details of the movie. In the narrative recognition task, participants were presented with either the true or false version of 75 statements, depicting things that happened in the movie. On each trial, participants decided whether the statement was true or false via button press. For the perceptual recognition task, across 36 trials, participants viewed target and lure images side by side and were asked to click on the image that they think was from the movie. The order of the narrative and perceptual recognition tasks was fixed across participants such that all participants completed the narrative recognition task first, followed by the perceptual recognition task in order to prevent intrusions from the perceptual to the narrative task. The recognition tasks were followed by a free recall task in which participants in both retrieval goal groups recalled the movie with an accuracy goal, responses for which were audio recorded (n.b., data from this free recall task is not analyzed in the current study). Schematic of the experimental procedure is depicted in Figure 1.1.

1.4. Data Preparation

All recordings were transcribed using an automated transcription tool (Rev AI; https://www.rev.ai/). The accuracy of the automated transcriptions was verified by the researchers who reviewed the transcriptions for errors by comparing them to the audio recordings of the recall.

1.5.Measures

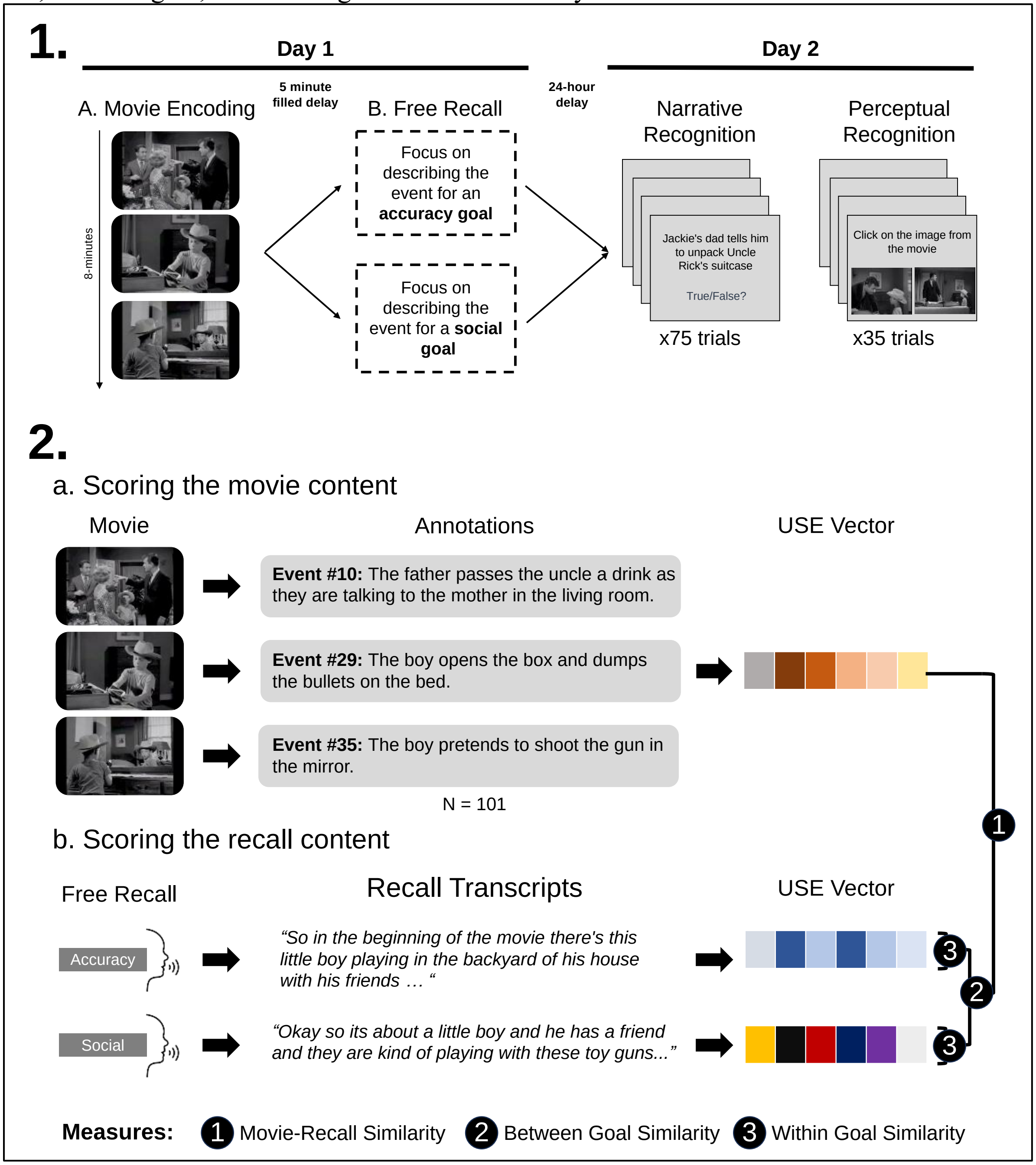
1.5.1. Memory Content

We scored the recall transcripts using a previously generated list of event annotations as a scoring template (Fenerci et al., 2023). Briefly, these annotations were written descriptions of what was happening in each scene of the movie as well as descriptions of where the events took place and the names of the characters involved in the scene (e.g., "*The boy thanks his uncle for the surprise.*"; for a similar procedure, see Chen et al., 2017). This procedure produced 101 unique event annotations (M = 4.70 seconds; Range = 1 —16 seconds). To score participants' recollections of movie events, we first segmented participants' narrative recalls into unique event details, which described the unfolding of the story, moved the story further, and captured the happenings/actions in the movie. We then scored each event detail against the event annotation list and calculated hits as the proportion of recollected movie events by dividing the number of unique event details participants remembered (i.e., matched to the events in the annotation list) by the total events in the movie (N = 101). We refer to this measure as recall hits from hereon.

Our main analysis was to use an automated approach to probe participants' memory content (illustrated in Figure 1.2.a). Prior to implementing this approach, we preprocessed the text data. First, each recall transcript was parsed into individual words (i.e., tokens), which were then labeled with a parts-of-speech (POS; e.g., noun, adjective, verb, etc.) tags using the Natural Language Toolkit (NLTK; Bird et al., 2009). Following, the recall transcripts were filtered for tokens with 2 or fewer letters (e.g., "by", "a") as well as function words (i.e., adpositions, determiners, and coordinating conjunctions), which signal grammatical relationships rather than carrying a lexical meaning in a sentence. After text preprocessing, each participant's recall was encoded into high dimensional vectors using Google's Universal Sentence Encoder (USE; Cer et al., 2018). USE is a natural language processing model that converts text into 512 dimensional, numerical vectors. USE is trained and optimized for greater-than-word length text, including paragraphs, which enabled us to obtain one 512-dimensional vector for each participant's recall. This model has been previously to embed descriptions of movie events (Lee & Chen, 2022; Sava-Segal et al., 2023) and validated for producing accurate representations of narrative memory for both younger and older adults (Shen et al., 2023). Finally, event annotations, previously generated for the movie were used to encode the movie events into the same high dimensional space as participants' recall. Then, the above-described preprocessing was applied to the movie annotations —such that the annotations were first concatenated into the same document, tokenized, 2 or fewer letter tokens along with function words were filtered. The preprocessed event annotations were transformed into a high dimensional vector via USE.

From these data, we derived three measures to test our predictions (see Figure 1.2.b.). First, we examined the content that was shared between the movie and participants' recall by calculating the cosine similarity between each participant's recall vector and the vector encoding movie event annotations. Cosine similarity is the cosine angle between two vectors, and it is calculated as the dot product of the vectors divided by the product of their Euclidean magnitudes. Here, higher values indicate greater content similarity between participant's recall and the movie, reflecting greater accuracy (for a similar method, see Houser et al., 2022). Second, we examined the similarity amongst the participants' recollections by computing cosine similarity between each participant's recall vectors and constructing a one subject-by-subject similarity matrix where each cell was the cosine distance between two participants' recalls ($N_{participants}$ x $N_{participants}$). For each participant, we then computed two types of recall similarity: (1) average recall similarity with all the other participants in their retrieval goal and age group (e.g., YA_{Acc} x YA_{Acc}; hereon *within* goal similarity) and (2) average recall similarity with all the participants in the other retrieval goal, but the same age group (e.g., YA_{Acc} x YA_{Soc}; hereon *between* goal similarity).

Figure 1. 1. Schematic of the experimental procedure. On Day 1, all participants encoded a short movie and after a brief delay recalled it with either accuracy or social retrieval goals. 24-hours later, all participants completed recognition memory tasks assessing their memory accuracy for the narrative and perceptual details of the movie. 2. Scoring the (a) movie and (b) recall content. (a) Each scene in the movie was assigned a brief annotation describing what was happening in the scene. These annotations were concatenated and transformed into a high dimensional vector via USE. (b) Scoring the recall content. Participants' recalls were transcribed and transformed into a 512-dimensional vector via USE. From these data, three measures were created, movie-recall, between goal, and within goal content similarity.



1.5.2 Recognition Memory Performance

For the narrative recognition memory task, we calculated two separate measures of memory performance: 1.) Hits: proportion of true statements that were correctly identified as true [i.e., p(True|TRUE)]; 2.) Narrative false alarms: proportion of false statements, which were erroneously endorsed as true [i.e., p(True|FALSE)]. For the perceptual recognition memory task, memory performance was scored as the proportion of trials in which participants correctly selected the target image from the movie.

1.6. Statistical Analysis

First, we compared the event specific details between the age and retrieval goal groups by conducting a linear regression on the recall hits (i.e., proportion of verifiable event details participants remembered out of all 101 movie events) with the age group (younger, older) and retrieval goal (accuracy, social) as independent variables.

Next, we examined age and retrieval goal effects on memory content. We conducted a linear regression, predicting fisher-z-transformed cosine similarity values between participants' recall and the movie. This model included the age group (younger, older) and retrieval goal (accuracy, social) as independent variables, and word counts for participants' free recall as a covariate to control for the length of the recall transcripts, which is known to impact embedding computation (Cer et al., 2018).

To examine the age effects on the overlap in content for memories recalled with different retrieval goals, we conducted a linear regression analysis on the fisher-z-transformed cosine similarity values with age (younger, older) and goal comparison (within-accuracy, within-social, and between) as the independent variables with a covariate for free recall word count. Prior to model fitting, we centered and scaled the word count covariate by 2 standard deviations (Gelman, 2008) and specified between group similarity (i.e., ACC-SOC) as the reference level.

Finally, to examine age and retrieval goal effects of recognition memory performance after the 24-hour delay, we conducted separate analyses of variance for the narrative hits and false alarms with the age group (younger, older) and retrieval goal (accuracy, social) as independent variables. For the perceptual recognition task, we used the same model structure but with the memory accuracy as the dependent variable.

Results

Memory Content

First, we examined the proportion of recollected events from the event annotations between the age and retrieval goal groups. We found a significant main effect of retrieval goals [β = -0.18, $t(120.00) = -5.30$, $p < 0.01$]—such that participants in the accuracy condition recalled a greater proportion of verifiable event details than those in the social goal condition [Estimated Marginal Means $(EMM)_{ACC} = 0.43$; $EMM_{SOC} = 0.19$; $EMM_{Difference} = 0.24$; see Figure 2.a.]. While we found a significant interaction between age and retrieval goal groups [β = -0.12, $t(120.00) = -2.52$, $p = 0.01$], post-hoc comparisons with Tukey correction for multiple comparisons revealed differences between the retrieval goal groups were comparable between the age groups [accuracy goal group: $t(120) = -0.06$, $p = 0.26$; social goals group: $t(120) = 0.31$, $p = 0.31$].

Next, we examined the effect of age and retrieval goal groups on the USE-derived measures of content similarity between the event annotations and participants' recollections. Confirming the above presented results, we found a significant main effect of retrieval goals [β = -0.17, $t(117.00) = -3.26$, $p < 0.01$]—with both younger and older participants in the accuracy group showing significantly higher movie-recall similarity than those in the social group (see Figure 2.b.). We did not find a main effect of age group nor an interaction between age and retrieval goal groups (all *p*s > 0.23), suggesting that when given the same retrieval goals younger and older adults recall the encoded movies with the same levels of content similarity to the encoded movie.

Next, we examined retrieval goal effects on the content recollected from the movie for younger and older adults by comparing content similarity for memories retrieved for accuracy goals, social goals, and between these goal conditions (reference level). We found a significant main effect of age group [$ß = -0.15$, $t(241.00) = -5.23$, $p < 0.01$] indicating that older adults showed greater between group similarity than younger adults. In addition, we found a significant main effect of goal group —such that within group similarity in the accuracy goal group was higher than between goal similarity for both younger and older adults [$ß = 0.23$, $t(241.00) = 6.42$, $p < 0.01$]. In addition, we found a significant interaction between age and goal groups —with older adults showing greater between compared to within group similarity than younger adults for both accuracy [$ß = 0.21$, $t(241.00) = 4.21$, $p < 0.01$] and social goals [$ß = 0.17$, $t(241.00) = 3.39$, $p < 0.01$]. Results of the linear regression models are presented in Table 2.

Table 2.

Results of the linear regression models, predicting memory content measures

Predictors	*ß*	*SE*	*95% CI*	*t-value*	*df*	*p*
Recall Hits						
(Intercept)	0.39	0.02	[0.35 —0.44]	16.22	120	**<0.01**
Age Group	0.06	0.03	[-0.01 —0.13]	1.83	120	0.07
Retrieval Goal	-0.18	0.03	[-0.25 —-0.11]	-5.30	120	**<0.01**
Age Group * Retrieval Goal	-0.12	0.05	[-0.21 —-0.03]	-2.52	120	**0.01**
Movie-Recall Similarity						
(Intercept)	0.67	0.04	[0.60 —0.74]	18.43	119	**<0.01**
Age Group	0.05	0.05	[-0.04 —0.15]	1.09	119	0.28
Retrieval Goal	-0.17	0.05	[-0.27 —-0.07]	-3.24	119	**<0.01**
Word Count	0.34	0.04	[0.25 —0.42]	8.03	119	**<0.01**
Age Group * Retrieval Goal	-0.09	0.07	[-0.23 —0.05]	-1.27	119	0.20
Subject-Subject Recall Similarity						
(Intercept)	0.63	0.02	0.59 —0.67	31.02	241	**<0.01**
Age Group	-0.15	0.03	-0.20 —-0.09	-5.23	241	**<0.01**
Within ACC	0.23	0.04	0.16 —0.30	6.42	241	**<0.01**
Within SOC	0.00	0.04	-0.07 —0.07	0.1	241	0.92
Word Count	0.11	0.02	0.07 —0.16	5.16	241	**<0.01**
Age Group * Within ACC	0.21	0.05	0.11 —0.31	4.21	241	**<0.01**
Age Group * Within SOC	0.17	0.05	0.07 —0.26	3.39	241	**<0.01**

Note: SE = Standard Error, CI=Confidence Interval; Word Count variable was centered and scaled by 2 standard deviations prior to model fitting. In the model with Subject-Subject Recall Similarity as the dependent variable, between group similarity was specified as the reference level.

Figure 2

Age and retrieval goal effects on a) Recall Hits, which is the proportion of verifiable event details participants remembered from the movie and b) Movie-Recall Content Similarity, which is the content similarity between the movie and participants' recall.

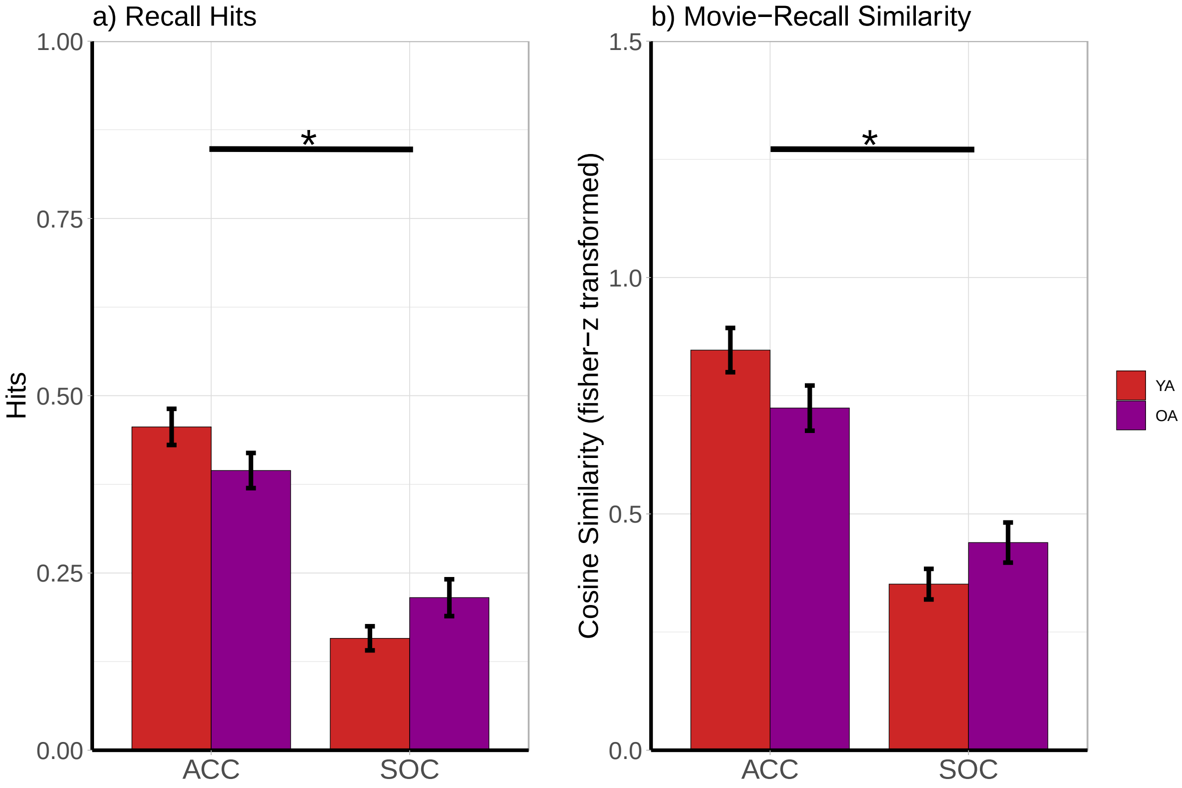
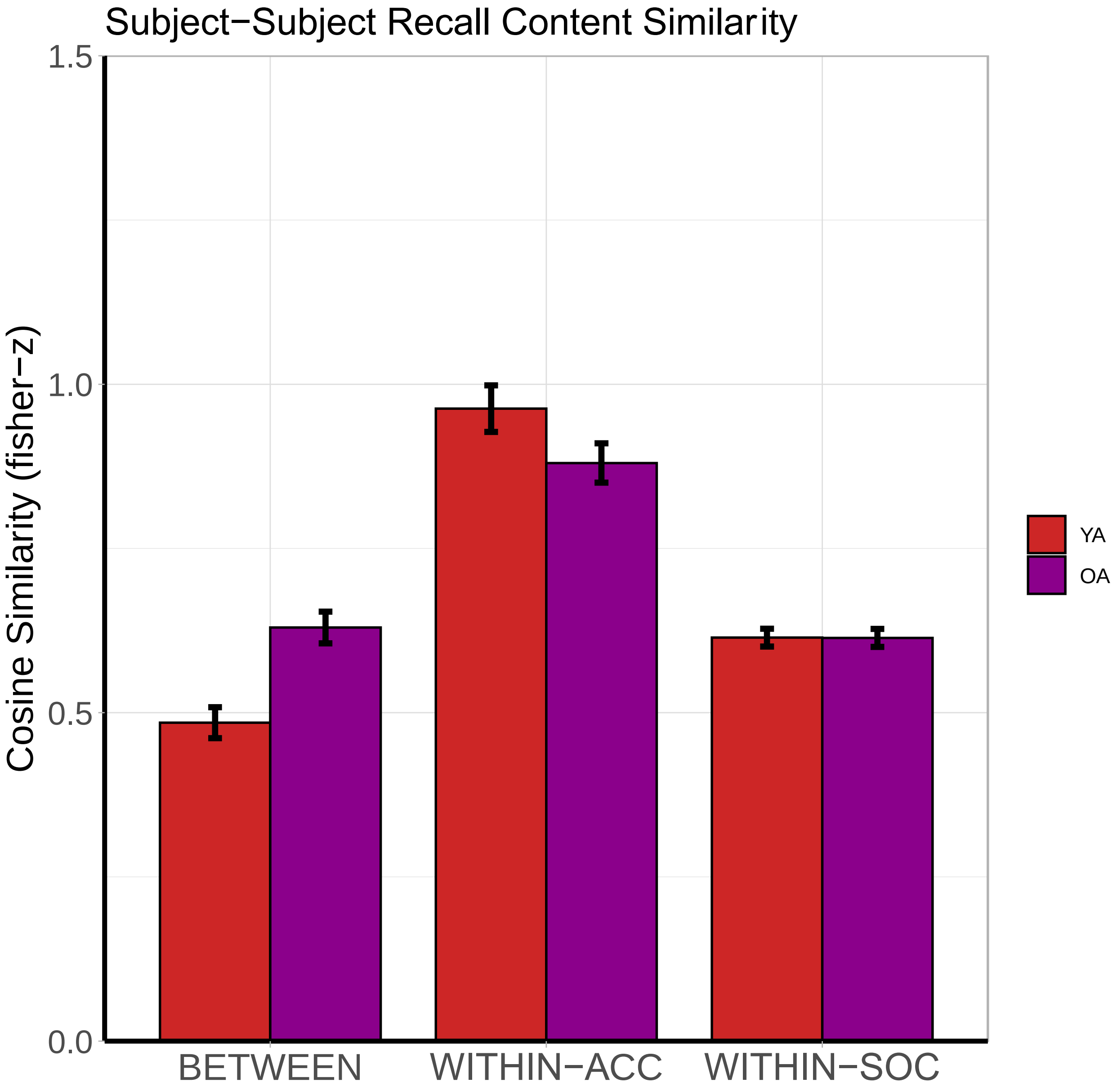


Figure 3

Age and retrieval goal effects on subject-subject recall content similarity for subjects in the same retrieval group (calculated separately for Accuracy and Social retrieval goal groups) and between the retrieval goal groups (Accuracy-Social).



Recognition Memory Performance

Next, we assessed whether there was a difference in the ability to later recognize narrative or perceptual content from the movie across the retrieval goal and age groups. For the recognition memory task probing narrative content, we found no significant effects of retrieval goals nor age group on the hits (all ps > 0.1), suggesting that neither age nor retrieval goals affect correctly identifying true information from the encoded movie (Figure 4.a.). However, there was a significant effect of age group on false alarms [$F(1,120)=5.73$; $p < 0.05$] —with older adults showing greater false alarm rates than younger across goal conditions ($EMM_{YA} = 0.37$; $EMM_{OA} = 0.43$; see Figure 4.b). We also found a significant main effect of age on accuracy for the perceptual recognition memory task, [$F(1,120)= 28.62$; $p < 0.01$]. Regardless of the retrieval goal condition, younger adults had greater perceptual recognition memory than older adults [$EMM_{YA} = 0.82$; $EMM_{OA} =0.72$; see Figure 4.c.]. No other significant effects emerged (all *p*s > 0.52). Results of the ANOVAs are provided in Table 3.

Finally, we compared the age effects on recognition memory tasks between the test domains (narrative vs. perceptual). To this end, we calculated an overall accuracy score for the narrative recognition task by combining the proportion of hits and correct rejections. We fit a linear mixed effects model with recognition memory accuracy as the dependent variable and age group (younger vs. older), goal group (accuracy vs. social), task (narrative vs. perceptual) and the interaction between age group and task as fixed effects, with a by-participant random intercept. We found a main effect of age group [$\beta = 0.05$, $t(228.00) = 3.07$, $p < 0.01$], task [$\beta = 0.09$, $t(122.00) = 6.07$, $p < 0.01$]. Post-hoc tests with Tukey correction for multiple comparisons revealed that younger adults outperformed older adults across both tasks and retrieval goal groups [$t(121)=-5.62$, $p < 0.001$, $MD_{OA-YA} = -0.07$] and that both younger and older adults had lower memory accuracy for the perceptual, compared to the narrative recognition task, regardless of goal group [t(122)=-11.00, $p < 0.001$, $MD_{\text{Narrative-Perceptual}} = -0.11$]. Importantly, we found an interaction between age group and task [$\beta = 0.04$, $t(122.00) = 2.25$, $p < 0.05$] such that age effects on memory accuracy was greater for perceptual compared to the narrative recognition task.

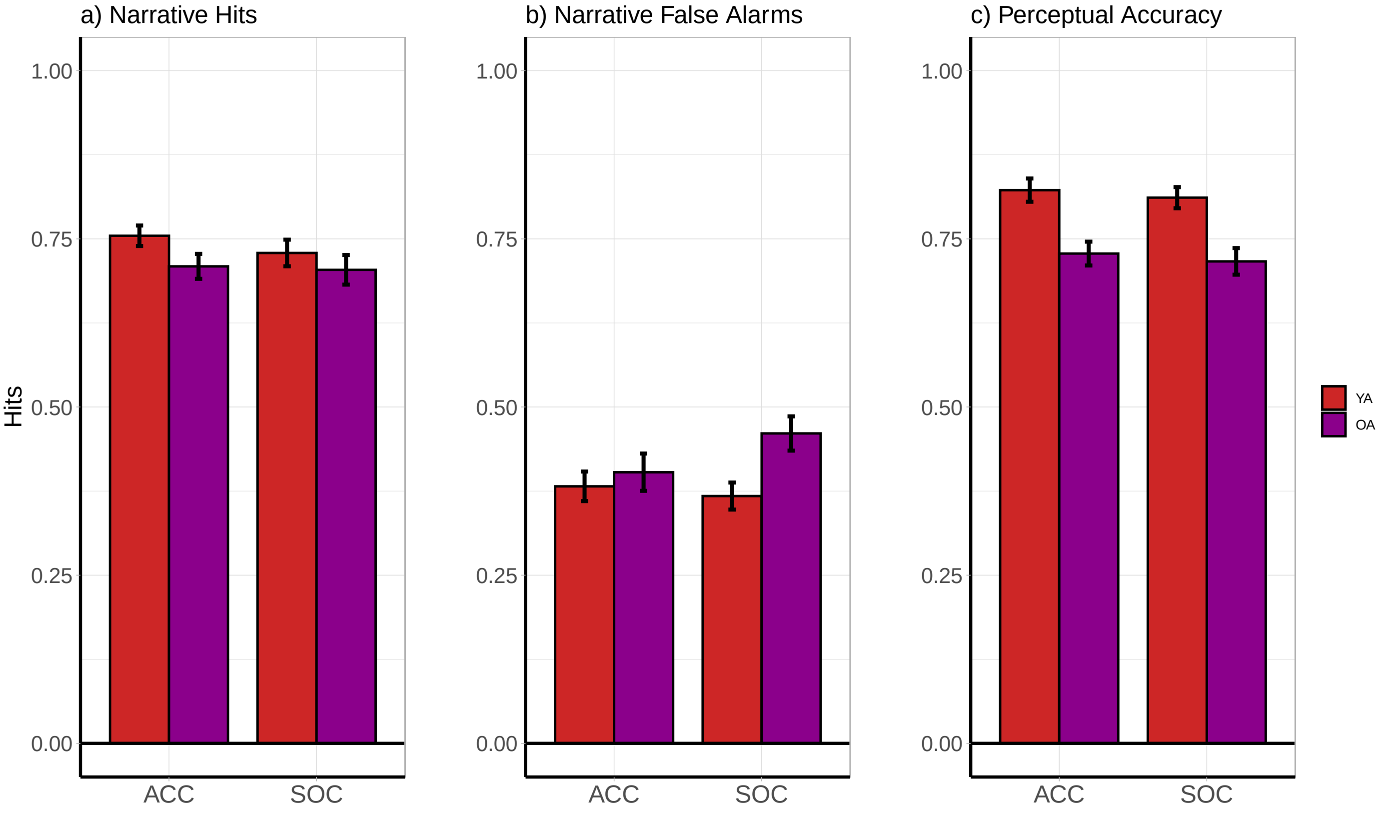
Table 3.
Memory performance for the narrative and perceptual recognition tasks as a function of age group and retrieval goal condition.

Predictors	*df*	*F*	*GES*	*p*
Narrative Recognition				
Hits				
Age Group	1,120	3.45	0.03	0.10
Retrieval Goal	1,120	0.65	0.01	0.42
Age Group * Retrieval Goal	1,120	0.29	0.02	0.59
False Alarms				
Age Group	1, 120	5.73	0.05	**<0.05**
Retrieval Goal	1, 120	0.82	0.01	0.37
Age Group * Retrieval Goal	1, 120	2.29	0.02	0.13
Perceptual Recognition				
Accuracy				
Age Group	1, 120	28.62	0.20	**<0.01**
Retrieval Goal	1, 120	0.42	0.00	0.52
Age Group * Retrieval Goal	1, 120	0.02	0.00	0.99

Note: GES = Generalized Eta Squared as a measure of effect size.

Figure 4

Age and retrieval goal effects on recognition memory performance after a 24-hour delay for Narrative (panels a & b) and Perceptual recognition tasks (panel c).



Discussion

We remember our past experiences in service of various goals (i.e., directive, social; Alea & Bluck, 2003; Bluck, 2003; Bluck et al., 2005), yet the effects of these goals on episodic memory are largely unknown. Understanding how retrieval goals affect episodic memory is especially relevant for cognitive aging research as aging is associated with parallel changes in episodic memory ability and goals that motivate remembering (Grilli & Sheldon, 2022b; Hess, 2005). In the current study, we examined the effect of accuracy (i.e., describing the event in a precise manner) and social retrieval goals (i.e., describing the event as if socializing with friends) on the recall content for younger and older adults. Additionally, we assessed whether retrieval goals, implemented shortly after encoding, affect subsequent memory for these age groups. To these ends, younger and older participants encoded a short movie and remembered it with either accuracy or social retrieval goals. After 24-hours, participants completed recognition memory tests, assessing their memory performance for narrative and perceptual information. We found that both younger and older adults showed greater recall content overlap with the encoded movie in the accuracy compared to the social group. As well, memories retrieved for different goals were more similar for older than younger adults. Finally, regardless of retrieval goals, younger adults outperformed older adults in the recognition memory tasks, especially when memory was tested for perceptual information. Overall, these results suggest that shifting the retrieval goals for recollecting an event affects recall content similarly for younger and older adults, but older age impacts both the ability to tune recollections towards these goals and the precision of the underlying memory trace.

1.6. Retrieval goals but not age affect recall content

Our first finding was that when recalling events with similar retrieval goals, younger and older adults describe events with similar reflections of the encoded events. Previous work that examined how younger and older adults describe past personal experiences (i.e., autobiographical memories) differently has found that older adults tend to describe these experiences with fewer event-specific (i.e., episodic) details but with more non-episodic content, particularly those that convey semantic knowledge (Levine et al., 2002a; Piolino et al., 2009, 2010; St. Jacques & Levine, 2007). This well-reported pattern is taken as reflecting episodic memory decline that is a hallmark of cognitive aging (Nyberg, Backman, et al., 1996; Simpson et al., 2023) —showcasing older adults' inability to remember specific details and the increased number of non-episodic details compensating for this decline (Devitt et al., 2017). However, a parallel line of work has attributed this pattern in part, to other changes that accompany older age, such as changes in retrieval/communicative goals adopted by older adults (Bluck et al., 1999; Bluck et al., 2016; Trunk & Abrams, 2009; Grilli & Sheldon, 2023). That is, differently from younger adults, older adults increasingly adopt retrieval goals that prioritize forming social bonds and reflect on the past, which manifests as age differences in the recollected content (Bluck & Alea, 2008; Demiray et al., 2019; Hess, 2005). Based on this work, we reasoned that if age differences in recall content emerges from distinct retrieval goals adopted by younger and older adults, then retrieving events with similar retrieval goals should result in similar recalled content. Our findings support this hypothesis and show that retrieval goals similarly shape the content younger and older adults recall from a past event.

1.7. Older adults' recollections are less distinct across different retrieval goals

Even though our initial set of results suggest that age differences in episodic memory content are largely due to age-related shifts in retrieval goals, we found evidence that older adults are less effective in tuning their recall to different retrieval goals than younger adults. Specifically, when comparing recall content similarity within and between the retrieval goals, we found that older adults showed greater content similarity between the different retrieval goals compared to younger adults. This finding dovetails with a long line of research showing that episodic memories become less distinct in older age (Koen & Rugg, 2019; Melega et al., 2024; Srokova et al., 2021; Strikwerda-Brown et al., 2021). For example, in one study, younger and older adults encoded words superimposed on different scene images and these word-image pairs were presented in one of three locations of the screen (Srokova et al., 2021). After a delay, participants were required to remember either the scene image, paired with the word or the location of the word-image pairs on the screen (i.e., different retrieval goals). The results showed that younger adults selectively reinstated scene information only when required to remember the scene image but not the location on the screen, whereas older adults reinstated this information irrespective of their retrieval goals, even when it was not relevant. Similarly, in Strikwerda-Brown et al., (2021), younger and older participants completed various narrative tasks requiring them to either describe past personal experiences, describe a picture, or describe any information the comes to their mind in relation to a presented image (Strikwerda-Brown et al., 2021). The results showed that younger adults modulated the number of event-specific details they reported across the different narrative tasks, whereas older adults' descriptions were more similar across these tasks (also see: Ford et al., 2014; Melega et al., 2024).

The reduced distinctiveness of memories in older age is couched in support of age-related deficits in cognitive control (Amer et al., 2016; Hasher et al., 1991). For example, a large body of work has shown that older adults are unable to inhibit distracting or off-target information (Hasher et al., 1997; Hasher & Campbell, 2020; Lustig et al., 2007). As a consequence, older adults integrate more goal-irrelevant details into their memories, resulting in less differentiated, "cluttered" memory representations across different goals (Amer et al., 2016, 2022b). In addition, previous work has shown deficits in domain-general cognitive control processes in older age, which are crucial for monitoring and maintaining ongoing goals (Braver et al., 2002; J. D. Cohen et al., 1997). Thus, a non-mutually exclusive possibility is that older adults are unable to continuously monitor ongoing task goals (i.e., accuracy and social), which converges how memories are recollected across these retrieval goals (Daigneault & Braun, 1993; Paxton et al., 2008; Salthouse, 1990). Future research should examine whether the observed similarity in recall content between the retrieval goals in older adults relates to cognitive control abilities.

1.8. Age but not retrieval goals determine the content of the underlying memory trace

We found evidence that retrieval goals near the time of encoding an event do not affect subsequent memory, rather, older age determines what content is accessible to participants. First, our results showed that neither age nor retrieval goal group affected hits (i.e., correctly identified target statements). However, older adults showed heightened false alarms to narrative lures and reduced accuracy for perceptual details after the 24-hour delay, regardless of their initial retrieval goals. The relative preservation of target recognition, accompanied by an increase in false alarms to lures in older age dovetails findings from a large body of work (Delarazan et al., 2023; Koutstaal & Schacter, 1997; Norman & Schacter, 1997; S. M. Stark et al., 2013, 2015). This pattern is commonly interpreted as older adults' tendency to form gist-based representations, capturing the meaning and core aspects of an experience rather than specific representations, which reproduce the precise, high fidelity details of that experience (Castel, 2005; Flores et al., 2017; Gallo et al., 2019; Greene et al., 2022; Greene & Naveh-Benjamin, 2023; Grilli &

Sheldon, 2022). Thus, even though relying on gist-based representations are sufficient to correctly identify target information, they additionally lead to erroneous endorsement of related, unseen lures (Devitt & Schacter, 2016).

In our study, retrieval goals did not affect subsequent memory for younger nor older adults. One possibility for this finding could be that the fate of the memory trace is determined by goals at the time of encoding rather than retrieval. In support of this possibility, previous work has shown that in younger adults, different encoding instructions lead to differences subsequent memory performance (Garcia-Bajos et al., 2014). Thus, an important future avenue is to manipulate goals prior to encoding and examine the downstream effects on subsequent memory. Our finding also deviates from previous work showing that accuracy and social retrieval goals, when implemented shortly after encoding, have dissociable mnemonic consequences for older but not younger adults (Barber & Mather, 2014). One possibility for this discrepancy could be due to the different methods used to probe participants' subsequent memory. That is, previous work has predominantly used free recall paradigms to assess episodic memory, which raises the possibility that participants simply omitted details rather than these details being forgotten or removed from the memory trace. As well, it could be that instead of recalling the original event, participants remembered and re-described their recollections of this event, which manifested as distinctions in subsequent memory given the initial differences in memory content. In this way, recall paradigms are limited in determining what content becomes part of the memory trace —a limitation that is addressed in our study by employing recognition memory tasks, which probed for specific narrative and perceptual details from the encoded event.

Our work advances previous findings in important ways. To begin, subsequent memory effects are commonly tested following short delays (e.g., minutes to hours), which does not allow for sleep-dependent consolidation, known to affect episodic memory (Diekelmann & Born, 2010). To this end, we administered the recognition memory tasks following a critical 24-hour period, allowing for sleep dependent consolidation. In addition, we tested subsequent memory for different kinds of content from the movie, namely, narrative and perceptual details. This choice was based on previous work showing that episodic memory for perceptual details are forgotten at a much faster rate than narrative details (e.g., “He took a bite of his sandwich.”; Sekeres et al., 2016), suggesting that retrieval goal effects might not be uniform across these detail categories. In addition, there is evidence to suggest that age differences in memory emerge for perceptual but to a lesser extent for narrative details of an event (Delarazan et al., 2023). In fact, in line with this work, our results showed that age differences were stronger for perceptual, compared to the narrative task.

2. Conclusion

In the current study, we examined the effect of accuracy and social retrieval goals on how younger and older adults recollect complex events. We found that for both age groups, retrieving an event for an accuracy goal resulted in greater production of event-specific details, greater alignment between the recalled and encoded content, and reduced subjectivity (i.e., more factual) than memories retrieved for social goals. However, our results showed that age group but not retrieval goals determined subsequent memory after a 24-hour delay. Specifically, regardless of initial retrieval goals, older adults committed a higher rate of false alarms to narrative lures and showed reduced perceptual accuracy. Together, our results suggest that previously reported age-related differences in memory content can in part, be explained by age-related distinctions in retrieval goals, yet retrieval goal differences are insufficient to explain what content becomes part of younger and older adults’ memories.

Statements and Declarations / Compliance with Ethical Standards

Ethical Approval: All experimental procedures were approved by the Office of Research Ethics.

Competing interests: The authors have no relevant financial or non-financial interests to disclose.

Author's contributions: C.F.: Conceptualization, Methodology, Data Collection, Formal Analysis, Visualization, Validation, Software, Writing-Reviewing and Editing. S.O.: Data Collection, Data Curation, Validation. E.R.: Data Collection, Data Curation, Validation. K.S.: Software. S.S.: Writing-Reviewing and Editing, Conceptualization, Supervision, Resources, Funding Acquisition

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Trial Registration Number (TRN): N/A

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Appendix

Task Instructions

Accuracy Retrieval Goal Group:

"I would like you to close your eyes and imagine the movie you watched earlier. Now, I would like you to retell this story in a precise manner. It is very important that you describe the movie exactly as you watched it, as close to the original movie. So be as accurate as you can. Tell me how you remember this movie as if you were trying to tell someone exactly what happened, what the scenes looked like, almost like you are narrating a script of the movie. It is important to keep this goal of remembering in mind."

Social Retrieval Goal Group:

"I would like you to close your eyes and imagine the movie you watched earlier. Now, I want you to imagine a scenario in which you would talk about this movie like it was a memory. I want you to imagine you are surrounded by your friends. You are comfortable and relaxed. One of your friends asks you to tell everyone about the movie. Tell me how you would describe this movie in this situation. You don't need to tell me the movie as it occurred but tell me how you would talk about the story when socializing with your friends. It is important to keep this goal of remembering in mind. You may want to imagine yourself as a storyteller with your friends."

Narrative Recognition Task:

"In this experiment you will see statements related to the video you watched. Your job is to decide whether each statement is True or False. You will first read the statement carefully, and press the 1 if you think the statement is TRUE, and the 2 if you think it is FALSE. The task is self-paced, so you may take as long as you like to remember and answer each question. Do you have any questions before we begin?"

Perceptual Recognition Task:

"In this experiment you will be presented with two images side by side. One of these images will be from the video you watched. The other image will be one you haven't seen. Your job is to select the image from the video by clicking on it. You will first view both images carefully, and using the mouse CLICK on the image you think is from the video. The task is self-paced, so you may take as long as you like to remember and answer each question."

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General Discussion

Older adults favor the gist over the specific details of past experiences. This is thought to emerge from functional brain changes as well as motivational shifts that accompany aging. To understand age-related episodic memory shifts in in real world settings, the experiments presented in this dissertation examined younger and older adults' episodic memory for complex events at the neural, behavioural, and motivational levels of inquiry. Findings from the current experiments provide evidence that aging shifts the neural and behavioural correlates of episodic memory for complex events, which might in part be due to age-related motivational shifts in why events are remembered. Specifically, I find that older adults increasingly rely on brain regions that process and form gist-based representations during encoding. In turn, during retrieval, their memories contain greater coarse-level, conceptual content. While retrieval goals alter how older adults remember events to an extent, they are insufficient to rescue the reduced precision with which events are remembered by older adults.

The present work adds on to a growing body of studies suggesting that for complex events, age-related episodic memory changes are best described as a shift towards forming more integrated, gist-based memory representations and that this shift emerges from and is shaped by brain changes as well as motivational changes that accompany older age. Thus, the current work offers a new perspective on how aging affects episodic memory, focusing on shifts rather than decline, and uses naturalistic, complex events to explore these shifts. In this concluding chapter, I begin by summarizing key findings and interpretations from the three manuscripts included in this dissertation, discuss their theoretical as well as practical implications and provide directions for future research.

Summary of findings

In Chapter 1, I tested the hypothesis that aging will be associated with shifts in hippocampal subregion connectivity during encoding, as measured during movie watching. Importantly, I examined connectivity patterns both between the hippocampal subregions and between the subregions and the rest of the brain. Key findings from this chapter were as follows: older age reduced contralateral subregion connectivity (e.g., left and right anterior hippocampus) for both subregions; anterior hippocampal connectivity increased, bilaterally, with regions in the prefrontal cortex, whereas posterior hippocampal connectivity decreased, also bilaterally, and with regions in the posterior, visual cortex. As well, the latter, cortico-subregion connectivity patterns, were associated with lower performance on the standard story recall measures collected outside the scanner. Together, these findings align with and extend the neural dedifferentiation frameworks, suggesting that functionally specialized hippocampal subregions increasingly show integrated connectivity patterns in older age, which negatively impacts task performance. Further, these results suggest that while encoding complex events, older adults increasingly rely on brain regions that process coarse-level, gist-representations such as the anterior hippocampus and the prefrontal cortices and rely less so on those that process fine-grained details (e.g., posterior hippocampus, visual cortices; Moscovitch et al., 2016; Robin & Moscovitch, 2017; Sheldon et al., 2019). Together, the results from Chapter 1 show that older adults' gist-based focus is reflected as shifts in how the hippocampus and its functionally specialized subregions support episodic memory encoding.

In light of these age-related functional brain shifts during complex event encoding, in Chapter 2, I investigated whether younger and older adults recall the same complex event (i.e., the movie) differently. To this end, in Chapter 2, I focused on key aspects of recalling complex events: accuracy, organization, and content. Here I tested the hypothesis that older adults' gist-based focus should shift what details they assemble from memory and how they would assemble them. I applied a novel scoring technique to identify the movie events participants accurately remembered, the order in which they remembered them, as well as other kinds of content they remembered (sensory perceptual, conceptual, and non-episodic details). Across two independent samples, I found that when younger adults recalled a higher proportion of event specific information, older adults' recall contained more conceptual and non-episodic content than younger adults. However, these age-related content shifts were accompanied by comparable memory accuracy and temporal organization of the movie events between the age groups. Together, these results showcase that older adults' tendency to form gist-based representations (Abadie et al., 2021; Grilli & Sheldon, 2022; Koutstaal & Schacter, 1997) shifts the content of their episodic memory. This shift emerges in the absence of, or perhaps compensate for, episodic memory deficits or age differences in temporal organization while recalling complex events.

Finally, in Chapter 3, I linked older adults' gist-based focus and biases in their recalled content to shifts in *why* younger and older adults remember past experiences (i.e., retrieval goals). This is based on psychosocial frameworks of cognitive aging, which propose that older adults increasingly take on socially oriented, rather than accuracy-oriented retrieval goals compared to younger adults, which can alter what is remembered from past events. In light of these frameworks, I first examined whether different retrieval goals changed the content of an encoded event for younger and older adults. An additional goal of this experiment was to assess the effect of different retrieval goals, implemented shortly after encoding an event, on younger and older adults' subsequent memory for the complex event. To this end, after a 24-hour delay, I examined younger and older adults' memory for movie's coarse-grained, narrative and fine-grained perceptual details. I used a Natural Language Processing model to examine the content overlap between the recalled and encoded content for each participant, as well as the recalled content between the participants. I found greater content overlap with the encoded movie in the accuracy group compared to the social group in both age groups. However, memories retrieved for different retrieval goals were more similar for older than younger adults. As well, regardless of retrieval goals, younger adults outperformed older adults in the recognition memory tasks and this effect was most pronounced for the perceptual details. These findings suggest that retrieval goals similarly shape the content younger and older adults recall from a past event, yet older adults' recollections are less distinct across these goals than younger adults. As well, age but not retrieval goals determine the content of the underlying memory trace. Together, these results indicate that previously reported age differences in memory content can in part, be explained by distinctions in retrieval goals, yet retrieval goal differences are insufficient to explain the differences in precision with which younger and older adults remember.

Theoretical implications

To begin, my findings suggest that for complex events, age-related memory differences are best characterized as distinctions in how younger and older adults represent past events, which have significant theoretical implications for neurocognitive models of aging. According to Fuzzy-trace Theory, advanced age is associated with a reliance on gist-based rather than verbatim memory representations (Brainerd & Reyna, 2015). Recently, this framework was extended to complex event memories, proposing that aging shifts how past experiences are represented – with older adults forming gist-based and younger adults, specific representations (Grilli & Sheldon, 2022). In line with these proposals, in Chapter 1, gist-based focus in older age was evident in the brain regions engaged while encoding the movie. That is, increased age was associated with greater connectivity of the anterior hippocampus, which is thought to represent coarse-grained, gist-based representations of an event and decreased connectivity of the posterior hippocampus, representing fine-grained specific representations (Robin & Moscovitch, 2017; Sheldon et al., 2019). In Chapter 2, older adults' gist-focus manifested as content shifts in how they recalled the movie —with older adults remembering more conceptual and non-episodic content and younger adults remembering more event specific details. These results provide evidence for neurocognitive frameworks proposing an age-related shift towards forming gist-based representations of events to suggest that while encoding and retrieving complex events, older adults prioritize the coarse, gist-level details of these events, which differs from younger adults' focus on more fine-grained specific details.

The current results also align with recent theoretical frameworks suggesting that the age-related shift toward representing memories at the gist level is not exclusively driven by decline (Grilli & Sheldon, 2022). In line with this proposal, in Chapters 2 and 3, I found that older age was associated with shifts in the recalled content in the absence of memory deficits or temporal organization, and when given the same retrieval goals, younger and older adults showed comparable recall content similarity with the encoded movie. If older adults' gist-focus was exclusively driven by their inability to encode and retrieve event-specific details, than the content shifts I observed in Chapter 2 would be accompanied by age group differences in memory accuracy. Similarly, if episodic memory deficits completely accounted for older adults' gist-based focus, then different retrieval goals would be ineffective in shaping older adults' recall, which was not the case in Chapter 3. Thus, the findings presented here provide empirical evidence for the proposal that older adults' gist-focus is a multifactorial outcome and cannot be exclusively tied to their episodic memory deficits.

In fact, the results of my dissertation suggest that older adults' gist-focus can at times, even supplement their episodic memory deficits. For example, in Chapter 2, I found that both younger and older adults showed typical features of temporal organization. This finding deviates from previous work using list learning paradigms, in which temporal organization of recall is impaired in older age (Diamond & Levine, 2020a; Howard et al., 2006; Kahana et al., 2002). A common finding from this literature is that older adults tend to regroup and recall list items based on their semantic meaning, which results in temporally "disorganized" recall of these items. I suggest that complex events, akin to those in the real world, provide the optimal conditions — enriched encoding and retrieval contexts —for older adults to leverage their gist-focus to their advantage. For example, for real world events, temporal organization is often accompanied by causal or higher-level associations between events. Two events that happen successively tend to also be causally (e.g., pouring a cup of coffee, drinking the coffee), logically (e.g., can't drink coffee without first pouring it into a cup), and thematically related (e.g., both events are coffee related). These higher-level, conceptual associations between individual events can be leveraged by older adults and supplement their deficits in forming fine-grained associations (Greene & Naveh-Benjamin, 2023), such as those based on temporal context. In support of this proposal, previous work has shown that older adults' associative memory deficits are limited to specific, fine-grained but not gist-based associations (Castel, 2005; Gallo et al., 2019; Greene & Naveh-Benjamin, 2020). For example, older adults successfully remembered that a face was associated with a park rather than a kitchen context but failed to identify the exact park scene that had been associated with the face (Greene & Naveh-Benjamin, 2020). Furthermore, there is evidence to suggest that older adults leverage higher forms of knowledge for episodic recollection (Castel, 2005; Umanath & Marsh, 2014) and that age differences are minimized when to be remembered information is consistent with prior knowledge (Mather et al., 1999). When participants read passages about a character who performed typical (e.g., “Jack asked the waiter for the check.”) and atypical (e.g., “Jack put a pen in his pocket.”) actions, older adults showed a larger memory advantage for typical over atypical actions than younger adults (Hess, 1985). Based on these findings, I propose that complex events allow older adults to leverage their intact, higher-level forms of knowledge, which can benefit their episodic recollection. This benefit, conferred by complex events to older adults, could be why I observed a negative association between the increased anterior hippocampal connectivity and performance in standard laboratory tasks in older age (Chapter 1). I speculate that the increased reliance on anterior hippocampus and accordingly the coarse-level, gist-based representations it supports, would be positively related to memory for complex events such as the encoded movie. An important future direction is to examine whether forming gist-based representations pose distinct consequences for laboratory based and real-world, complex events.

Another notable finding from the current work is that to some extent, motivational differences, in this case *why* younger and older adults remembered an event, can account for differences in memory content. In Chapter 3, I found that both younger and older adults showed greater content overlap with the encoded movie in the accuracy compared to the social group, suggesting that when given similar retrieval goals, younger and older adults perform comparably. This finding potentially explains previously reported age differences in recall content, which is pervasive in the autobiographical memory literature (Simpson et al., 2023). A common finding in this body of work is that older adults provide fewer event-specific details and more non-episodic, general knowledge statements than younger adults (Addis et al., 2008, 2011; Levine et al., 2002; Simpson et al., 2023). Such patterns are considered to reflect age-related deficits in the ability to access specific details from past experiences, which older adults compensate for by generating more non-episodic details. Based on the results presented here, it stands to reason that previously reported age differences in recall content could be due to differences in what motivates younger and older adults during these tasks. For example, in autobiographical memory studies, older adults often remember and relate their memories to younger experimenters. Thus, it is plausible that in these contexts, with a younger audience, older adults are spontaneously motivated to provide more background information and share their past with goals that emphasize teaching/informing others, which results in greater production of "external" details, particularly personal and general semantic information (Simpson et al., 2023). In contrast, younger adults, might not feel the need to provide such background context to a younger audience, which results in a greater proportion of event specific details in their recall. In support of this speculation, previous work has shown that older adults are more likely to tune their retellings to their audiences (Adams et al., 2002) and that older adults' memories are often rated as more interesting and informative by independent sample of younger and older raters (James et al., 1998). Future work can address this possibility by having younger and older adults remember and share autobiographical memories with other younger and older adults to examine if the increased generation of external details are still present when older adults share these events with other older adults with whom they likely have shared knowledge context.

Last but not least, the presented research also contributes to the recent theoretical and empirical movement towards naturalistic assessments of memory (Diamond & Levine, 2020b; Grall & Finn, 2022; Kringelbach et al., 2023; Sonkusare et al., 2019). In all 3 Chapters, I used an audiovisual movie to probe age-related shifts in encoding and retrieving complex events. This choice was based on recent trends in the cognitive neuroscience research, which is increasingly using these stimuli to study cognitive processes embedded in real-world like contexts. By using these stimuli, it was possible to assess key behavioural and neural correlates of how we encode and remember past events within a single, extended, and complex episode. For instance, in Chapter 1, participants were scanned as they watched this movie, which allowed me to examine hippocampal subregion patterns under conditions where functional patterns relevant to episodic memory encoding are likely to emerge. This approach differs from and extends a large body of work, which has examined age differences in subregion functional connectivity at rest —with no externally imposed task or stimulation (Damoiseaux et al., 2016; Panitz et al., 2021; Salami et al., 2014; Setton, Mwilambwe-Tshilobo, Sheldon, et al., 2022). The resting state scan protocols have their advantages (Lee et al., 2013): they are easy to standardize across sites and more feasible for hard-to-scan populations, yet also suffer from several confounds, especially when used to study age effects or cohort differences (Campbell & Schacter, 2017). One such confound is that the experimenter has little to no control over participants' internal thoughts. As a result, one possibility is that younger and older adults engage in different tasks or thought patterns at rest. Earlier work has suggested that differences in resting state thought patterns emerge even in younger adults (Fox et al., 2015), and these individual differences correspond to distinct patterns of resting-state functional connectivity (Gorgolewski et al., 2014). More recently, these differences have been extended to aging to show that older adults experience more positive thoughts than younger adults at rest (Stoica et al., 2024) and that they experience mind wandering less frequently than younger adults (Maillet et al., 2018; Maillet & Schacter, 2016), reflecting broader age differences in spontaneous cognition. Thus, the distinctions in younger and older adults' resting state thoughts can cloud the interpretation of any neural differences observed during these scans. This potential source of variability, however, is functionally eliminated by movie watching paradigms since these paradigms constrain attention with a shared, time locked stimulus across subjects, while exposing them to a detail rich, dynamic content (Finn, 2021). In this way, movie watching provides the optimal conditions to study age effects on hippocampal functional connectivity.

In a similar vein, using movies provided experimental control over the encoded event, enabling me to calculate memory accuracy in Chapters 2 and 3. Measuring memory accuracy for complex, naturalistic events has been elusive, especially in autobiographical memory studies (although see: Diamond et al., 2020; Diamond & Levine, 2020). This is because autobiographical events are retrospectively sampled in these studies and as a result, these experiences are uncontrolled, unverifiable and idiosyncratic to each individual. Thus, researchers cannot objectively measure the accuracy with which an autobiographical memory corresponds to the experience it represents. In addition, movie watching provided control over the encoded sequence of events and enabled comparison between the original and remembered order of movie events, in turn, allowing for the assessment of temporal organization of recall for complex events. In Chapter 2, I leveraged this feature of the movies and borrowed well-established measures of temporal organization and temporal context reinstatement (i.e., temporal contiguity, forward-bias) from the word-list learning literature (Howard & Kahana, 2002; Polyn et al., 2009) to compare these measures between younger and older adults. Differently from previous work using list-learning paradigms, I found no age differences in the temporal organization of recall, suggesting that with naturalistic stimuli, older adults, just as well as younger adults, can transform the experienced structure of events into structure in memory. These findings showcase the fact that naturalistic assessments can capture different aspects of episodic memory (e.g., accuracy, content, organization) in a single episode, providing a more comprehensive and nuanced view of how memory changes in older age. In fact, I suggest that movies as memoranda bridge the gap between traditional laboratory-based methods that are devoid of realism as well as real-world autobiographical memories that lack experimental control, making them ideal for studying episodic memory processes for complex events and age-related changes in these processes.

Another proposal based on the present work is that age-related shifts in how past experiences are represented can be best studied with naturalistic assessments of memory. This is because naturalistic stimuli such as movies —due to their rich and dynamic content, and the flexibility in which the constituent details can be combined —allow for different representations to be formed. For example, several theoretical frameworks have proposed that the detail content used to remember an event can be selectively emphasized, giving rise to qualitatively different memory representations (Robin & Moscovitch, 2017; Sheldon et al., 2019; Sheldon & Levine, 2016). For complex memories, one distinction is made between representing an event's content by focusing on the specific, perceptual details (e.g., "I had a blue shirt on.") versus higher-order, conceptual details that capture one's evaluations and inferences about the event (e.g., "I was so happy to see all my friends together."; Sheldon et al., 2019; Gurguryan et al., 2019). It has been proposed that focusing on perceptual details results in highly precise, specific memory representations, whereas focusing on conceptual details results in gist or meaning-based memory representations (Grilli & Sheldon, 2022). Since naturalistic stimuli include both specific perceptual and higher order conceptual details, the associated memories can be formed by different weighing of these details, consequently giving rise to different kinds of representations.

The fact that much of the extant evidence for older adults' specific-to-gist focus comes from studies examining memory for individual items (e.g., false recall of critical lures, incorrect recognition of synonyms or perceptually similar images) might explain why older adults' specific-to-gist focus has been primarily viewed from a decline-oriented lens thus far. The metrics derived from these tasks are informative for assessing age-related deficits in memory, yet neglected in these studies is whether there are age related shifts in the representational quality of memories. For example, standard tests, such as item recognition or recall, require individuals to remember a specific item from a list. Since these tasks demand the recall of precise details, such as whether it was a park or a beach that appeared on a list, if older adults do not form specific representations, they may perform worse than younger adults on these tests. However, it is possible that older adults retain gist-based representations of the items (e.g., "I remember seeing an outdoor scene") or representations that are comprised of different kinds of content (e.g., “I remember thinking how I wish I was outdoors.”) that are not typically measured or can be expressed in these procedures. As a result, these paradigms are limited in that age-related specific-to-gist shifts can only emerge as a deficit on older adults' part. In contrast, naturalistic assessments provide conditions under which gist-representations can emerge and perhaps be adaptive to older adults' memories as shown in the present work.

Finally, the presented results underscore the value of studying aging and its impact on episodic memory through an integrated lens that combines neural, behavioral, and psychosocial factors. This integrated approach provides a comprehensive understanding of older adults' episodic memory, offering deeper insights into both the challenges and adaptive changes in older age, and characterizing the relationship between aging and episodic memory beyond a decline-oriented lens. Specifically, the current work suggests that age-related episodic memory changes are apparent in the neural (Chapter 1) and behavioural levels (Chapter 2) of analyses, which can emerge in the absence of episodic memory deficits (Chapter 2) and be mitigated by motivational factors (Chapter 3). Thus, by integrating these levels, the current work provides a more nuanced description of age-related episodic memory changes —both in terms of gains and losses. This nuanced understanding has several practical implications, which are reviewed below.

Practical applications

It is estimated that by 2068 more than 1 in 4 individuals in Canada will be over the age of 65. This increase in senior population will have significant implications for health, housing, transportation, and care services, making it imperative that we understand what aspects of cognition are lost and what is preserved in older age, especially in real world settings.

The preserved aspects of episodic memory in older age can be leveraged for developing targeted memory interventions for older adults. For example, in Chapter 3, I found that older adults can, to some extent, align their recall content with their on-line retrieval goals, suggesting that the flexibility with which memories can be represented remains somewhat intact in older age. This flexibility can be capitalized on to improve older adults' memory, for example, by promoting both specific and gist-based representations of events and importantly, flexible transitions between these types of representations. For example, this idea is central to MemFlex, a memory flexibility training that has been administered to patients with major depressive disorder (MDD), which is marked by memory biases towards over-general rather than specific memories (Hitchcock et al., 2016). MemFlex encourages flexibility in alternating between retrieving over-general and specific memories and has been shown to reduce overgeneral memory bias in patients with MDD. Thus, a similar training program can be designed to overcome older adults' specific-to-gist bias. To this point, the current work additionally suggests that an integrated approach to design interventions targeting behavioural strategies is essential, as these interventions may be less effective if they do not consider the underlying neural limitations such as those observed in Chapter 1 or motivational shifts that accompany aging (Chapter 3). Thus, tailoring interventions to the individual's motivational state, neural and behavioural performance could lead to more personalized and effective solutions for mitigating age-related memory changes.

In addition, by highlighting the aspects of episodic memory that are preserved or change rather than exclusively decline in older age, the current work promotes positive aging stereotypes. While much of cognitive aging research considers aging and older adults' gist-focus to be synonymous with decline, the present work suggests a different story for complex events. For example, in Chapter 2, I found comparable memory accuracy and temporal organization of the remembered events between younger and older adults. I interpret this lack of age difference as reflecting older adults' preserved ability to remember complex events akin to our experiences in the real world. The broader knowledge of abilities that are maintained or even improved in older adulthood is important to highlight as it can enhance older adults' perception of themselves, which has a potential to increase older adults' wellbeing and even cognitive functioning. For example, previous work has shown that older adults who hold negative views of aging report experiencing higher levels of stress (Levy et al., 2016), show a steeper hippocampal volume loss and greater accumulation of neurofibrillary tangles and amyloid plaques, predictive of pathological aging such as Alzheimer's disease (Levy et al., 2016). As well, the effect of stereotype threat —when an individual feels they will confirm a negative stereotype about their group and consequently underperforms on stereotype related tasks —on memory performance has been well-documented in older adults (Lamont et al., 2015). These studies have shown that negative, age-related stereotypes, experimentally induced prior to completing a memory task, impairs older adults' performance (Armstrong et al., 2017; Lamont et al., 2015). Thus, given that negative views of aging are prevalent in society and these views are becoming increasingly more negative (Mason et al., 2015; Ng et al., 2015), showcasing the preserved aspects of cognition in older age is important for improving not only the well-being of older adults but also possibly their memory.

Moving forward, focusing on the preserved aspects of episodic memory in healthy aging can help distinguish between healthy and pathological aging. That is, by characterizing the adaptive shifts in memory, such as the specific-to-gist and recall content shifts reported in the present work, researchers and clinicians can establish benchmarks for healthy aging and identify deviations that might signal pathological conditions such as amnestic mild cognitive impairment (aMCI) or Alzheimer's disease (AD). In support of this point, previous work has reported severe gist memory impairments in patients with AD compared to healthy older adults (Hudon et al., 2006) and that gist-memory decays at a much faster rate for patients with aMCI than age-matched healthy controls (Lin et al., 2023; Taler et al., 2021), suggesting that reductions in gist-based recall can be a particularly sensitive marker for unhealthy aging. As well, age-related content shifts in the absence of episodic memory deficits observed in the current work (Chapter 2) can serve as a reference point for pathological aging. In fact, recent work has begun to uncover content-specific differences in the recollections of healthy versus pathological agers (Grande et al., 2021). For example, in a recent meta-analysis, Simpson et al., (2023) found that the increased generation of non-episodic (i.e., external) details, well-reported in healthy older adults, is reduced in patients with MCI and AD (Simpson et al., 2023), suggesting that this pattern of recollection can in fact be a sign of adaptive aging. To sum, the extent to which older adults exhibit adaptive shifts in memory, such as those that are observed in current work, can potentially predict their cognitive status or pathology in the brain.

Limitations and future directions

Like all research, the presented work has its limitations that future work can address. To being, in all 3 Chapters, I used movies as memoranda to approximate the complexity and dynamicity of our experiences in the real world. However, these stimuli are approximations rather than simulations of how we experience and remember events in the real world. For example, differently from real world experiences, commercial movies are produced —such that they are deliberately structured to evoke certain senses, percepts, and emotions. As well, participants passively view these stimuli, often depicted from a third-person perspective, whereas in the real-world participants are free to explore and engage with their environments egocentrically. In this way, movies are fundamentally not natural per se but naturalistic in that they depict subjective and goal directed tellings of fictional or non-fictional events. An interesting future direction is to study age-related shifts in event cognition and memory using even more naturalistic paradigms, such as stimuli that mimic real-life familiar, repetitive and first-person experiences (Pooja et al., 2024). To this point, previous work has used "lifelogging", which is the digital logging of an individual's daily life activities via a device that automatically (Sreekumar et al., 2018) or through human intervention (Martin et al., 2022) records events. Although these methods bring real-world events into the laboratory, a limitation of this approach is that the recorded events are idiosyncratic to each individual and this variability removes experimental control over the types of events participants record and subsequently remember. Another method that marshalled significant attention in recent years is virtual reality (VR), likely due to its ability to create immersive and egocentric experiences (Brugada-Ramentol et al., 2022; Kisker et al., 2021; Mueller et al., 2012). These methods immerse individuals in the same detail rich, virtual environments that participants are free to explore, which allows researchers experimental control over the encoded details while preserving participants' agency. However, these environments are often digitally created with low visual fidelity —such that they do not faithfully reproduce the visual qualities and details of real world settings (Smith, 2019). In this way, as with any scientific method or stimuli, using movies as memoranda has its limitations. While they can be powerful tools for certain research questions, they fall short for others.

Another limitation is that the movie I used in all three Chapters might be more familiar to older than younger adults, which can explain the neural and behavioural shifts observed in the current study. For example, given that the movie was from the 1970s, an era that is likely more familiar to older adults, it contained details and contexts for which older adults have presumably greater prior knowledge (e.g., a mechanical horse, rotary phone, etc.). This extant prior knowledge could have been leveraged by older adults to bolster memory for the movie, which might explain why differences in memory accuracy did not emerge between younger and older adults in Chapter 2. To this point, several studies have shown that episodic memory performance in older adulthood may be supported by preserved cognitive functioning in other domains, such as semantic knowledge (Umanath & Marsh, 2014). In addition, there is evidence to suggest when participants leverage their extant prior knowledge during episodic memory tasks (e.g., when the encoded material is congruent with such knowledge), they recruit different brain regions than when this knowledge is not available or useful (e.g., incongruent material). Given that in Chapter 1, such knowledge was presumably available to older but not younger adults, the observed differences in the subregion connectivity patterns across the lifespan could be attributed to this factor. Although participants in all three Chapters were naïve to the movie and reported having not seen it before, familiarity of the movie elements or its era was not directly controlled. Thus, an interesting future direction is to examine whether similar patterns emerge for movies that are unfamiliar to both older and younger adults.

Finally, an important future direction is to consider age-related changes to complex event memory within the context of demographic variables other than chronological age. Chief among these variables is the sex and gender of the participants —with evidence suggesting that these variables can interact with age and shift the observed results at all three levels of analyses (Miller et al., 2017; Subramaniapillai et al., 2024). To begin, the neural correlates of age-related episodic memory changes have been shown to differ between women and men —with older women showing greater between network integration more broadly (Subramaniapillai et al., 2022) and greater intrinsic coupling between the posterior hippocampus and medial prefrontal cortex than men (Damoiseaux et al., 2016). Behaviourally, there is evidence to suggest that older men and women draw upon different kinds of content when recalling autobiographical memories, with women integrating more conceptual details than men (McLean, 2008; Pillemer et al., 2003). Lastly, given that gender as a construct encompasses an individual's societal interactions and socially constructed roles (National Academies of Sciences, 2022), it is likely that the psychosocial factors I explored in relation to age-related episodic memory changes may not generalize across the entire gender spectrum. For example, one potential confound with socially oriented retrieval goals is that these goals may be interpreted differently by individuals of different genders, likely due to known differences in socialization experiences (Leaper & Friedman, 2007). In this way, older men and women in the social goal group may have prioritized different memory content and consequently, formed different memory representations of the movie in Chapter 3. To sum, applying a sex and gender-dependent lens to study the relationship between age and episodic memory is an important future avenue. This lens can enhance the translation of the emerging findings for both sexes and all gender expressions, ensuring that the full benefit of the research efforts is accessible to all.

Beyond sex differences, another important variable that is increasingly being considered is the reproductive stage of the participants (Jacobs & Goldstein, 2018; LaPlume et al., 2024). For example, menopause is an important and significant period of neuroendocrine change in a woman's life and a period when many women report changes in memory (e.g., "menopause fog"; Greendale et al., 2011). A growing body of evidence suggests that menopause status has substantial impact on the behavioural and neural correlates of episodic memory (Crestol et al., 2023; Jacobs et al., 2016; Rentz et al., 2017). For example, post-menopausal women show enhanced bilateral hippocampal connectivity relative to pre- and peri menopausal women (Jacobs et al., 2016). As well, in early midlife, encompassing pre- and peri-menopausal periods, women outperform men across a wide range of episodic memory measures but these sex differences are attenuated in late life, post-menopausal stage (Rentz et al., 2017). Since reproductive stage is strongly correlated with chronological age, accounting for this variable is an important future avenue for research examining age-related changes to complex event memory. By accounting for the reproductive stage, researchers can gain a more accurate understanding of how biological changes impact episodic memory across the lifespan, differentiating between age-related and hormonally driven changes.

Finally, age-related episodic memory changes should be considered in the context of cultural differences, especially if assessing memory for complex events. As reviewed above, the complexity inherent to our experiences allow for different kinds of representations to be formed —depending on what content is prioritized (Grilli & Sheldon, 2022; Sheldon et al., 2019). In this respect, it is possible that cultural context and background can shape how people encode, organize, and retrieve their experiences. For one, culture can operate as a lens that brings to focus aspects of an experience that aligns with the cultural priorities and values, in turn determining what is accessible for or preferentially accessed from memory (Gutchess & Siegel, 2012). In support, cross-cultural research has consistently demonstrated cultural differences in what information is selectively encoded and retrieved (Millar et al., 2013; Wang et al., 2018; Wang, 2009; Wang & Conway, 2004). For example, East Asian participants tend to place a greater emphasis on social interactions and produce more information about people compared to Westerners during recall, whereas Westerners tend to recall more self-related as opposed to social information than East Asians (Wang & Conway, 2004). In addition, European and European Americans tend to retrieve more specific details of events than do their Asian and Asian American counterparts (Wang, 2006, 2009). These patterns align well with the age-related content shifts reported in Chapter 2, and the well-reported reductions in memory specificity (Levine et al., 2002). One speculation emerging from these findings is that the reported patterns may be seen as a byproduct of aging in Western cultures, yet these patterns could reflect a normative way of remembering in other cultural contexts. In other words, what is considered an age-related deficit in one culture may be considered normative, culturally appropriate way of remembering in another. By taking culture into account, researchers can ensure that findings on episodic memory and aging reflect the diverse cognitive landscapes shaped by cultural backgrounds, avoiding biases that arise from culturally narrow frameworks. This understanding is critical for developing more effective, culturally sensitive interventions to support healthy memory aging.

Conclusion

How we remember the past changes in older age along with why we remember it. The findings from this thesis highlight the nuanced ways in which these age-related episodic memory changes manifest for complex events. Across three levels of analyses —neural, behavioural, and psychosocial —I have demonstrated that episodic memory in older age is a multifactorial outcome that is best characterized as differences in how younger and older adults represent past experiences. By integrating insights from these levels, the current dissertation draws a comprehensive picture of how episodic memory evolves with age, moving beyond a decline-oriented perspective to emphasize the preserved aspects and adaptability of memory in older adulthood. This integrated approach is crucial for bringing cognitive aging research from silos to synergy.

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