“In the mind’s eye” – Exploring the interaction between oculomotor behaviour and memory-related processes in ageing and neurodegeneration

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List of abbreviations

ACC	Anterior cingulate cortex
ACE-III	Addenbrooke’s Cognitive Examination – Third Edition
AD	Alzheimer’s disease
ADL	Activities of daily living
AEM	Amount of eye movements
ANOVA	Analysis of variance
bvFTD	Behavioural variant of frontotemporal dementia
dlPFC	Dorsolateral prefrontal cortex
DSB	Digit Span Backward
DSF	Digit Span Forward
EEG	Electroencephalography
FEF	Frontal eye fields
FTD	Frontotemporal dementia
GLM	Generalized linear model
η_p^2	Partial eta-square
LME	Linear mixed-effects modelling
MCI	Mild cognitive impairment
MEG	Magnetoencephalography
MRI	Magnetic resonance imaging
MTL	Medial Temporal Lobe
PCC	Posterior cingulate cortex
PPA	Primary progressive aphasia
RAVLT	Rey Auditory Verbal Learning Test
RCFT	Rey Complex Figure Test
ROI	Region of Interest
RSC	Restrosplenial cortex
SD	Semantic Dementia
SPSS	Statistical Package for the Social Sciences
SYDBAT	The Sydney Language Battery
vmPFC	Ventromedial prefrontal cortex
VOSP	Visual Object and Space Perception Battery
$\chi 2$	Chi-Square Test

List of publications

The following first-author publication forms part of this thesis. Materials published in this peer-reviewed article are presented in Chapter 1.

Conti, F., Irish, M. (2021) Harnessing visual imagery and oculomotor behaviour to understand prospection. *Trends in Cognitive Sciences*, 25(4), 272-283.

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Co-author declaration

We, the undersigned, acknowledge that the publication included in this thesis is predominantly the work of Federica Conti and that the information provided regarding the co-author contribution is accurate.

Professor Muireann Irish

12th December 2023

Professor Olivier Piguet

12th December 2023

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Statement of originality

This is to certify that, to the best of my knowledge, the content of this thesis is my own work. This thesis has not been submitted for any degree or other purposes. I certify that the intellectual content of this thesis is the product of my own work and that all the assistance received in preparing this thesis and sources have been acknowledged.

All studies were carried out during my PhD candidature under the supervision of Professor Muireann Irish and Professor Olivier Piguet. The studies contained within this thesis were conducted at FRONTIER, the frontotemporal dementia research clinic, based at the Brain and Mind Centre, the University of Sydney. The data collected from this thesis were collected by me alongside senior neurologists, neuropsychologists, psychologists, occupational therapists, and other experienced research assistants at FRONTIER. All data were collected through direct contact with participants, with written informed consent obtained from all participants or their person responsible.

In accordance with the Declaration of Helsinki, ethical approval for these studies was obtained from the Human Research Ethics Committee (HREC) of the South Eastern Sydney Local Health District as part of the following two projects: “Memory and imagination in ageing” (approval number 2018/479) and “Clinical Assessment for Ageing and Neurodegeneration Research” (approval number 2020/224).

12th December 2023

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The past five years have been incredibly challenging, mentally, and emotionally. I have seen myself grow as a person and as a scientist in ways that I would have never imagined. I found joy and passion in the quest for knowledge, and I am excited for what lies ahead.

This thesis is dedicated to my mother. Despite the considerable geographical distance between us, she has always been in my corner, cheering and rooting for me every step of the way. She taught me and inspired me to build resilience in the face of adversities and never once did she doubt that I would make it through. I could not be more grateful. I hope I made her proud and that I will continue to do so in the years to come.

Abstract

Much of the rich internal world constructed by humans is derived from, and experienced through, visual mental imagery. Despite growing appreciation of visual exploration in guiding imagery-rich construction-based processes, extant theories of memory retrieval and prospection have yet to accommodate the precise role of visual mental imagery and corresponding oculomotor dynamics in the service of past and future-oriented thinking, particularly as we age and in the presence of neurodegenerative syndromes.

This thesis comprises three experimental studies investigating the above issues. **Chapter 2** demonstrates distinct signatures of oculomotor behaviour during visual exploration and memory retrieval in younger and cognitively healthy older adults, as well as patients with either Alzheimer's disease or semantic dementia. The relative contributions of the episodic and semantic memory systems in supporting task performance, as well as the potential relationship between participants' oculomotor patterns and underlying cognitive mechanisms are discussed in the context of both healthy ageing and neurodegeneration. In **Chapter 3**, I extend my enquiries into age-related changes in oculomotor dynamics to alterations in eye movement metrics during the endogenous construction of atemporal scenes in the absence of externally cued visual stimuli and examine how they relate to participants' self-reported phenomenological experience of the mental simulation. Results from this study suggest a shift away from the production of eye movements specifically in older adults as a function of increasing task complexity as cognitive demands exceed working memory capacities. Finally, **Chapter 4** expands on these findings in the context of episodic future thinking. While no age effects were found in either the provision of episodic content, or any of the oculomotor and behavioural measures considered, results indicate that the temporal distance and the level of plausibility of hypothetical future events strongly influence participants' performance by encouraging the elaboration of scenarios that are particularly rich in contextual detail in selected experimental conditions (near future, plausible scenarios and far future, implausible scenarios). Current theories looking at the potential mechanisms driving these behavioural responses are discussed, particularly the respective contributions of the episodic and semantic representational systems in response to the generative demands of the constructive endeavour.

The work presented in this thesis adds to the extant literature by demonstrating and characterising the relationship between oculomotor behaviour and imagery-rich construction-based processes. Future enquiries exploring the potential and diverse applications of oculomotor metrics to neuropsychological and clinical research will further elucidate the complex adaptive mechanisms supporting cognitive performance in both healthy ageing and neurodegeneration.

Chapter 1

Introduction

> "*The mind is a kind of theatre, where several perceptions successively make their appearance; pass, re-pass, glade away, and mingle in an infinite variety of postures and situations*."
>
> David Hume (1739-1740)

Memory is arguably one of the most remarkable aspects of the human experience. For thousands of years, the capacity to encode, store and retrieve information has allowed us to evolve as a species by shaping our perception and understanding of the external world. Without memory, learning from, and adaptation to, new situations and challenges could not occur. When we reflect on the past, we extract valuable knowledge that informs our decision-making and behaviour, allowing us to navigate life's complexities with greater clarity and purpose.

Memories also contribute to the construction of our identity. We nurture and cherish memories of what is important to us, such as meaningful events or encounters, alongside the emotions and impressions they generated. This ever-growing repository of personal stories ultimately makes us who we are and helps us define and reappraise our fundamental values, beliefs, and desires (Wilson & Ross, 2003). Most importantly, memories are not just mere recollections of the past that pile up in our minds. The episodic content they are comprised of provides a rich catalogue of images and feelings we naturally draw from every time we fabricate or (re-)play a hypothetical scenario in our head (Schacter, Addis, & Buckner, 2007). By flexibly combining and integrating these perceptual elements into a coherent representation, we can construct entirely new narratives, projecting ourselves into the future in anticipation of what lies ahead (see Figure 1.1). For example, imagining the outcomes of our actions and simulating possible alternatives enable us to rule out undesirable consequences and move progressively towards our goals in a directed manner (Bulley & Irish, 2018; Schacter, Benoit, & Szpunar, 2017). By recombining details extracted from previously experienced events, we can construct a vivid future scenario, irrespective of its truthfulness or plausibility (Thakral, Madore, & Schacter, 2019).

Figure 1.1 Examples of construction-based processes.

A hypothetical PhD student in cognitive neuroscience at The University of Sydney engaging in various forms of mental simulations such as thinking about a childhood memory (memory retrieval, on the left), visualising the different steps required to prepare her favourite recipe (atemporal scene construction, in the centre), and envisaging the completion of her doctoral degree (episodic future thinking, on the right). Images sourced from Canva.

1.1 The debilitating consequences of memory and visuospatial impairment

Given the fundamental role memory plays in most aspects of human cognition, loss of memory integrity can have deleterious effects on the person affected. Memory lapses can influence every aspect of our everyday life, from cognitive health and emotional wellbeing to our personal identity and social interactions (Parikh, Troyer, Maione, & Murphy, 2015). While memory loss can be the result of a traumatic event, brain injury, or simply occur to some extent as part of the ageing process, compelling research unequivocally indicates that disturbances in memory functioning are prominent features of neurological conditions, for example mild cognitive impairment (MCI) and Alzheimer's disease (AD). In fact, individuals affected by these conditions generally present a complex and multi-faceted cognitive profile, as well as a constellation of behavioural and personality changes including anxiety, apathy, depression, and sleep disturbances (Peter-Derex, Yammine, Bastuji, & Croisile, 2015; Robins Wahlin & Byrne, 2011). Most often, however, they report having trouble with a number of memory-related tasks and activities of daily living such as finding their way in places they used to know well, remembering the name of people they recently met or the flow of a recent conversation, as well as misplacing common, everyday objects somewhere that does not make contextual sense (Hamilton, Fay, & Rockwood, 2009; Vlček & Laczó, 2014; Werheid & Clare, 2007).

It is believed that the above symptomatology results from the progressive damage to brain regions traditionally associated with memory encoding, consolidation, and retrieval (particularly the hippocampus, Allen et al., 2007; Mu & Gage, 2011), and posterior brain structures (the primary visual and visual association cortices) devoted to visual perception, construction, and memory (Geldmacher, 2003). From a cognitive perspective, these atrophy profiles are often accompanied by deficits in episodic and autobiographical memory, future thinking, and more generally in the ability to mentally envisage and provide accurate descriptions of visuospatial scenes (El Haj, Moustafa, Gallouj, & Robin, 2019; Irish et al., 2015; Irish, Hornberger, et al., 2011). Interestingly, in conditions such as Alzheimer's disease, impairment of episodic memory often goes hand in hand with visuospatial dysfunction (Salimi et al., 2018b), suggesting that these capacities interact in a functionally relevant way.

1.2 The inherently visual nature of mental simulations: an overview

One noteworthy characteristic all expressions of memory and introspection have in common is that they are inherently visual in nature. Indeed, we tend to reexperience emotionally charged episodes in flashbacks, we routinely 'look ahead,' 'envisage,' or 'see ourselves' at future time points and, perhaps unsurprisingly, health, business and life coaches often speak of the importance of *having a vision* as a stepping stone to our happiness and success. The language we typically use to describe these mental feats undeniably reflects the strong contribution of visual mental imagery to human cognition, a captivating idea that can be traced back to Aristotle's prescient observation that 'the soul never thinks without a phantasma' (Aristotle, 1984). Much of the rich internal world constructed by humans is in fact derived from, and experienced through, visual mental imagery and subsequently recapitulated in the form of episodic memories or prospective thoughts. Converging lines of evidence suggest that mental imagery plays a fundamental role in supporting both past- and future-oriented forms of cognition, yet its precise contribution to the retrieval and dynamic recombination of perceptual content, as well as to the resulting phenomenology associated with the constructive endeavour remains poorly understood. While the fields of vision science and memory have largely proceeded in parallel up to this point in time, recent approaches suggest that we might now be able to unite these disciplines (Ryan, Shen, & Liu, 2020).

Concerted efforts to investigate memory and construction-based processes from a broader, more integrative standpoint have originated from the recognition that the visuo-oculomotor system and the memory system comprise cortical areas located in close proximity to each other and which are structurally interconnected (see Figure 1.2). Furthermore, their reciprocal interaction also appears to produce functionally relevant outcomes. For example, neuroimaging studies of memory retrieval and episodic future thinking consistently demonstrate increased activation and functional coupling between medial temporal regions and neocortical sites classically associated with visual imagery (Schacter et al., 2012).

Compelling proof of the tight relationship between these systems also comes from clinical studies of visual imagery impairment, whereby visuospatial imagery loss is often reported alongside autobiographical amnesia and in the context of posterior cortical atrophy (Ahmed et al., 2018; Ramanan, Alaeddin, et al., 2018). Furthermore, it has recently been discovered that some individuals (approximately 2-5% of the general population) experience a complete inability to engage in mental imagery in the absence of any acquired neurological damage or coinciding psychopathology (Dawes, Keogh, Andrillon, & Pearson, 2020). This condition, now referred to as “aphantasia” (Zeman, Dewar, & Della Sala, 2015, 2016), is often accompanied by deficits in episodic and semantic memory, as well as future prospection, demonstrating the foundational role of visual mental imagery in the construction of episodic events (Dawes, Keogh, Robuck, & Pearson, 2022). As a result, examining potential alterations in imagery capacities and cognitive performance between healthy and clinical populations where memory deficits are traditionally observed may provide a unique opportunity to deconstruct the complex interrelationship between visual mental imagery and episodic simulation.

1.3 Anatomical contiguity and functional interplay between the visual system and the memory system

From an anatomical perspective, the visuo-oculomotor system lies adjacent to posterior nodes of the core episodic network, placing it in a unique position to supply the visual elements necessary to remember past events and simulate the future (see Figure 1.2). This spatial contiguity enables the seamless and bidirectional exchange of information between the visual system and the medial temporal lobe (MTL), where hippocampal activity has been shown to augment visual imagery processes and produce observable responses in oculomotor areas within the time span of a typical gaze fixation (Parr & Friston, 2017; Rosen et al., 2018; Ryan, Shen, Kacollja, et al., 2020). Strong evidence for this interactive relationship also comes from studies on non-human primates (Leonard et al., 2015). In exploring the structural connectivity between the oculomotor and construction systems, these studies point to key cortical areas within the oculomotor circuitry, namely the frontal eye fields (FEF), dorsolateral prefrontal cortex (dlPFC) and anterior cingulate cortex (ACC), that appear to play a pivotal role in directing and integrating the flow of information from one system to the other to further guide visual behaviour (Shen, Bezgin, Selvam, McIntosh, & Ryan, 2016).

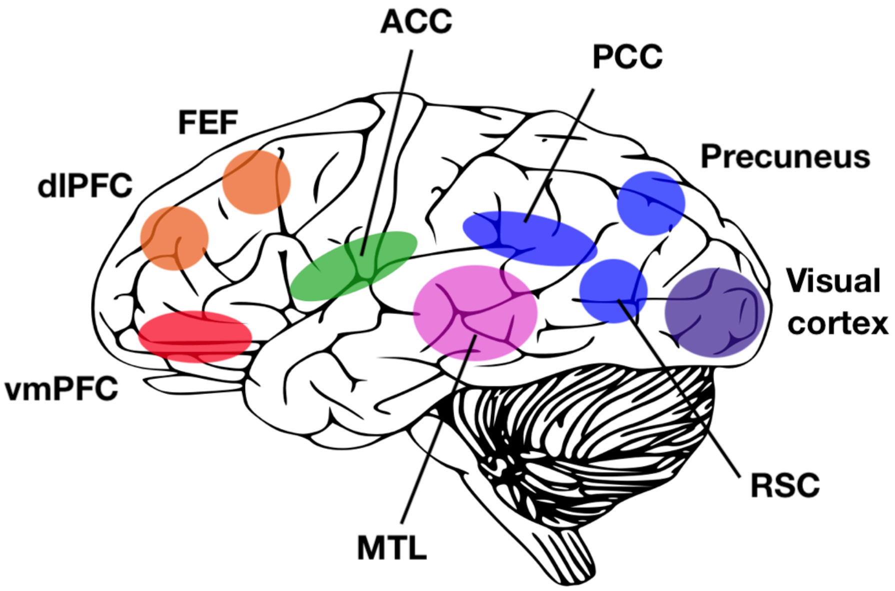

Figure 1.2 Anatomical contiguity between key cortical areas within the visual and the memory system.

Notes: ACC = Anterior Cingulate Cortex, PCC = Posterior Cingulate Cortex, RSC = Retrosplenial Cortex, MTL = Medial Temporal Lobe, vmPFC = ventromedial Prefrontal Cortex, dlPFC = dorsolateral prefrontal Cortex, FEF = Frontal Eye Fields. Brain template sourced from Canva.

From a functional standpoint, neuroimaging studies independently exploring visual mental imagery (Winlove et al., 2018), memory retrieval and episodic future thinking capacities (Beaty, Thakral, Madore, Benedek, & Schacter, 2018) consistently converge on a distributed set of posterior parietal and occipital cortical regions. In doing so, these studies therefore evoke common underlying functional properties above and beyond the anatomical co-location of the underpinning systems. More precisely, the deliberate instantiation of mental imagery has been suggested to reflect the operations of a so-called "reverse hierarchy mechanism" (Dentico et al., 2014; Dijkstra, Zeidman, Ondobaka, van Gerven, & Friston, 2017). According to this theory, it is the frontal cortex that kickstarts the imagery process by triggering a cascade of activation travelling backwards in the cortical hierarchy and leading to the reactivation of sensory content from posterior cortices (reviewed by Conti & Irish, 2021). This proposed mechanism bears strong similarities to prominent theories on the dynamic reconstruction of episodic memories (Ranganath & Ritchey, 2012; Renoult, Irish, Moscovitch, & Rugg, 2019) and has been observed in conjunction with increased functional connectivity between the hippocampus and regions of the visual cortex during past and future event elaboration (Addis, Wong, & Schacter, 2007).

1.4 The neural basis of imagery-rich simulations

Memory retrieval and construction-based mechanisms such as episodic future thinking may be endogenously generated or triggered by external stimuli, which are often visual in nature. Regardless of the trigger, theoretical accounts of mental construction emphasise the ventromedial prefrontal cortex (vmPFC) as an important driver of activity in the anterior hippocampus during mental construction (Monk, Dalton, Barnes, & Maguire, 2021). The necessary spatial backdrop of the simulation is assembled in the anterior hippocampus (Zeidman & Maguire, 2016), anchored on a conceptual semantic framework, which guides event construction according to a prescribed semantic script/schema (Gilboa & Marlatte, 2017; Irish & Piguet, 2013). This scaffold is embellished with sensory-perceptual elements, sourced from neocortical sites, and merged into a rich contextual layer via lateral posterior parietal convergence zones (e.g., angular gyrus and posterior cingulate cortex, Ramanan, Piguet, & Irish, 2018). These contextually rich assemblies are relayed to the hippocampus, where they can be reinstantiated in the form of an episodic memory or flexibly recombined into novel future simulations (Schacter et al., 2012). The precise pattern of neural activation in both visual and construction systems hinges upon the representational content invoked – the richer and more fine-grained the sensory-perceptual details, the greater the posterior parietal and posterior hippocampal activation and corresponding functional connectivity between the construction and visuo-oculomotor systems (Brunec et al., 2018; Irish & Vatansever, 2020). These proposed changing dynamics confer immense flexibility in how visual elements supplied by the visuo-oculomotor system are co-opted by the construction system into a multidimensional mental experience (Addis, 2018; Irish, 2020) that is predominantly visual in nature and subjectively conveys a strong sense of vividness (Richter, Cooper, Bays, & Simons, 2016).

1.5 Individual differences in imagery capacities

Imagery abilities vary considerably in the healthy population at large, prompting calls for the reconceptualisation of imagery strength as a dimensional construct (MacKisack, 2018). As such, individuals can be situated along a continuum of imagery strength ranging from completely absent (aphantasia) to extremely strong and photo-like (hyperaphantasia, Zeman et al., 2020). This naturally occurring variation in imagery strength has important implications for how we reconstruct the past and envisage the future (D'Argembeau & Van der Linden, 2006). Consistent with prominent theoretical accounts emphasising the shared nature of memory and imagination (Addis, 2018), discrete aspects of visual mental imagery underwrite many of the processes common to past and future thinking. For example, contemporary theories of scene construction emphasise the notable contribution of spatial imagery in providing the requisite backdrop for all forms of mental simulation (Mullally & Maguire, 2014). Indeed, studies of past retrieval and future thinking have found differences in spatial imagery to be the sole predictor of the level of episodic detail participants generated (Aydin, 2018), while at the most impoverished extreme of the putative imagery continuum, aphantasic individuals who experience an absence of internally generated mental imagery display parallel difficulties in retrieving past events and imagining hypothetical scenarios in the future (Dawes et al., 2020).

These commonalities aside, an individual's proclivity for different imagery strategies (e.g., object versus spatial) likely confers distinct benefits depending on the temporal demands of the constructive task. For past retrieval, stronger object but not spatial imagery is consistently associated with higher levels of sensory detail and a greater sense of autonoetic re-experiencing (Sheldon, Amaral, & Levine, 2017). Furthermore, object imagery is also positively correlated with discrete aspects of recollection, including the number of visual details successfully retrieved, the overall coherence, and the emotional intensity of the recalled experience (Aydin, 2018). In contrast, object imagery has been found to predict only the emotional intensity of simulated events projected into the future (Aydin, 2018), whereas emerging evidence points to spatial imagery as the main actor in supporting the mental construction of prospective thoughts (Wiebels et al., 2020). As such, individual differences in object imagery may diverge across past and future contexts at the level of generated content versus subjective experience, respectively.

1.6 Alterations in visual imagery and constructive abilities in healthy ageing

Age-related changes in vision (Owsley, 2011), visuospatial and visual exploration processes (Wynn, Amer, & Schacter, 2020) also provide important convergent evidence regarding the potential synergies between visual imagery and constructive endeavours. Functional MRI studies in healthy ageing reveal a strong association between diminished imagery strength and age-related memory impairment, attributable to reduced selectivity of visual cortex activation during visual imagery, alongside decreased functional connectivity between the prefrontal cortex and visual association cortices (Kalkstein, Checksfield, Bollinger, & Gazzaley, 2011). The reinstatement of cortical activity in posterior parietal brain regions involved in the encoding of complex visual stimuli is further compromised in healthy ageing (Folville et al., 2020), disrupting the flow of information between these regions and other components of the core network during the elaboration of vivid, imagery-rich scenarios. Mounting evidence from the memory literature highlights a unique age-related disruption in the fidelity, specificity, and precision of contextual and item-specific information, even when age-related decreases in perceptual sensitivity are accounted for (Korkki, Richter, Jeyarathnarajah, & Simons, 2020). These interesting findings predict that tasks that load heavily on visuospatial processes should be disproportionately affected in older adults, as has been demonstrated in studies of mental imagery (Castellano, Guarnera, & Di Nuovo, 2015) and future thinking (Gaesser, Sacchetti, Addis, & Schacter, 2011). An intriguing observation in this context is that the novelty of future simulations may be particularly vulnerable to ageing effects because older adults often default to previously generated mental representations rather than constructing future scenarios ex novo (Schacter, Gaesser, & Addis, 2013). By this view, older adults are likely to recapitulate previously experienced events in their entirety (i.e., "recasting", see Irish, 2016) and to perform particularly poorly on experimental tasks that require the extraction and flexible integration of multiple sensory and visuospatial elements (Schacter et al., 2013).

1.7 Insights from dementia syndromes

Further compelling insights have been gleaned from studying alterations in memory and future thinking capacity in dementia populations, where underlying pathological processes result in a significant departure from the cognitive trajectory of healthy ageing (Andrews-Hanna, Grilli, & Irish, 2019). To date, however, the study of mental imagery in neurodegenerative disorders has proceeded largely independently from the literature on memory-based processes, with little to no crosstalk between these fields. The capacity for future thinking is particularly vulnerable in Alzheimer’s disease, with the suggestion of a common pathological process driving disturbances across past and future contexts (Addis, Sacchetti, Ally, Budson, & Schacter, 2009). Compromised retrieval of semantic information, coupled with visuospatial and executive functioning deficits, has been shown to dramatically impair Alzheimer’s disease patient performance on complex imagery tasks (Hussey, Smolinsky, Piryatinsky, Budson, &

Ally, 2012), with such impairments attributable to degeneration of posterior parietal brain regions (Salimi et al., 2018b). On formal tasks of both memory retrieval and episodic future thinking, patients with Alzheimer's disease display a specific inability to access and harness visual elements to furnish their mental constructions. Such selective decay of visual aspects leads to autobiographical memories that more closely resemble static snapshots rather than temporally extended events (Irish, Lawlor, O'Mara, & Coen, 2011; Irish, Lawlor, O'Mara, & Coen, 2010), comprise tangential or non–self-referential imagery, or are devoid of any visual imagery altogether (Irish, Lawlor, et al., 2011). Unsurprisingly, the capacity to mentally construct spatially contiguous scenes in the mind's eye is grossly impaired in Alzheimer's disease, with patients rating their constructions as vague, divested of rich perceptual detail, and typically re-experienced in black and white (Irish et al., 2015; Wilson et al., 2020).

Although performance deficits in both past and future thinking tasks have been investigated mostly in the context of Alzheimer's disease, an impaired capacity to imagine hypothetical future scenarios is in fact ubiquitous across several dementia subtypes (Irish & Piolino, 2016). For example, patients affected by semantic dementia, a subtype of frontotemporal dementia whereby memory of facts and conceptual knowledge is markedly impoverished, also exhibit diminished ability to engage in prospection (Irish, Addis, Hodges, & Piguet, 2012a). Presumably, this loss is because semantic information aids the recall of perceptual elements associated with one another to support the construction of a spatially coherent, imagery-rich representation in the mind's eye (Irish & Piguet, 2013; Ji, Kavanagh, Holmes, MacLeod, & Di Simplicio, 2019). Importantly, beyond the constraints imposed by the specific profile of cognitive dysfunction, the use of narrative-based tasks in the assessment of autobiographical memory and future thinking in these clinical populations has been recently criticised (Miloyan & McFarlane, 2019), conveying the need for a new breed of objective measures.

1.8 Limitations of commonly employed methodologies in exploring constructive processes

Although it is now well-established that humans largely apprehend, perceive, and experience the world through the visual system, current methodological approaches to evaluate performance in imagery-driven cognitive tasks are limited in their capacity to probe the visual contribution in all its complexity. Contemporary lines of enquiry investigating the neural and behavioural mechanisms in operation when remembering the past and imagining the future have traditionally turned to language as the preferred representational system to index episodic content. Words and images have long been regarded as orthogonal cognitive strategies to each other[1] and given that imagery, by its subjective nature, has proved particularly elusive to formal enquiry, language has often been considered the most accessible pathway to internal cognition. Such language dominance has permeated through to experimental methods, whereby participants are typically asked to describe the contents of their simulations via verbal report. While intuitive and certainly practical, the reliability of this approach has been critiqued, given the requirement for participants to verbalise phenomenological characteristics such as vividness and sensory detail that would otherwise be inaccessible to the investigators (Miloyan & McFarlane, 2019). This is especially the case when constructive endeavours are projected into the future or unfold on temporal scales that are not anchored to a specific past experience or event, since the accuracy or veracity of the simulated scenario cannot be objectively determined (Redshaw & Bulley, 2018). Additionally, when evaluating the richness and coherence of an episodic representation where sensory and perceptual detail is cued, recollected, and further integrated in verbal rather than visual form, more demand is placed on inputs from semantic knowledge. This methodological bias inherently undermines

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[1] Such tendency can be traced back to Ancient Greece, where Socrates affirmed that 'the soul is 'like a book' into which 'a writer within us' inscribes 'statements' and 'opinions' (*doxa*). This writer, however, does not work alone, because there is 'a painter, who paints in our souls pictures (*eikones*) to illustrate the words which the writer has written' (reviewed by MacKisack et al., 2016).

performance in clinical cohorts where the capacity to form and retrieve semantic associations between items and their surrounding contexts progressively deteriorates (Hodges & Patterson, 2007a; Irish, 2020). On such measures, it is difficult to disentangle whether task performance is determined by language proficiency, imagery ability, or the capacity to successfully introspect on one's internal milieu and to adequately capture the complexity of the scenario via verbal report (Conti & Irish, 2021). As one of more of these faculties gradually decline throughout the ageing process or following the onset of a neurodegenerative condition, the reduced viability of currently employed methodologies calls for alternative analytical strategies allowing a systematic evaluation of cognitive performance using objective measures applicable at large.

1.9 Oculomotor behaviour as an adjunct objective measure

In recent years, mounting evidence has increasingly recognised the potential of oculomotor measures in providing a powerful tool to explore foundational processes of episodic memory and future thinking that are otherwise not amenable to self-report (Wynn, Amer, et al., 2020). From a practical perspective, experimental protocols incorporating eye-tracking are not only inexpensive and non-invasive, but they can also be applied to a large number of populations ranging from prelingual infants to clinical cohorts who have lost the capacity to articulate their thoughts and mental experiences, as well as non-human species (Hannula et al., 2010). Most importantly, neuroimaging studies simultaneously recording MEG/EEG data and eye movements during tasks involving attentional and memory processes (e.g., reading, perceptual switching) have consistently found that oculomotor responses are time-locked to the phases of alpha oscillations (Drewes & VanRullen, 2011; Nakatani, Orlandi, & van Leeuwen, 2011; Pan, Popov, Frisson, & Jensen, 2023; Popov, Miller, Rockstroh, Jensen, & Langer, 2021). These findings demonstrate that eye-tracking measures may be employed to complement task-evoked neural activity and provide insight into cognitive mechanisms on comparable timescales (Popov et al., 2021).

Early studies of visual exploration and recognition memory assessing task-concomitant voluntary eye movements in ageing and clinical populations provide strong, auxiliary evidence for several age-related phenomena such as impaired inhibition and relational binding (Ryan, Leung, Turk-Browne, & Hasher, 2007), as well as attentional and visuospatial deficits typical of dementia syndromes (Molitor, Ko, & Ally, 2015). For example, older adults are often found to generate more saccades towards exogenously salient cues, even when explicitly instructed to ignore them or previously warned of their imminent appearance (Erel & Levy, 2016), while also producing more anticipatory saccades towards the location of expected cues (Ryan, Shen, & Reingold, 2006). In contrast, patients with Alzheimer’s disease tend to exhibit atypical fixational patterns by preferentially directing their gaze towards a limited set of visual areas, and largely ignoring novel, unfamiliar, and irregular aspects of the visual environment (Daffner, Scinto, Weintraub, Guinessey, & Mesulam, 1992). These behavioural features have been found to undermine performance in an array of cognitive tasks where timely and efficient processing of visual information is required (Chau et al., 2017; Wynn et al., 2016).

Oculomotor signatures of visual exploration have long been proposed to reliably predict successful encoding and consolidation of to-be-learned information (Fehlmann et al., 2020; Johansson, Nyström, Dewhurst, & Johansson, 2022), as first suggested by the “scanpath hypothesis” (Noton & Stark, 1971). More specifically, converging evidence indicates that in healthy individuals the original eye movement patterns generated during visual inspection of a stimulus or event are spontaneously re-enacted across repeated exposure and during recollection at later timepoints, even when the visual cue is no longer present (Ferreira, Apel,

& Henderson, 2008; Richardson & Spivey, 2000). This unconscious mechanism, referred to as *gaze reinstatement*, is thought to help consolidate relational binding between items and the surrounding context, thus facilitating access to previously formed memories about those items (Wynn, Olsen, Binns, Buchsbaum, & Ryan, 2018; Wynn, Shen, & Ryan, 2019). The acknowledgement that eye movements play an active role in memory encoding is further corroborated by studies comparing performance in free- versus fixed-viewing conditions, whereby recognition accuracy is significantly attenuated when participants are required to maintain fixation or engage in concurrent, guided saccades or smooth pursuit activities (Damiano & Walther, 2019; Henderson, Williams, & Falk, 2005; Ryan, Shen, & Liu, 2020). At the neural level, this drop in performance is accompanied by reduced activation and functional connectivity between cortical regions heavily involved in memory and visuospatial processing, including the hippocampus and the parahippocampal place area (Z. X. Liu, Rosenbaum, & Ryan, 2020). Accordingly, research studies combining eye movement monitoring and neuroimaging techniques indicate that specific patterns of oculomotor behaviour are not only guided by, but also actively support, memory-related processes (Wynn, Liu, & Ryan, 2022). Nonetheless, recent evidence suggests that the bidirectional relationship between memory and active vision may incur a dynamic recalibration in response to increasing task demands up to a critical point beyond which the production of eye movements may no longer be necessary, beneficial, or indeed available, to support performance (Conti & Irish, 2021; Wynn et al., 2019).

Along the same lines, preliminary evidence from studies of episodic future thinking reveals that cognitive load and competition for available resources play a prominent role in constructive endeavours involving complex forms of mental imagery in the absence of externally cued visual stimuli (El Haj & Lenoble, 2018). Indeed, when participants are required to engage in concurrent activities, including voluntary eye movements towards task-irrelevant stimuli, fewer episodic details are generated (de Vito, Buonocore, Bonnefon, & Della Sala, 2015), alongside an abundance of external (non-episodic) details, often taken to reflect off-target or compensatory processes (Strikwerda-Brown, Mothakunnel, Hodges, Piguet, & Irish, 2019). Such reduction in available cognitive resources compromises the curation and/or integration of relevant sensory-perceptual details into the event simulation, further precipitating a compensatory mechanism whereby participants recruit accessible yet tangential, external details to 'fill in the blanks' (Irish, Addis, Hodges, & Piguet, 2012b).

It remains unclear, however, whether spontaneous expressions of oculomotor behaviour such as gaze reinstatement may facilitate future thinking. The additional cognitive effort imposed by the associative demands of future thinking may be predicted to produce a quantitative reduction in eye movements. This would be most evident on open-ended laboratory-based tasks where participants are instructed to envisage an unspecified event that will occur at some point in the future (typically within the next 12 months). Such ambiguity disproportionately taxes the semantic memory system, whereby participants must first generate an appropriate semantic scaffold into which event details can be assimilated (Irish, 2020). Under such conditions, the heightened constructive demands imposed by the open-ended nature of most prospective thoughts would preclude spontaneous oculomotor behaviour. By contrast, on well-defined tasks where the requisite semantic scaffold is embedded in task instructions (e.g., scene construction tasks), greater incidence of spontaneous eye movements may be predicted because the provision of the event cue considerably reduces the generative demands of the mental simulation (Irish, 2020; Sheldon & Levine, 2016).

In summary, the extant literature converges to implicate oculomotor behaviour as central to visually laden forms of memory (Wynn et al., 2019). Compelling evidence indicates that eye movement metrics represent a promising tool to investigate the neural and cognitive mechanisms supporting memory-based constructive endeavours and their respective phenomenology. Furthermore, emerging research suggests that oculomotor variables may prove to be especially informative in the appraisal of dementia-related impairment by enhancing the accuracy of cognitive assessments and diagnosis (Parra, Granada, & Fernández, 2022).

1.10 Summary and overall aims of this thesis

Humans constantly engage in various forms of mental construction, whether it be the result of a dynamic recombination of perceptual and semantic detail retrieved from the past, an episodic simulation projected into the future, or the atemporal construction of scenes. Disentangling the neural and cognitive mechanisms at play as we elaborate and maintain a coherent representation in the mind's eye is a challenging feat. A comprehensive understanding of these processes necessarily relies upon behavioural strategies that can reliably and efficiently index episodic content as experienced through visual mental imagery. Experimental approaches designed to deconstruct these fascinating, complex phenomena must also be comparable with objective standards and applicable to both clinical and healthy populations, as well as developmental cohorts and non-human species. In recent years, mounting evidence has pointed to oculomotor behaviour as one such candidate (Hannula et al., 2010; Z. Liu, Yang, Gu, Liu, & Wang, 2021; Ryan, Shen, & Liu, 2020). This thesis seeks to explore some of the avenues where eye movement measures may provide insight into the mechanisms involved in imagery-driven constructive tasks, by highlighting commonalities and differences in healthy ageing and neurodegeneration.

Specifically, I will examine the contribution of oculomotor behaviour to different expressions of imagery-rich mental constructions through three novel experimental studies. First, I will characterise the relationship between commonly employed measures of visual exploration and memory performance in healthy ageing as well as in selected neurodegenerative conditions where episodic and semantic memory are differentially impaired, namely Alzheimer's disease and semantic dementia, respectively (Chapter 2). In doing so, I will demonstrate that oculomotor profiles may predict deficits in task performance by reflecting potential compensatory mechanisms as the encoding and consolidation of new memories is impeded on the one hand, and the semantic knowledge base progressively deteriorates on the other.

Next, I will investigate how the production of eye movements during atemporal scene construction relying solely on internally generated mental imagery is affected by increasing task complexity in both youth and healthy ageing (Chapter 3). This will enable me to demonstrate how the production of eye movements serves different functions at different stages of the constructive process and to elucidate how such variables are affected when cognitive resources run low, and task demands progressively increase.

Finally, and building on the results of the previous study, I will examine age-related changes in oculomotor profiles in the absence of externally cued visual stimuli during prospection. I will explore how these changes relate to discrete and subjective aspects of the resulting hypothetical scenarios such as the richness in episodic detail and the perceived phenomenology (Chapter 4). Task complexity will be manipulated by adjusting the temporal scale (near vs far future) and level of plausibility (low vs high) of the task stimuli to demonstrate how competition for available cognitive resources differentially affects the production of eye movements in youth and healthy ageing.

It is the intention of this thesis that the findings from these experimental studies will contribute to deepening our comprehension of the behavioural strategies and adaptations supporting cognitive performance in healthy ageing and neurodegeneration. Importantly, the results from the studies presented in this thesis will inform the development of an integrative framework including oculomotor measures as an additional, reliable, and ecologically inexpensive tool to better understand the interplay between imagery-driven and memory-related processes and how this relationship breaks down in healthy ageing and clinical populations.

Chapter 2

Alterations in schema-driven eye movements during visual exploration and episodic memory performance in healthy ageing and neurodegenerative disorders

2.1 Introduction

In recent years, contemporary theories of cognitive and social behaviour have pointed to the role of semantic knowledge in modulating how we perceive, experience, and subsequently remember information (Gilboa & Marlatte, 2017). Prior expectations about people, objects, contexts and events and their corresponding associations in space and time, significantly influence our actions and reactions. Semantic knowledge is also particularly well suited to extracting statistical regularities within the environment to scaffold complex expressions of memory (Irish & Piguet, 2013). Conversely, social environments are often conceived and constructed as expressions of a specific semantic context. For example, places meant for frictionless, almost transactional human interaction such as airport terminals, hotel lounges and grocery stores, rarely come across as foreign or disorienting, even when we have never been there before. The reason for this curious, perhaps striking, feature is that such places tend to present similar layouts (e.g., fresh produce, dairy and other perishable or refrigerated items are usually located along the perimeter of a grocery store), display easily recognisable visual cues (e.g., stick figure bathroom signs, exit signs, disabled parking, etc.), and are generally designed based on widely accepted conventional rules (e.g., the checkouts should be conveniently located somewhere near the exit of a store). These semantic attributes act as a compass to help us navigate our surroundings and ultimately direct human interaction by priming us towards the behaviours that are most appropriate for the situation at hand.

Mounting evidence further indicates that schema-based knowledge structures are not fixed in nature but are regularly updated in the face of new information (Gilboa & Marlatte, 2017). As we age, however, domain-specific knowledge assumes an increasingly prominent role in driving how we perceive, process, and recall external stimuli (Umanath & Marsh, 2014). As such, an active topic in the research literature concerns how schema-based updating influences task performance across the adult lifespan (Kan, Rosenbaum, & Verfaellie, 2020).

2.1.1 Semantic knowledge in healthy ageing

Reliance on prior knowledge in older age may drive proactive interference, whereby older memories disrupt access to recently encountered information (see Umanath & Marsh, 2014 for a review). Similarly, studies of remote memory reveal a natural shift in autobiographical narrative style, whereby cognitively healthy older adults increasingly provide non-episodic details at the expense of episodic specificity (Delarazan, Ranganath, & Reagh, 2022; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). This age-related shift towards off-target information is also evident during future simulation; future narratives are often rich in semantic information that is related, but slightly tangential, to the main event of interest (Schacter, Devitt, & Addis, 2018). While typically interpreted in terms of age-related decline, this shift towards gist-based representations may serve an adaptive purpose (Andrews-Hanna et al., 2019), enabling older adults to circumvent natural reductions in the availability of specific details whilst prioritising information that is familiar and consistent with prior knowledge (Grilli & Sheldon, 2022).

2.1.2 Insights from oculomotor studies

Age-related changes in memory extend beyond narrative style to the domain of visual exploration (see Ryan, Shen, & Liu, 2020; Ryan, Wynn, Shen, & Liu, 2022; Wynn, Amer, et al., 2020 for comprehensive reviews). Recent studies leveraging oculomotor behaviour demonstrate that older adults are more likely to employ gaze reinstatement (i.e., rehearse the eye movement patterns they produced at an earlier time point, Wynn et al., 2019) to support the consolidation and recollection of previously encountered visual stimuli (Wynn et al., 2018; Wynn et al., 2019). Increased reliance on semantic memory and deficits in inhibitory control have further been associated with measures of oculomotor behaviour in ageing (Crawford, Smith, & Berry, 2017), including anticipatory saccades towards locations that are consistent with prior expectations (Ryan et al., 2006), and selective fixation of exogenously salient but contextually irrelevant cues (Nuthmann, Schütz, & Einhäuser, 2020).

A recent study offers important insights into the contribution of semantic knowledge to active vision in the context of healthy ageing. Wynn, Ryan, and Moscovitch (2020) implemented a visual search task with concurrent eye-tracking in younger and older adults in which target objects were displayed in semantically congruent (e.g., a kettle on the stovetop) or incongruent (e.g., a kettle on the floor) locations. The authors examined participants' eye movements as they attempted to locate each target object within the corresponding scene, while also measuring reaction times, the proportion of initial saccades terminating in target congruent areas, as well as the overall percentage of viewing time spent in such areas. Stimuli for this study consisted of naturalistic scenes, such as a kitchen, bathroom, or other real-life setting, paired with common, everyday objects, such as a toaster, toothbrush, and coffee cup. Accordingly, object-location associations were likely to evoke well-established semantic representations, thus providing the opportunity to assess whether younger and older adults differed in the way they deploy this information. This was hypothesised to be further reflected in their oculomotor patterns during task completion. Indeed, analysis of oculomotor behaviour revealed that schema-based knowledge and expectations differentially influenced visual search performance in older adults, resulting in longer search times and greater viewing of target congruent areas across repeated search blocks. Further, older adults showed disproportional impairment in detecting target objects displayed in semantically incongruent locations (Wynn, Ryan, et al., 2020). Taken together, these findings suggest that prior knowledge becomes increasingly important in guiding visual exploration during episodic encoding and retrieval in healthy ageing and may hinder performance when such knowledge is incongruous with to-be-learned information. Nonetheless, whether and to what extent such processes are affected in the face of semantic knowledge loss remains unclear.

2.1.2 Preliminary evidence from dementia syndromes

Semantic dementia is a neurodegenerative disorder characterised by progressive deterioration of the conceptual knowledge base in the context of relatively preserved episodic memory (Hodges & Patterson, 2007b; Irish et al., 2016b). Given the distinctive nature of the semantic impairment, semantic dementia offers a unique opportunity to explore how degradation of prior knowledge impacts performance on tasks involving memory and active vision (Conti & Irish, 2021). In contrast, other forms of dementia such as Alzheimer's disease are characterised by profound episodic memory disturbances alongside visuospatial dysfunction (McKhann et al., 2011; Salimi et al., 2018a), while semantic processes remain relatively intact, at least in the earlier stages of the disease. Eye-tracking studies in dementia have largely focused on Alzheimer's disease, although the majority of work in this area has been conducted under carefully controlled scenarios, such as monitoring oculomotor abnormalities while reading (Fernández et al., 2016) or during laboratory-based recognition tasks (Loftus, 1972).

Importantly, these studies have relied almost entirely on basic, often guided, oculomotor measures such as prosaccades, antisaccades and smooth pursuit analyses to characterise changes in visual attention and inhibitory control (Chau et al., 2017; Crawford & Higham, 2016; see also Molitor et al., 2015 for a comprehensive review; Noiret et al., 2017). Perhaps not surprisingly, these studies converge to suggest alterations of fixational eye movements, increased latency of saccadic movements, as well as reduced accuracy of smooth pursuit performance in Alzheimer's disease. While informative, such approaches fail to capture the dynamic way in which humans apprehend and encode information in daily life (Seligman & Giovannetti, 2015).

Studies coupling exploratory eye movements with incongruous or unpredictable targets in dementia populations are rare. An early study on curiosity in Alzheimer's disease examined the preference for directing visual gaze to novel, unfamiliar, and irregular aspects of the visual environment (Daffner et al., 1992). Relative to age-matched healthy controls, patients with Alzheimer's disease spent significantly less time looking at incongruous stimuli; an effect which was not explained by attentional deficits or impairment in ocular motility. The authors interpreted this pattern in terms of diminished novelty-seeking and impaired identification of novel, complex, or incongruous stimuli in Alzheimer's disease (Daffner et al., 1992). These findings were corroborated by a later study investigating visual exploration in Alzheimer's disease using complex scenes with unpredictable targets (Moser, Kömpf, & Olschinka, 1995). Again, saccadic eye movements analyses indicated that Alzheimer's disease patients often overlooked scene regions with unusual or incongruent elements or discovered them later in the viewing session.

While a handful of studies have probed the dynamic interaction between memory and active vision in Alzheimer's disease, just one study, to my knowledge, has explored oculomotor behaviour during cognitive task performance in semantic dementia. Mengoudi et al. (2020) applied a self-supervised machine learning algorithm to oculomotor data obtained under free-viewing conditions in semantic dementia during scene exploration, semantic processing, and recognition memory. Using this approach, the authors revealed less extensive and slower visual sampling in semantic dementia as well as repeated fixation patterns directed towards a limited set of visual areas (Mengoudi et al., 2020). These oculomotor signatures support the hypothesis that early cognitive dysfunction is detectable through the analysis of eye movement patterns, at least to some extent, thus paving the way for future research on cognitive function in dementia syndromes incorporating eye-tracking paradigms.

2.1.3 Study objectives

In summary, the available evidence points to qualitative differences in how neurodegenerative disorders sample the visual world. It remains unclear, however, how pathological changes in oculomotor behaviour impact the recollection and dynamic integration of previously encountered visual stimuli in the context of existing prior knowledge. The present study sought to address this gap in the literature by adapting the visual search and memory task paradigm employed by Wynn, Ryan, et al. (2020) for use in a well-characterised group of patients with semantic dementia and Alzheimer's disease. First, I sought to replicate the results of the original study by comparing memory and oculomotor performance in healthy younger and older participants. Subsequently, I set to establish how the progressive and cross-modal degeneration of the semantic knowledge base impacts the relationship between memory performance and active vision in semantic dementia. Given that performance in congruous trials requires the deployment of prior knowledge, I expected greater impairments in congruous relative to incongruous trials in semantic dementia compared to control participants (i.e., Congruous < Incongruous). In contrast, for Alzheimer's disease, I predicted greater impairments in visual search and memory performance compared to both controls participants and semantic dementia in incongruous relative to congruous trials (i.e., Congruous > Incongruous), reflecting marked episodic memory dysfunction in the context of less severe semantic memory impairment.

2.2 Methods

2.2.1 Participants

A total of seventy participants were recruited for this study including 24 young adults, 24 older adults, and 22 patients diagnosed with either semantic dementia (SD; 10 participants) or Alzheimer's disease (AD; 12 participants). A posteriori power calculations on sample sizes were performed using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007). The results of such analyses are presented in the corresponding sections based on the participant groups considered and the statistical tests employed therein. The demographic data for the study participants are presented in Table 2.1.

Table 2.1 Demographic information for study participants.

	Younger adults (n = 24)	**Older adults (n = 24)**	**Alzheimer's disease (n = 12)**	**Semantic dementia (n = 10)**
Sex (M : F)	5 : 19	7 : 17	6 : 6	3 : 7
Age (y)	19.79 (1.74)	66.66 (5.95)	65.08 (6.16)	69.1 (6.40)
Education (y)	14.38 (0.47)	13.90 (2.66)	14.92 (2.12)	12.7 (3.48)

Notes: Years of age and education presented as means with corresponding standard deviations in parentheses.

Younger adults were undergraduate Psychology students at the University of Sydney recruited via the Sydney University Psychology SONAPsych Research Participation System and took part in the study in exchange for course credit. Older adults and participants with dementia were recruited through FRONTIER, the frontotemporal dementia research clinic based at the Brain and Mind Centre, University of Sydney, Australia. A comprehensive clinical investigation, along with cognitive assessment and structural brain imaging was conducted in the older and the dementia groups. Older adults were required to score above 88/100 in the Addenbrooke's Cognitive Examination-III (ACE-III; Hsieh, Schubert, Hoon, Mioshi, & Hodges, 2013; So et al., 2018), 0 on the Clinical Dementia Rating Scale (Knopman et al., 2008) and to perform within normal limits on all behavioural and cognitive measures. Dementia patients scoring <45 on the ACE-III test were excluded from the study due to the severity of their cognitive impairment. Exclusion criteria for younger and older participants included concurrent psychiatric, depression and/or anxiety diagnosis, presence of other dementia or neurological syndrome, traumatic brain injury and/or history of alcohol or substance abuse. All participants had normal or corrected-to-normal vision.

Dementia diagnosis was established by a multidisciplinary team including a senior neurologist, neuropsychologist, and an occupational therapist, based on clinical investigations and structural MRI. Briefly, semantic dementia (SD) was diagnosed in line with current clinical diagnostic criteria (Gorno-Tempini et al., 2011) based on the presence of word finding and comprehension difficulties as well as progressive loss of knowledge about objects and people in the context of relative preservation of phonology and fluency, visuospatial and everyday episodic memory function. On structural neuroimaging, SD patients displayed marked anterior temporal lobe atrophy, including 6 cases with greater left- relative to right-sided atrophy and 4 cases with the converse profile. A linear mixed effects model revealed no significant differences between the left and right SD subgroups in terms of the key outcome measures of the present study, namely task accuracy, reaction time, and time spent in target congruent areas (all p-values > .05), thus enabling me to combine the data into a single SD group. Participants were diagnosed with clinically probable Alzheimer's disease according to current diagnostic criteria (McKhann et al., 2011), based on the presence of episodic memory and visuospatial dysfunction, compromised functional impairment, and significant medial temporal and posterior parietal atrophy on structural MRI. Patients with atypical presentations of AD such as posterior cortical atrophy or logopenic progressive aphasia were excluded.

2.2.2 Cognitive Testing

Prior to the experimental task, older adults and dementia participants completed a comprehensive neuropsychological test battery covering the domains of attention, memory, language, and visuospatial processing. Tests included the Addenbrooke's Cognitive Examination-III (ACE-III; Hsieh et al., 2013; So et al., 2018), the Sydney Language Battery (SYDBAT; Savage et al., 2013), the Rey–Osterrieth Complex Figure Test (RCFT; Rey, 1941), Digit Span Forwards and Backwards (Wechsler, 1997), and the Trail Making Test (TMT; Reitan, 1958).

2.2.3 Eye tracking apparatus

Participants performed the experimental task while seated in a neutral upright position 50 cm from a 1920 x1080 resolution, 19″ Dell M991 monitor. The height of the chair and the chinrest utilized during the task were adjusted so that participants' gaze was directed to the centre of the screen. We used an Eyelink II eye tracking system (SR Research Ltd., Mississauga, Ontario), with a sampling rate of 500Hz, to record monocular eye movements of the right eye. Prior to the first block of the task, a 9-point calibration and validation procedure was conducted. Participants were allowed to wear glasses during the task provided no reflexes were detected during the calibration and the Eyelink could successfully recognise participants' pupils.

2.2.4 Experimental task design

A modified version of the task developed by Wynn, Ryan, et al. (2020) was used, whereby participants performed a visual search task across 3 learning blocks, followed by a surprise memory block. To ensure suitability for dementia populations, the task was shortened from 4 learning blocks to 3, and a total of 32 trials were completed per block (instead of 72 trials per block in the original study).

2.2.5 Task stimuli

Stimuli comprised 32 naturalistic scenes selected from the Berlin Object in Scene Database (Mohr et al., 2016) and divided into 4 groups of 8, based on the following four scene categories: kitchen, bathroom, office, and garden. Each image contained one everyday target object (e.g., a rubber duck in a bathroom), that was displayed in either a semantically congruent (e.g., on the bathtub) or incongruent (e.g., somewhere on the floor) location (see Figure 2.1). Target locations were counterbalanced across participants. Importantly, images were photographed under carefully controlled conditions with respect to photographic parameters and were corrected for optical distortions (see Mohr et al., 2016). Target objects were consistently kept clear of the centre of the image and its outer margin, while congruent and incongruent target locations had a comparable distance from the image centre, as well as a comparable spatial distribution over the entire collection of scenes.

Figure 2.1 Example of stimuli for the visual search and memory task.

Notes: Bathroom scene displaying a rubber duck in a semantically congruent (left) and incongruent (right) location. The wider rectangle in the congruent scene denotes the target congruent area.

2.2.6 Procedure

The experimental task consisted of 4 blocks with 32 trials each. Blocks 1-3 were identical and constituted the visual search task, while Block 4 served as a surprise memory task.

Visual search task (Blocks 1-3)

On each trial, participants were first shown a fixation cross at the centre of the screen (1 second), followed by the name of the target object to search for in the upcoming trial (1.5 seconds). After a short gap interval of 400ms (black screen), a picture appeared in the centre of the screen and participants were given 4.5 seconds to locate and click on the target object using a computer mouse. Participants were not allowed to click multiple times and once they selected a particular location, a red square would appear to confirm that their answer had been recorded. Regardless of individual reaction times or participant group, each image remained on the screen for the entire 4.5 seconds allocated for the visual search, following which the next trial automatically began. Figure 2.2 illustrates the task design for a sample trial from the visual search task.

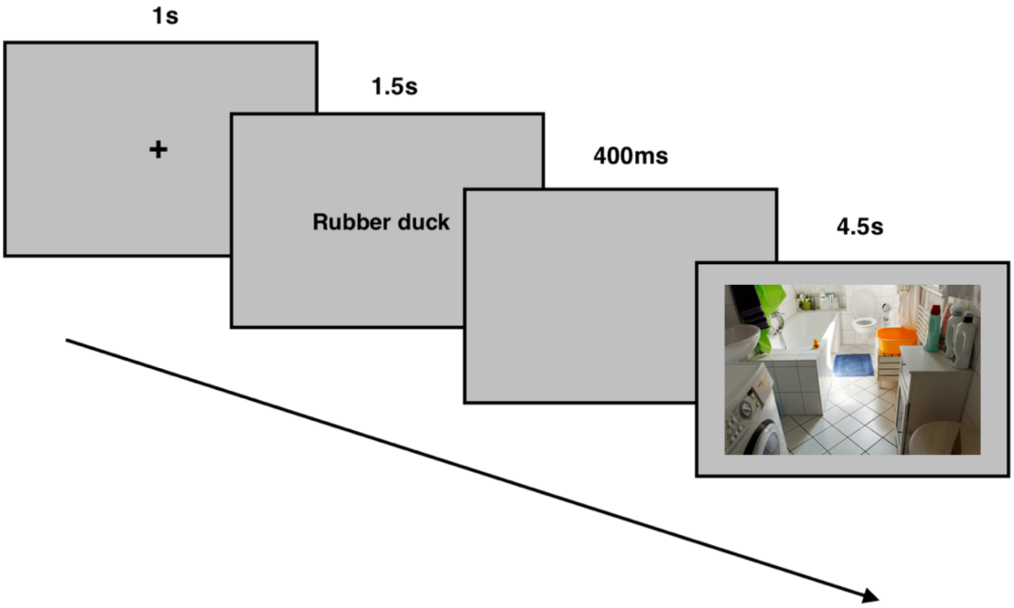

Figure 2.2 Visual search and memory task design.

Notes: Timeline of a sample trial from the visual search task. Each trial started with a fixation cross displayed in the centre of the screen for 1s, followed by the name of the target object (1.5s). After a short gap interval (400ms), a picture of the scene in question would appear and participants were given 4.5 seconds to locate and click on the target object with a computer mouse.

Memory task (Block 4)

Once the visual search task was completed, participants were informed that they would perform a surprise memory task. The experimental procedure (fixation cross, target object name, etc..) was the same as for Blocks 1-3 (i.e., 32 trials), and scenes were presented in the same order as in previous blocks. The only difference between Block 4 and the previous visual search blocks was that the target objects were now absent from the scenes. As a result, participants had to recall and indicate (via a mouse click) the locations where target objects had been displayed in the visual search.

2.2.7 Statistical analyses

Potential group differences in neuropsychological test performance between older controls and the dementia groups were explored using one-way ANOVAs with Games-Howell post-hoc tests. Benjamini-Hochberg corrections were employed to control for multiple comparisons.

Oculomotor performance on the visual search task (Blocks 1-3) and memory task (Block 4) was analysed via linear mixed effects analyses and Sidak post-hoc tests using R (R Core Team, 2012, version 4.2.0) and *afex* (Singmann, Bolker, Westfall, Aust, & Ben-Shachar, 2022) MATLAB (The MathWorks Inc, 2017). Normality of distributions and homogeneity of variances were examined using Kolmogorov–Smirnov tests and Levene tests, respectively. For the visual search task, the key variables of interest were: reaction time (i.e., time to target detection in seconds), task accuracy (% of trials where the target object was successfully located within the 4.5s time limit), and time spent in the semantically congruent area for each target object (measured in seconds). Similarly, for the memory task, the main outcome measures were: reaction time, task accuracy (i.e., % of successful trials where the location of the target object was successfully recalled within the 4.5s time limit), and time spent in the semantically congruent area for each target object (measured in seconds).

Linear mixed model analyses (LME) were run for each variable of interest, with "Group" as a fixed effect, and "Subject Number" and "Condition" (Congruent or Incongruent) as random effects. For the ageing replication component (section 2.3), "Group" comprised young adults and healthy older adults, while for the dementia component (section 2.4), "Group" comprised healthy older adults, SD, and ADs. The significance of each fixed and random effect was evaluated using ANOVAs, as were significant interactions between experimental factors. The accuracy data were transformed using a quadratic function prior to the linear mixed model analyses, due to the presence of a single outlier datapoint in the percentage of successful trials on both tasks. Pearson correlation analyses were conducted to explore potential associations between experimental task performance, oculomotor data, and key cognitive domains in the healthy control and dementia groups, separately.

For healthy older adults and both patient groups, I also calculated the degree of overlap of eye movement patterns over consecutive blocks in both the visual search task and memory task (referred to here as “gaze reinstatement”). For each participant and for each trial, I considered the scan paths generated in Blocks 2, 3 and 4 (memory block) and calculated a separate visual density map for each of these blocks. Given that each picture was displayed in the centre of the screen and measured 1000x667 pixels, I divided this visual array into rectangles of 25x23 pixels. I then constructed a density matrix where each entry corresponded to the number of datapoints in the participant’s scan path for that particular trial that were detected within the corresponding visual array. In the visual search task, I compared the density maps obtained from Blocks 2 and 3 by calculating their cosine similarity. For each participant, the resulting similarity scores were averaged within conditions (i.e., over the 16 congruent trials and 16 incongruent trials), to yield 2 values representing the participant’s average gaze reinstatement in the congruent and incongruent conditions, respectively. The same analytical procedure was adopted for the memory condition, but this time I compared the density maps obtained from Blocks 3 and 4. As before, I conducted LME analyses on the gaze reinstatement scores with “Group” as a fixed effect, and “Subject Number” and “Condition” (Congruent or Incongruent) as random effects. A logarithmic transformation of the data was applied due to the presence of a few outlier datapoints. Finally, for each experimental condition, I ran Pearson correlation analyses between gaze reinstatement scores in both tasks and performance scores in the memory task.

2.3 Replication study in healthy ageing

First, I sought to replicate the ageing effects reported by Wynn, Ryan, et al. (2020) in my cohort of healthy older participants. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample of 48 participants was sufficient to detect a significant main effect of size $f = 0.5$ with 97% power and an alpha level of 0.05 and a significant two-way interaction of size $f = 0.25$ with 99% power and an alpha level of 0.05.

2.3.1 Visual Search Task

Reaction times

Analyses from the linear mixed model for reaction time on the visual search task revealed a significant effect of Group ($F(1,46) = 10.40$; $p = .002$) whereby older adults performed more poorly relative to their younger counterparts ($p = .002$). A main effect of Condition ($F(1,46) = 96.06$; $p < .001$) further reflected the fact that irrespective of group, reaction times were significantly slower in the Incongruent relative to Congruent condition ($p < .001$, see Figure 2.3). The Group x Condition interaction was not significant ($F(1,46) = 2.55$, $p = .117$).

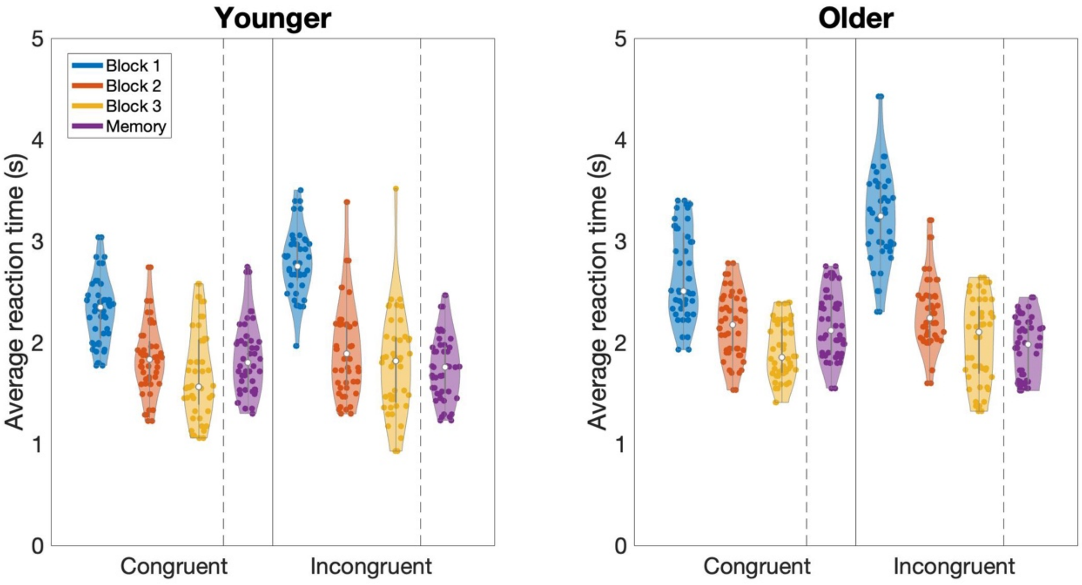

Figure 2.3 Reaction times in younger versus older participants in the visual search and memory tasks.

Notes: Mean reaction times (s) for younger (left) and older participants (right), by block and congruency (Congruent/Incongruent). Violin plots were obtained using the *violinplot* function from the Matlab repository Bechtold (2016).

Percentage of successful trials

The linear mixed model failed to reveal a significant effect of Group ($F(1,46) = 1.81, p =.186$). However, a significant main effect of Condition was found ($F(1,46) = 184.12$; $p <.001$) indicating that accuracy was significantly higher in the Congruent relative to Incongruent condition, irrespective of group ($p <.001$). Finally, the Group x Condition interaction was also significant ($F(1,46) = 9.71$; $p =.003$). Post-hoc tests on the interaction term indicated that older adults showed reduced visual search accuracy relative to their younger counterparts in Incongruent ($p = .02$), but not Congruent trials ($p = .57$). Post-hoc tests also confirmed that both groups performed better in Congruent relative to Incongruent trials (Mean difference in performance: Younger adults: 30.9%, $p <.001$; Older adults: 49.4%, $p < .001$, see Figure 2.4), although this discrepancy in performance accuracy between conditions was higher in older compared to younger participants (49.4% - 30.9% = 18.5%, $p = .003$).

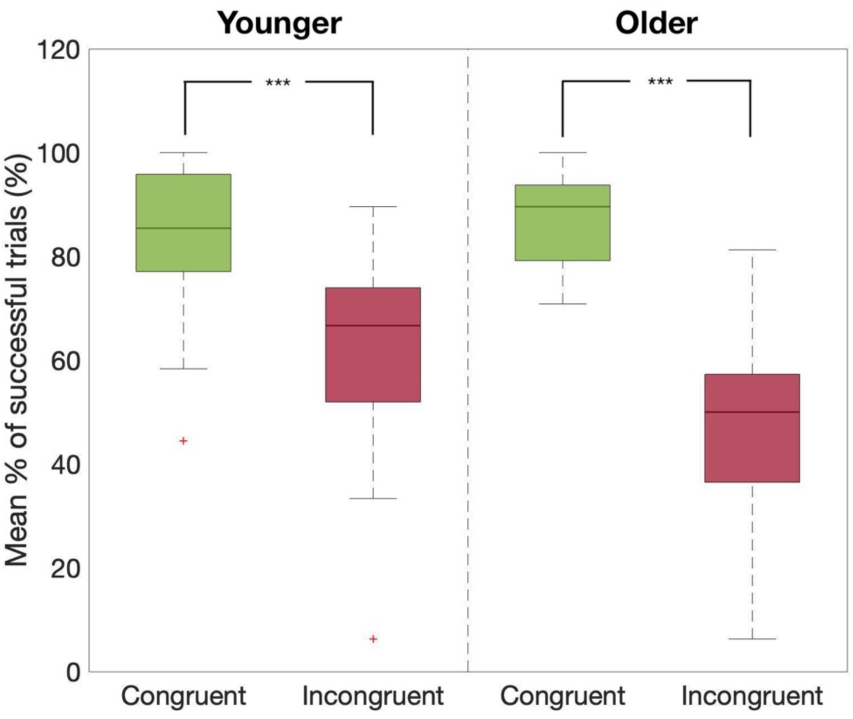

Figure 2.4 Performance scores in younger versus older participants on the visual search task.

Notes: Visual search task accuracy as indexed by the mean percentage of successful trials for healthy younger (left) and older adults (right) in Congruent (left side box plots, in green) and Incongruent trials (right side boxplots, in red). Visual search accuracy is averaged across the three visual search blocks. *$p < .05$; **$p < .01$; ***$p < .001$.

Time spent in target congruent areas

The linear mixed model revealed a significant main effect of Group ($F(1,46) = 4.79$; $p = .034$), indicating that older adults spent significantly more time in target congruent areas relative to their younger counterparts (see Figure 2.5). A significant main effect of Condition was also found ($F(1,46) = 149.72$; $p < .001$) whereby, irrespective of group, participants spent significantly more time in target congruent areas in Congruent versus Incongruent trials. The Group x Condition interaction was not significant ($F(1,46) = 0.58$; $p = .449$).

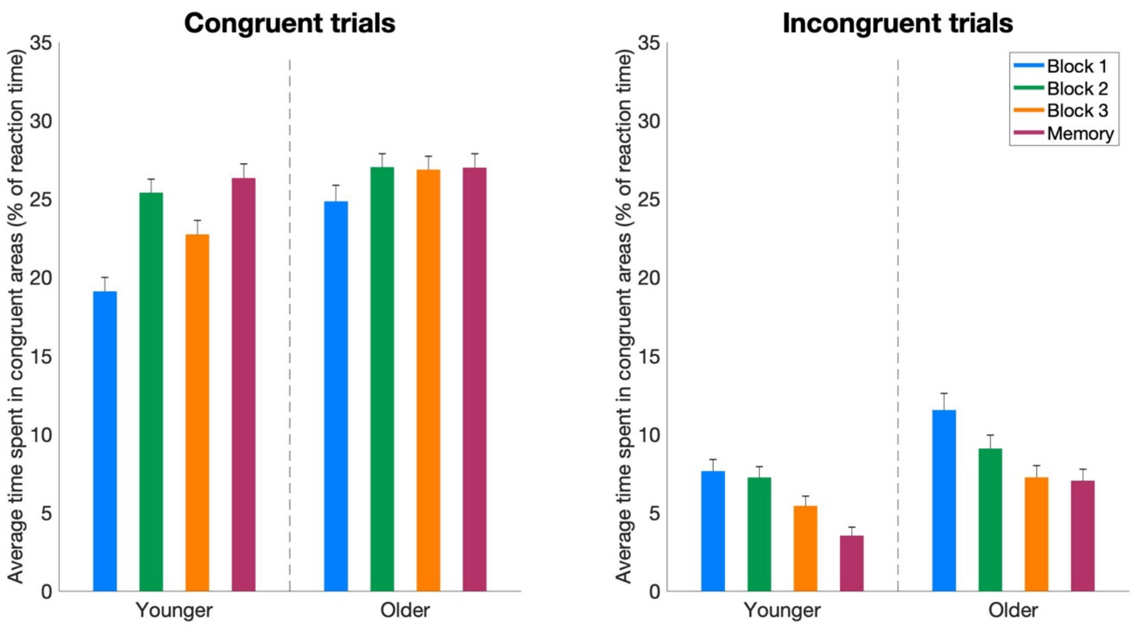

Figure 2.5 Average time spent in target congruent areas in younger versus older participants in the visual search task.

Notes: Average time younger and older participants spent in target congruent areas in the visual search task (Blocks 1-3) and memory task (Block 4) in Congruent (left bar plots) and Incongruent (right bar plots) trials. Data are calculated as a percentage of participants' reaction time. Error bars correspond to one standard error.

2.3.2 Memory Task

Reaction times

The linear mixed model for reaction time on the memory task revealed a significant effect of Group ($F(1,46) = 10.53$; $p = .002$) whereby older adults performed more poorly relative to their younger counterparts (see Figure 2.3). In contrast, the model failed to reveal both a significant main effect of Condition ($F(1,46) = 0.09$; $p = .776$) or a significant Group x Condition interaction ($F(1,46) = 0.09$, $p = .771$).

Percentage of successful trials

The linear mixed model failed to reveal a significant effect of Group (*F*(1,46) = 3.13, *p* =.083). However, a significant main effect of Condition was found (*F*(1,46) = 75.74; *p* <.001) indicating that accuracy was significantly higher in the Congruent relative to Incongruent condition, irrespective of group. The Group x Condition interaction was also significant (*F*(1,46) = 7.72; *p* =.008). As in the visual search task, post-hoc tests on the interaction term indicated that older adults showed reduced memory accuracy relative to their younger counterparts in Incongruent (*p* = .03), but not Congruent trials (*p* = .64). Post-hoc tests also confirmed that both groups performed better in Congruent relative to Incongruent trials (Mean difference in performance: Younger adults: 23.0%, *p* <.001; Older adults: 44.7%, *p* < .001, see Figure 2.6), although, once again, the discrepancy in performance accuracy between conditions was higher in older compared to younger participants (44.7% - 23.0% = 21.7%, *p* = .008).

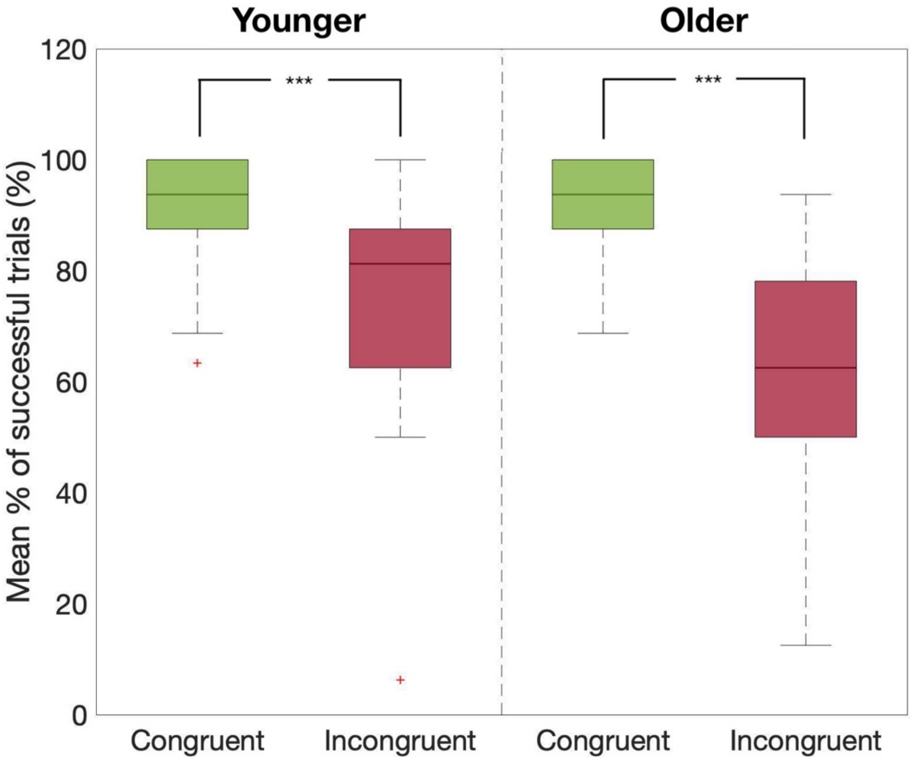

Figure 2.6 Performance scores in younger versus older participants on the memory task.

Notes: Memory task accuracy as indexed by the mean percentage of successful trials for healthy younger (left) and older adults (right) in Congruent (green) and Incongruent (red) trials. Visual search accuracy is averaged across the three visual search blocks. **p* < .05; ***p* < .01; ****p* < .001.

Time spent in target congruent areas

The linear mixed model failed to reveal a significant main effect of Group (*F*(1,46) = 1.09; *p* =.303). In contrast, a significant main effect of Condition was found (*F*(1,46) = 136.31; *p* <.001) whereby, irrespective of group, participants spent significantly more time in target congruent areas in Congruent versus Incongruent trials (see Figure 2.7). The Group x Condition interaction was not significant (*F*(1,46) = 0.48; *p* =.492).

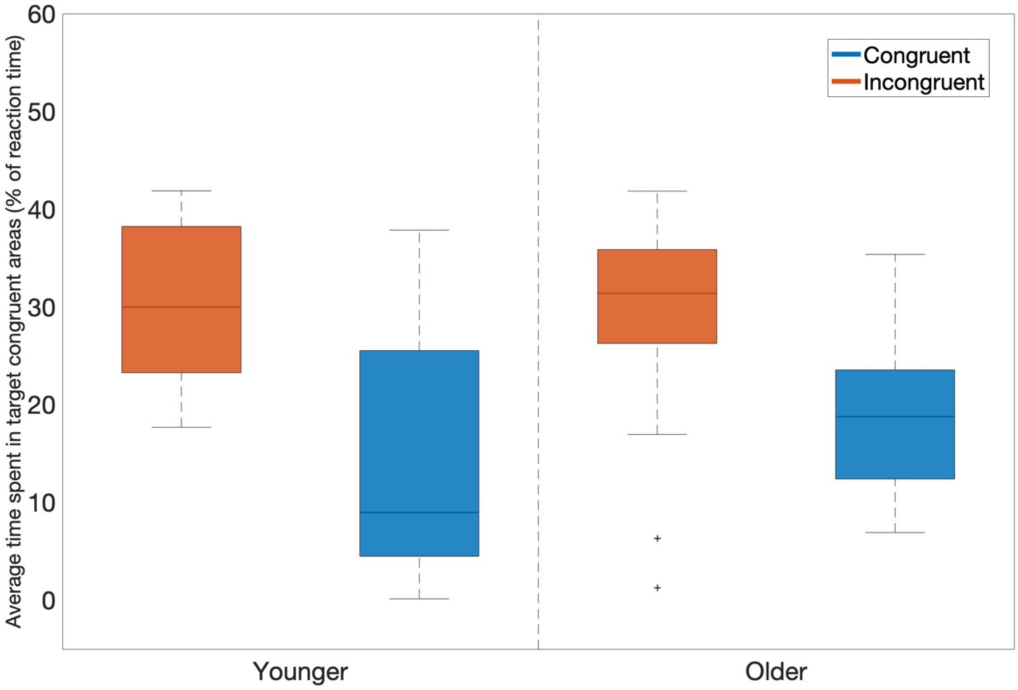

Figure 2.7 Average time spent in target congruent areas in younger versus older participants in the memory task.

Notes: Average time younger (left) and older participants (right) spent in target congruent areas in the memory task in Congruent (left side boxplots, in orange) and Incongruent (right side boxplots, in blue) trials. Data are calculated as a percentage of participants' reaction time.

2.3.2 Summary

Results from the linear mixed model analyses indicated that reaction times were slower in older relative to younger adults, irrespective of task or experimental condition. In both the visual search and the memory task, older adults exhibited reduced accuracy (i.e., lower percentage of successful trials), however this was exclusively in Incongruent trials. Older participants were also found to spend a significantly longer time in target congruent areas compared to their younger counterparts in the visual search task, whereas no significant differences or interactions were found for the time spent in target congruent areas in the memory task.

Overall, my results align well with the original study by (Wynn, Ryan, et al., 2020) in suggesting that older adults rely on semantic knowledge to a greater extent than younger adults and that this tendency undermines performance when target objects appear in locations inconsistent with prior expectations. More precisely, in Congruent trials older adults can draw from their rich conceptual knowledge base to inform visual exploration and therefore improve memory consolidation and subsequent recollection. In contrast, when pre-existing semantic associations are violated, as happens in Incongruent trials, prior expectations are not relevant to the task at hand and successful performance requires the inhibition of previous associations from conceptual knowledge and a greater reliance on perceptual features.

2.4 Oculomotor behaviour and memory performance in dementia

Following my analyses of oculomotor behaviour and memory performance in healthy ageing, I focused on potential group differences between cognitively healthy older adults, and two cohorts of patients affected by either Alzheimer's disease or semantic dementia. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample of 46 participants was sufficient to detect a significant main effect of size *f* = 0.5 with 93% power and an alpha level of 0.05 and a significant two-way interaction of size $f = 0.25$ with 99% power and an alpha level of 0.05.

2.4.1 Clinical and demographic information

Relative to Controls, both SD and AD groups displayed characteristic cognitive profiles in keeping with their clinical diagnoses (see Table 2.2). Direct comparison of the patient groups revealed comparable overall disease severity as indexed by disease duration (years elapsed since first reported symptoms; $p = .3$) and overall cognitive performance on the ACE-III screening tool ($p = .07$). SD patients showed disproportionate semantic processing impairments on the SYDBAT Naming, Comprehension, and Semantic Association subscales relative to AD (all p values $< .05$). In contrast, visuospatial memory was disproportionately affected in AD relative to SD as indicated by RCF % Retained scores ($p = .02$).

Table 2.2 Neuropsychological test performance for Control, Alzheimer's disease, and semantic dementia study participants.

	Controls (n=24)	AD (n=12)	SD (n=10)	*F*	*p*-adjusted	Post hoc tests	*p*-value
Disease duration [y]	N/A	4.79 (2.45)	6.42 (4.13)	1.20	.3	ns	n/a
ACE-III Total [100]	96.50 (2.52)	75.33 (11.05)	64.4 (10.93)	59.44	***	AD < C	***
						SD < C	***
ACE-III Attention [18]	17.54 (0.66)	13.75 (3.67)	15.40 (1.84)	11.84	**	AD < C	*
						SD < C	*
ACE-III Memory [26]	25 (1.02)	15.17 (4.86)	13.80 (4.85)	46.98	***	AD < C	***
						SD < C	***
ACE-III Fluency [14]	12.75 (1.36)	8.25 (2.05)	6.20 (2.62)	43.97	***	AD < C	***
						SD < C	***
ACE-III Language [26]	25.46 (0.78)	23.67 (2.81)	13.90 (4.02)	40.80	***	SD < AD	***
						SD < C	***
ACE-III Visuospatial [16]	15.75 (0.61)	14.50 (2.11)	15.10 (1.37)	2.78	.09	ns	n/a
Trails A [secs][a]	32.46 (9.00)	45.83 (11.07)	43.10 (18.99)	7.01	**	AD > C	**
Trails B [secs][a]	72.25 (29.10)	191.42 (118.63)	131.40 (85.10)	7.57	**	AD > C	*
Trails B-A [secs][a]	39.79 (26.92)	145.58 (115.10)	88.30 (72.02)	6.53	*	AD > C	*
Digit span Forwards [16]	12.04 (2.25)	8.50 (1.35)	10.10 (2.60)	9.41	**	AD < C	***
Digit span Backwards [14]	7.71 (2.31)	5.0 (1.54)	6.40 (2.55)	8.48	**	AD < C	***
RCF % Retained [%][b, c]	62.31 (15.85)	18.53 (21.98)	45.93 (26.20)	19.33	***	AD < C	***
						SD < C	*
						AD < SD	*
SYDBAT Naming [30][c]	27.83 (1.66)	24.75 (2.86)	7.89 (5.51)	58.12	***	AD < C	*
						SD < C	***
						SD < AD	***
SYDBAT Comprehension [30]	29.71 (0.55)	27.33 (2.19)	20.30 (5.44)	20.53	***	AD < C	**
						SD < C	**
						SD < AD	**
SYDBAT Semantic association [30][c]	28.29 (1.30)	25.58 (1.38)	18.67 (6.96)	22.17	***	AD < C	***
						SD < C	**
						SD < AD	*
SYDBAT Repetition [30]	29.96 (0.20)	29.58 (0.67)	27.80 (3.58)	3.42	**	ns	n/a

Notes: Data presented as mean values with standard deviations in parentheses. Maximum test score and unit of measurement presented in square brackets where appropriate. [a]Higher scores denote poorer performance. [b]RCF % retained = RCF 3min recall/ RCF Copy *100. [c]Missing data: 1 SD. P-adjusted values for omnibus test obtained using Benjamini-Hochberg procedure. Post hoc group differences established using Games-Howell tests. AD = Alzheimer's disease; C = Controls; SD = semantic dementia. *$p < .05$; **$p < .01$; ***$p < .0001$

2.4.2 Visual Search Task

Reaction Time

The linear mixed model for reaction time on the visual search task revealed a significant effect of Group (*F*(2,43) = 8.78; *p* <.001) whereby AD patients were significantly slower relative to Controls (*p* < .001). In contrast, no significant difference was observed between SD and Controls (*p* = .11). A main effect of Condition (*F*(1,43) = 76.70; *p* <.001) reflected the fact that irrespective of group, reaction times were significantly slower in the Incongruent relative to Congruent condition (*p* <.001; see Figure 2.8). The Group x Condition interaction was found to approach significance (*F*(2,43) = 2.88; *p* =.067). Exploratory post-hoc tests on the interaction term revealed that AD reaction times were slower compared to Controls irrespective of condition (both *p*-values = .002). In contrast, SD reaction times were slower in Congruent trials only (Congruent trials: *p* = .04; Incongruent trials: *p* =.33). No significant differences were found between the patient groups (both *p*-values >.1).

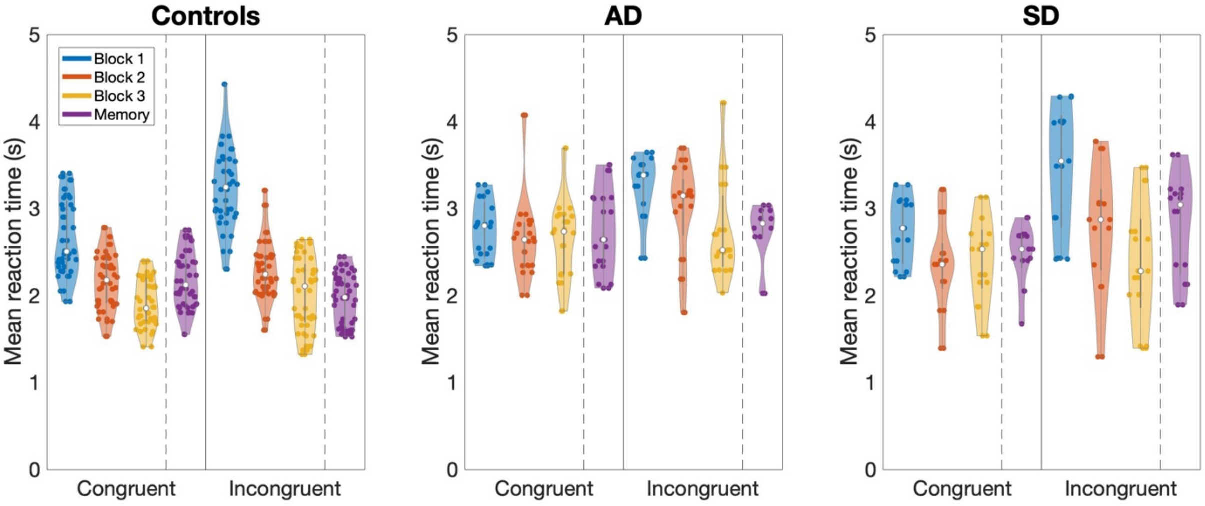

Figure 2.8 Reaction times in dementia syndromes versus controls in the visual search and memory tasks.

Notes: Mean reaction times for healthy older adults (left), AD (centre) and SD (right) participants according to block (Visual Search: Blocks 1-3; Memory task: Block 4) and congruency (Congruent/Incongruent). Violin plots were obtained using the *violinplot* function from the Matlab repository (Bechtold (2016).

Percentage of successful trials

The linear mixed model revealed a significant effect of Group ($F(2,43) = 15.47$; $p < .001$), whereby both patient groups significantly underperformed compared to Controls (AD: $p = .0001$; SD: $p = .003$). A significant main effect of Condition was also found ($F(1,43) = 128.62$; $p < .001$) indicating that accuracy was significantly higher in the Congruent relative to Incongruent condition, irrespective of group. Finally, the Group x Condition interaction was significant ($F(2,43) = 6.73$; $p = .003$). Post-hoc analyses on the interaction term using the Benjamini-Hochberg procedure indicated reduced visual search accuracy in AD relative to Controls irrespective of condition (Congruent: $p < .001$; Incongruent: $p = .03$). SD patients, by contrast, displayed poorer accuracy exclusively in Congruent trials ($p < .001$), scoring in line with Control performance in Incongruent trials ($p = .46$). Post-hoc tests on the interaction term further confirmed that all groups performed better in Congruent relative to Incongruent trials (Mean difference in performance: Controls: 49.4%, $p < .001$; AD: 36.4%, $p < .001$; SD: 22.2%, $p = .001$; see Figure 2.9), however the discrepancy in performance accuracy between conditions was found to be highest in Controls and smallest in SD. Comparisons of mean differences in performance were found to be statistically significant between control participants and SD (49.4% - 22.2% = 27.2%, $p = .002$), but not between control participants and AD or between patient groups (both $p > .05$).

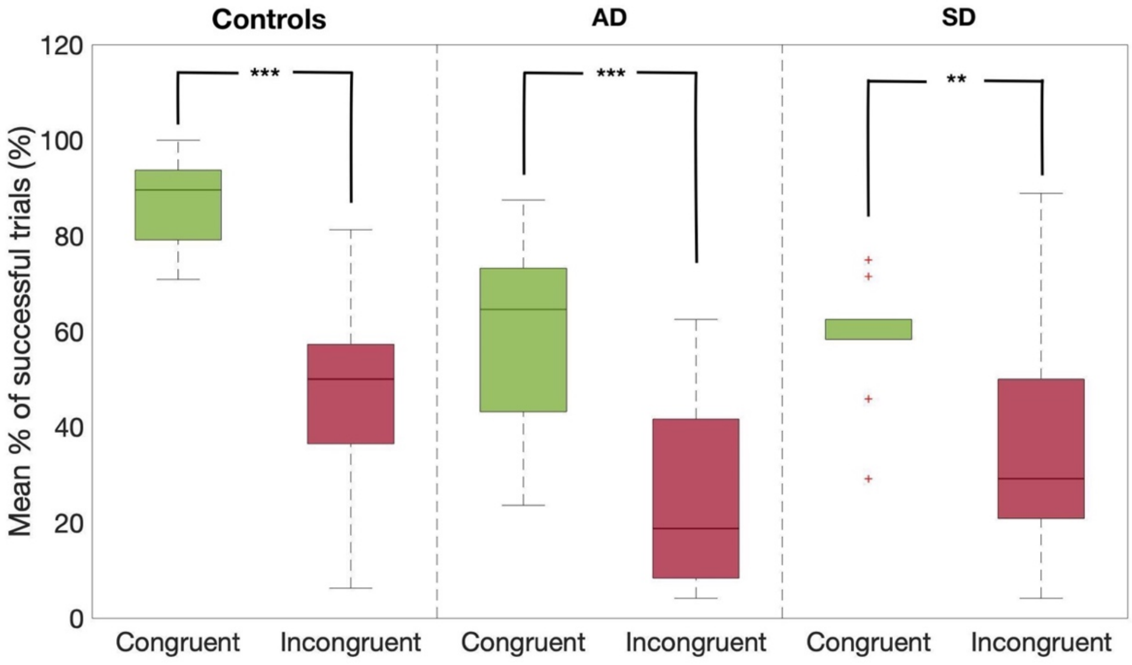

Figure 2.9 Performance scores in dementia syndromes versus controls on the visual search task.

Notes: Visual search task accuracy as indexed by the mean percentage of successful trials for healthy older adults (left), AD (centre) and SD (right) participants in Congruent (left side box plots, in green) and Incongruent trials (right side boxplots, in red). Visual search accuracy is averaged across the three visual search blocks. *$p < .05$; **$p < .01$; ***$p < .001$.

Time spent in target congruent areas

The linear mixed model failed to reveal a significant main effect of Group ($F(2,43) = 1.14$; $p = .33$), suggesting that all groups spent a comparable amount of time in target congruent areas (see Figure 2.10). However, a significant main effect of Condition was found ($F(1,43) = 86.64$; $p < .001$) whereby, irrespective of group, participants spent significantly more time in target congruent areas during Congruent as opposed to Incongruent trials ($p < .0001$). The Group x Condition interaction was not significant ($F(2,43) = 1.50$; $p = .24$).

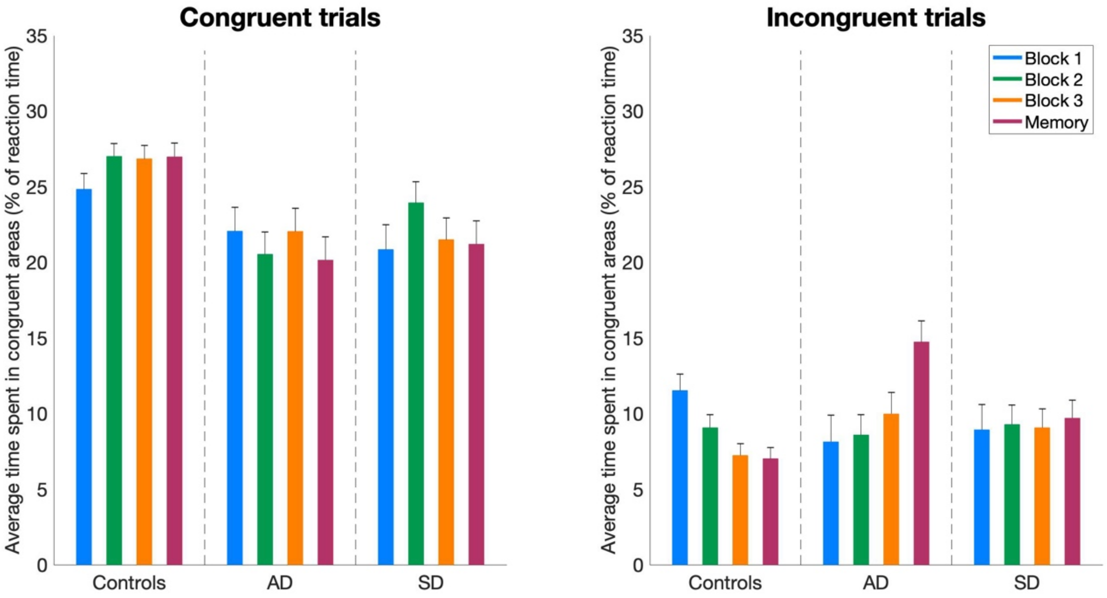

Figure 2.10 Time spent in target congruent areas in dementia syndromes versus controls in the visual search task.

Notes: Average time control participants (left), AD (centre) and SD (right) patients spent in target congruent areas in the visual search task (Blocks 1-3) and memory task (Block 4) in Congruent (left bar plots) and Incongruent (right bar plots) trials. Data are calculated as a percentage of participants' reaction time. Error bars correspond to one standard error.

Gaze reinstatement

The linear mixed model did not reveal a significant main effect of Group (*F*(2,43) = 0.83; *p* =.44) in terms of the degree of overlap of participants' eye movement patterns across adjacent search blocks (see Figure 2.11). However, a significant main effect of Condition was found (*F*(1,43) = 8.13; *p* =.007) whereby, irrespective of group, participants were found to reinstate their gaze to a greater extent in the Incongruent compared to Congruent condition (*p* =.007). The Group x Condition interaction showed a statistically non-significant trend (*F*(2,43) = 2.66; *p* =.08). Exploratory post hoc tests on the interaction term revealed significant differences in gaze reinstatement between Congruent and Incongruent conditions within AD (*p* = .005), but not SD (p = .51) or Controls (p = .51), suggesting that in AD the scan path overlap across subsequent blocks was greater in the Incongruent compared to the Congruent condition. Importantly, these results were not driven by the presence of a single, yet significant outlier in the Incongruent condition (see Figure 2.11), given that the same main effects and interactions described above could still be found when excluding this datapoint from the sample.

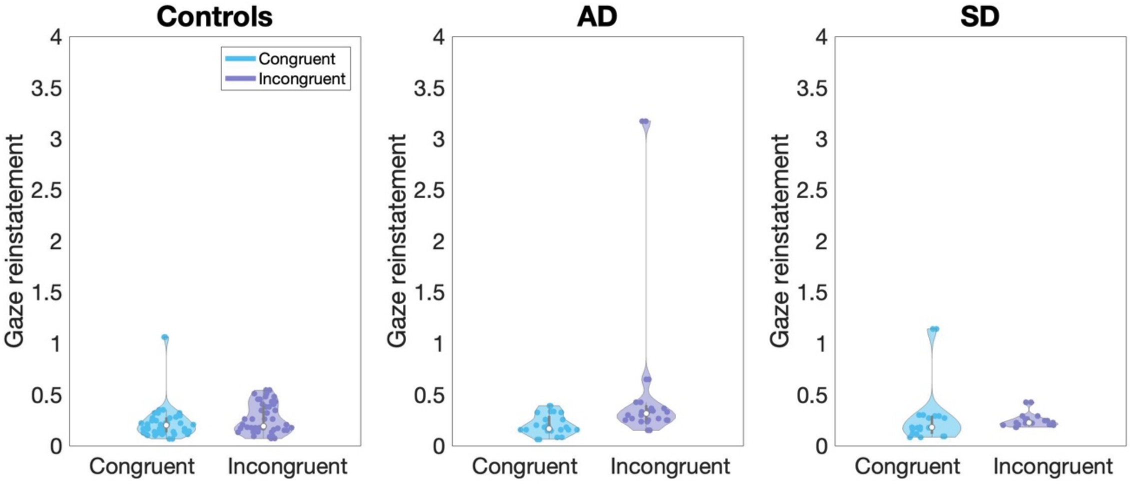

Figure 2.11 Gaze reinstatement in dementia syndromes versus controls in the visual search task.

Notes: Cosine similarity scores representing gaze reinstatement for healthy older adults (left), AD (centre) and SD (right) participants in the visual search task according to the experimental condition, i.e., Congruent (left side violin plots, in cyan) versus Incongruent (right side violin plots, in purple). Data shown are scaled by a factor 10^8. Violin plots were obtained using the *violinplot* function from the Matlab repository (Bechtold (2016).

2.4.3 Memory Task

Reaction Time

The linear mixed model revealed a significant effect of Group ($F(2,42) = 16.40$; $p <.001$) driven by overall slower reaction times in the dementia groups relative to Controls (AD: $p < .001$; SD: $p = .002$). A main effect of Condition ($F(1,42) = 14.59$; $p <.001$) indicated that reaction times were significantly slower in the Incongruent relative to Congruent condition, irrespective of group (see Figure 2.8). Finally, the Group x Condition interaction was significant (*F*(2,42) = 5.94; *p* =.005). Post hoc tests on the interaction term revealed significant differences in reaction times between Congruent and Incongruent conditions within the AD (Mean Difference: -0.27; *p* =.02) and SD (Mean Difference: -0.34; *p* =.005) groups, but not in Controls (Mean Difference: 0.02; *p* = .74). Post hoc tests further indicated that in AD reaction times were significantly slower relative to Controls, irrespective of condition (both *p*-values < .001). In contrast, reaction times in SD were slower in Incongruent trials only (Congruent: *p* = .08; Incongruent: *p* <.001). No significant differences were found between the patient groups (all *p*-values >.2).

Percentage of successful memory trials

The linear mixed model revealed a significant effect of Group (*F*(2,43) = 35.90; *p* <.001) reflecting significantly lower memory accuracy in both patient groups relative to Controls (both *p* < .0001). A significant main effect of Condition was found (*F*(1,43) = 72.63; *p* <.001), driven by significantly higher accuracy in Congruent relative to Incongruent trials, irrespective of group. Finally, the Group x Condition interaction was significant (*F*(2,43) = 4.09; *p* =.024). Post-hoc analyses on the interaction term further pointed to poorer memory accuracy in both patient groups relative to Controls irrespective of condition (AD: both *p values* < .0001; SD: Congruent: *p* < .0001, Incongruent: *p* = .01). As in the visual search task, post-hoc tests at the level of Condition confirmed that for all groups memory performance was higher in Congruent relative to Incongruent trials (Mean difference in performance: Controls: 44.7%, *p* < .001; AD: 33.9%, *p* < .001; SD: 18.9%, *p* = .02; see Figure 2.12), although, at the level Group, the discrepancy in performance accuracy between conditions was different, and was found to be highest in Controls and smallest in SD. Furthermore, comparisons of mean differences in performance were found to be statistically significant between control participants and SD

(44.7% - 18.9% = 25.8%, *p* = .02), but not between control participants and AD or between patient groups (both *p* >.05).

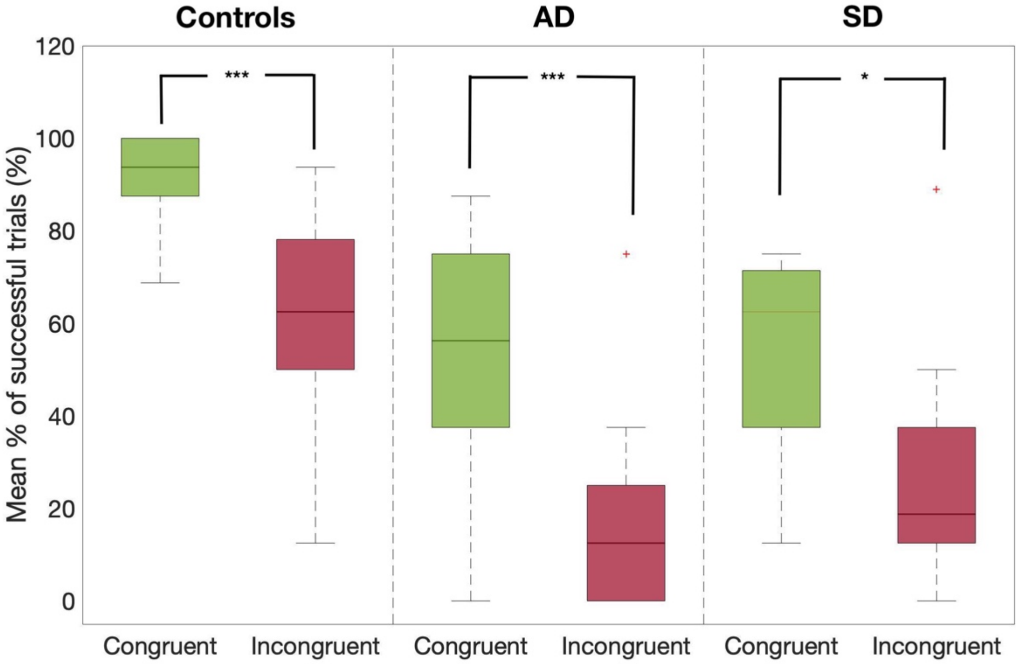

Figure 2.12 Performance scores in dementia syndromes versus controls on the memory task.

Notes: Memory task accuracy as indexed by the mean percentage of successful trials for healthy older adults (left), AD (centre) and SD (right) participants in Congruent (left side box plots, in green) and Incongruent trials (right side boxplots, in red). $*p < .05$; $**p < .01$; $***p < .001$

Time spent in target congruent areas during memory performance

The linear mixed model failed to reveal a significant main effect of Group ($F(2,42) = 0.24$; $p = .78$), indicating that participant groups spent a comparable amount of time in target congruent areas during the memory task. In contrast, a significant main effect of Condition was found ($F(1,42) = 35.86$; $p < .001$) reflecting the fact that, irrespective of group, participants spent significantly more time in target congruent areas in Congruent compared to Incongruent trials. In addition, a significant Group x Condition interaction was observed ($F(2,42) = 5.79$; $p = .006$). Post-hoc tests on the interaction term revealed that Controls and SD spent significantly more time in target congruent areas on Congruent vs Incongruent trials (Controls: *p* <.001; SD: *p* = .02), while this effect was not found in AD (*p* = .19; see Figure 2.13). Post hoc tests further indicated that AD patients spent significantly more time in target congruent areas compared to Controls in Incongruent (*p* = .007) but not Congruent trials (*p* = .38), while no statistically significant differences were observed between Controls and SD (all *p*-values >.1).

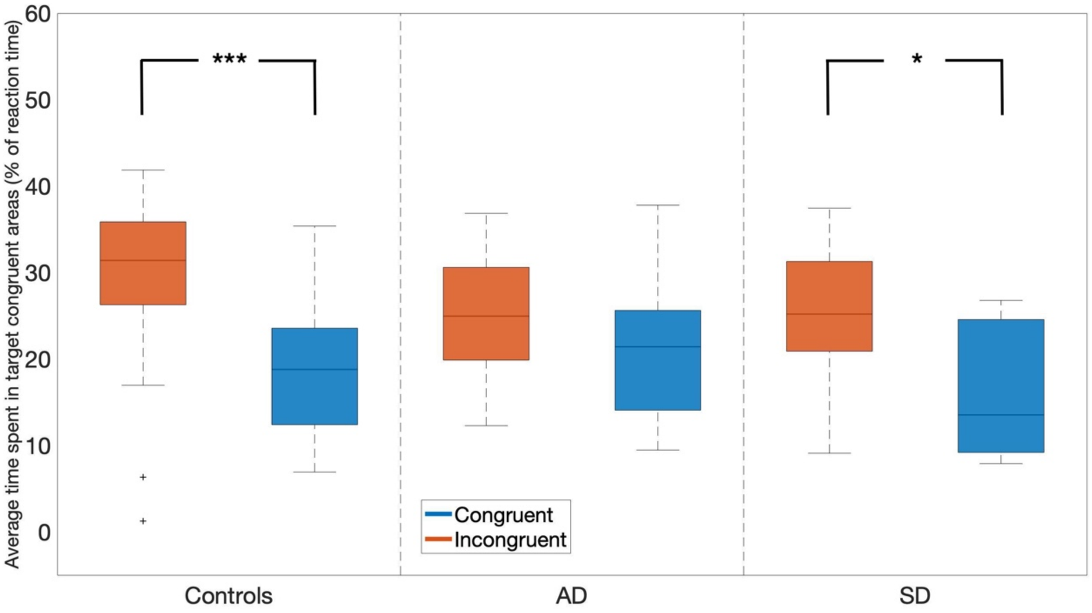

Figure 2.13 Average time spent in target congruent areas in dementia syndromes versus controls in the memory task.

Notes: Average time control participants (left), AD (centre) and SD patients (right) spent in target congruent areas in the memory task in Congruent (left side boxplots, in orange) and Incongruent (right side boxplots, in blue) trials. Data are calculated as a percentage of participants' reaction time. Significant within-group differences are shown with **p* < .05; ***p* < .01; ****p* < .001.

Gaze reinstatement

The linear mixed model failed to reveal a significant main effect of Group (*F*(2,43) = 0.38; *p* =.69) or Condition (*F*(1,43) = 2.47; *p* =.12), suggesting no significant differences between groups or across experimental conditions in terms of the degree of overlap of participants' eye movement patterns in Blocks 3 and 4 (see Figure 2.14). Similarly, the Group x Condition interaction was not significant ($F(2,43) = 0.46$; p =.64).

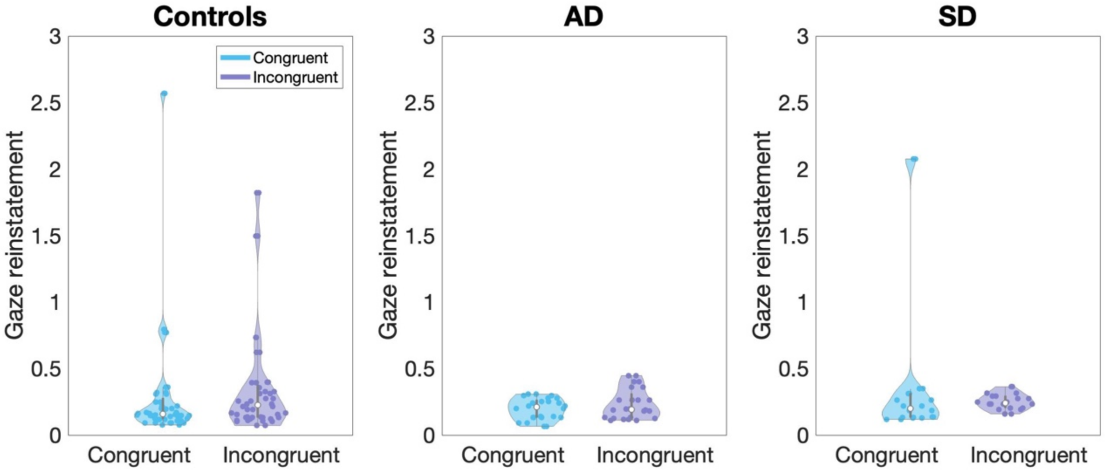

Figure 2.14 Gaze reinstatement in dementia syndromes versus controls in the memory task.

Notes: Cosine similarity scores representing gaze reinstatement for healthy older adults (left), AD (centre) and SD (right) participants in the memory task according to the experimental condition, i.e., Congruent (left side violin plots, in cyan) versus Incongruent (right side violin plots, in purple). Data shown are scaled by a factor 10^8. Violin plots were obtained using the *violinplot* function from the Matlab repository (Bechtold (2016).

2.4.4 Correlation analyses between oculomotor variables and neuropsychological data

A series of one-tailed Pearson correlation analyses were run in each group separately to explore potential associations between experimental task performance and relevant domains of cognitive function. I constrained my focus to two variables from the experimental task (i) memory accuracy (Block 4) and (ii) oculomotor time spent in target congruent areas during the memory block, and explored their respective associations with independent tests of episodic memory (ACE-III Memory subscale; RCF % retained) and semantic processing (SYDBAT Comprehension and Semantic Association subscales). Tables 2.3 and 2.4 present the results of the correlation analyses. When Bonferroni corrections were applied for multiple comparisons (*p* adjusted = .05 /4 = .0125) to guard against false positives, none of the associations remained statistically significant.

Table 2.3 Preliminary associations between average memory task performance and relevant domains of cognitive function for each participant group.

	CONTROLS N = 24	**AD N = 12**	**SD N = 10**
CONGRUENT			
Verbal episodic memory	**0.41***	-0.09	0.01
Visual episodic memory	0.19	-0.02	0.12
Semantic comprehension	-0.10	-0.10	-0.24
Semantic association	0.17	-0.03	0.53
INCONGRUENT			
Verbal episodic memory	0.26	-0.29	0.14
Visual episodic memory	-0.08	0.19	0.34
Semantic comprehension	-0.11	-0.15	0.27
Semantic association	-0.06	0.03	**0.64****

Notes. Verbal and visual episodic memory were measured via the ACE-III Memory subscale and the RCF % retained, respectively. Similarly, semantic comprehension and associations were measured via the corresponding SYDBAT subscales. Pearson R correlations presented uncorrected. Statistically significant trends are highlighted in bold where **p* = .024; ** *p* = .031.

Table 2.4 Preliminary associations between the time spent in target congruent areas during the memory task and relevant domains of cognitive function for each participant group.

	CONTROLS N = 24	**AD N = 12**	**SD N = 10**
CONGRUENT			
Verbal episodic memory	-0.06	**0.57***	-0.31
Visual episodic memory	0.04	0.01	0.24
Semantic comprehension	-0.21	0.27	-0.23
Semantic association	0.11	0.29	0.15

INCONGRUENT			
Verbal episodic memory	-0.28	**0.61****	-0.37
Visual episodic memory	0.20	-0.10	-0.11
Semantic comprehension	0.06	0.13	-0.40
Semantic association	0.27	0.07	-0.02

Notes. Verbal and visual episodic memory were measured via the ACE-III Memory subscale and the RCF % retained, respectively. Similarly, semantic comprehension and associations were measured via the corresponding SYDBAT subscales. Pearson R correlations presented uncorrected. Statistically significant trends are highlighted in bold where **p* = .032; ***p* = .018

2.4.5 Correlation analyses between gaze reinstatement and task accuracy

Finally, I sought to determine whether participants rehearsed their eye movement patterns over the course of the experimental task and whether such oculomotor behaviour was correlated with performance scores in the memory task. Pearson correlation analyses exploring the degree of overlap of participants' eye movement patterns across adjacent blocks failed to reveal any significant correlations between gaze reinstatement in the visual search task and performance scores in the memory task, in either Congruent or Incongruent trials (all *p*-values > .2). Similarly, no significant associations were observed between gaze reinstatement in the memory task and corresponding performance scores, in either experimental condition (all *p*-values > .5).

2.5 Discussion

Contemporary theories of episodic memory increasingly recognise the role of existing knowledge frameworks in supporting adaptive behaviour (Irish, 2020; Renoult et al., 2019). As we age, semantic knowledge assumes a prominent role in guiding sensory perception and recollection, preferentially directing our attention towards objects and areas within our surrounding environment that are consistent with prior expectations (Wynn, Ryan, et al., 2020).

In the present chapter, I explored oculomotor dynamics in healthy ageing and the dementia syndromes of semantic dementia and Alzheimer's disease to better understand the relationship between memory performance and active vision. Overall, my findings reveal how degradation of the semantic or episodic memory system differentially impacts visual exploration and memory retrieval, according to stimulus congruency. Further, I provide preliminary evidence to suggest a shift in the deployment of oculomotor strategies during these processes.

2.5.1 Insights from semantic dementia

Visual Search Task

Semantic dementia (SD) is characterised by the progressive deterioration of the conceptual knowledge base in the context of relatively preserved episodic memory and visuospatial function. My main finding in SD was that congruency of the semantic association between target locations and the surrounding context negatively influences visual search performance, likely because semantic-driven prior expectations have been degraded or cannot be effectively utilised to inform visual exploration. This was evident in significantly longer reaction times and reduced accuracy in SD relative to Controls, exclusively in Congruent trials. In Incongruent trials, by contrast, SD patients displayed comparable performance to Controls, with no significant differences in reaction times or task accuracy. These performance profiles can be interpreted relative to the inherent semantic processing demands of Congruent trials, where successful completion of each trial depends upon the invocation of prior semantic associations (e.g., rubber duck – bath). Incongruent trials, on the other hand, can be completed relatively free from semantic associations, as participants may rely more on salient perceptual features of the stimuli to guide task performance (Itti & Koch, 2000). My finding of intact performance in Incongruent trials in SD resonates with previous findings of relatively intact visuospatial (Salimi et al., 2018b) and episodic memory function in this syndrome (Irish et al., 2016a), particularly when stimuli are presented in a non-conceptually loaded manner. I note further parallels with the proposal that intact attentional mechanisms may support aspects of visual search in SD when semantic knowledge is not required. For example, Viskontas et al. (2011) demonstrated that SD patients perform in line with Controls when exposed to a large number of distractors in conjunction visual search tasks. The authors interpreted this behavioural feature as reflecting more efficient visual search strategies in SD, suggestive of enhanced visuospatial function particularly on cognitive tasks involving perceptual detail rather than semantic information (Viskontas et al., 2011).

Memory Task

Conversely, in the memory task, SD patients performed significantly worse than Controls across both Congruent and Incongruent conditions. While performance for both groups was better in Congruent vs Incongruent trials, post-hoc analyses revealed that the drop in performance between conditions was smallest in the SD group, suggesting that prior semantic knowledge influenced subsequent memory performance to a lesser degree in this group. Looking at potential underlying cognitive mechanisms in SD, I found trend-level associations between memory task accuracy in Incongruent trials and performance on the semantic association subscale of the SYDBAT. The semantic association subscale assesses the capacity to identify the link between visually presented targets (e.g., a butterfly and a net), which can sometimes be location-based. Considerable variability was evident in the performance profiles within the SD group potentially reflecting the breakdown of different aspects of semantic knowledge and semantic associations. For example, within semantic memory, concepts can be organised and represented at different levels of specificity, namely taxonomic (i.e., semantic associations based on shared features or functions allowing to group concepts into categories, e.g., a kettle and a toaster as kitchen appliances) vs thematic (i.e., contiguity relations based on co-occurrence in events or scenarios, e.g., a kettle and a tea bag as items required to make a cup of tea, Mirman, Landrigan, & Britt, 2017). This distinction is supported by neuroimaging studies pointing to different neural substrates: bilateral visual association areas and the anterior temporal lobe for the taxonomic system, and the posterior temporoparietal junction for the thematic system (Schwartz et al., 2011; Yangwen et al., 2018). How such aspects of conceptual knowledge are affected in SD remains unclear, although preliminary evidence points to a *semantic disequilibrium* in the disease, whereby overuse of one system may represent a compensatory strategy for the earlier, progressive deterioration of the other (Faria, Race, Kim, & Hillis, 2018; Kalenine, Mirman, & Buxbaum, 2012; Seckin et al., 2016). Indeed, a recent eye-tracking study exploring this dissociation through a simple word-to-picture matching task found an abnormal reliance on thematic vs taxonomic processing in patients compared with controls. More specifically, SD patients were more prone to confusion errors than healthy controls when taxonomic rather than thematic distractors were displayed, a behavioural result likely reflecting a potential semantic disorganization in SD (Merck et al., 2020). Nonetheless, the functional interplay between these systems is not well understood. Questions arise on how they might interact in more naturalistic tasks resembling activities of daily living, as these typically involve a hierarchical combination of both taxonomic and thematic associations.

Oculomotor Results

Looking next at the oculomotor variables, SD patients spent a comparable amount of time in target congruent areas in the memory task as Controls. Similarly, measures of gaze reinstatement were not found to differ between SD and Controls. Taken together, these results suggest that both groups were able to overcome prior expectations to a similar extent and redirect their attention based on episodic and perceptual features. Interestingly, my findings diverge somewhat from the recent study by Mengoudi et al. (2020) in which visual exploration in SD patients was found be less extensive and slower relative to Controls, comprising repeated fixation patterns directed towards a limited set of visual areas. Methodological differences likely play an important role here given that participants were not given explicit task instructions in the Mengoudi et al. (2020) study but were simply asked to look at the screen as stimuli were displayed in a sequential manner. Visual exploration in semantic dementia may therefore differ depending on the nature of the task across free-viewing passive settings versus perceptually guided cognitive tasks. Moreover, in the Mengoudi et al. (2020) study the congruent and incongruent stimuli selected for the analysis of semantic processing comprised sentences rather than images. This is an important distinction as the visual versus verbal presentation of stimuli dramatically influences task performance in SD (Lambon Ralph, Graham, Patterson, & Hodges, 1999). When new information is presented in the form of a visual stimulus, SD patients can leverage sensory/perceptual features of the stimulus to guide task performance (Graham, Simons, Pratt, Patterson, & Hodges, 2000). On the other hand, verbally-loaded tests do not afford such perceptual inputs and disproportionately tax semantic knowledge, resulting in performance impairments if access to such knowledge is reduced or compromised (Graham, Becker, & Hodges, 1997; Warrington, 1975).

2.5.2 Alzheimer’s disease

Considering the AD group next, perhaps not surprisingly, I found evidence of significant performance impairments irrespective of condition or task demands. Overall, AD patients displayed significantly slower reaction times and poorer accuracy compared to Controls in both Congruent and Incongruent trials, and this was the case for both the visual search task and subsequent memory task. These findings resonate with existing work on compromised visual exploration and memory in AD, impairments that have been attributed to poor attentional processing and canonical recognition mnemonic deficits in the visuospatial domain (Alescio-Lautier et al., 2007; Tales, Haworth, Nelson, Snowden, & Wilcock, 2005). Analyses of gaze reinstatement indicated that during the visual search task, AD patients had a greater tendency to rehearse the eye movement patterns previously produced compared to other participant groups, especially in the Incongruent condition. Additionally, AD patients were found to spend significantly more time in target congruent areas even when objects had been displayed in semantically incongruent locations. My analyses further revealed a trend-level positive association between this behavioural feature and task accuracy in the memory block. Given the decreased capacity to form and consolidate new memories typical of this syndrome, it is likely that AD patients defaulted to existing knowledge to support task performance, resulting in an increased propensity to direct their attention to target congruent areas despite repeated exposure to semantically incongruent associations. This reliance on residual semantic processing may reflect a compensatory strategy enabling the individual to harness information that remains accessible, at least in early stages of the disease (discussed by Irish, 2023; Strikwerda-Brown, Grilli, Andrews-Hanna, & Irish, 2019). My proposal that familiar stimuli and contexts may be preferentially attended to and processed in AD can explain previous findings of diminished visual exploration and decreased attention towards novel and incongruous stimuli (Daffner et al., 1992) as well as decreased capacity to perform tasks where stimuli parameters are ambiguous (Synn et al., 2018). Whether semantic memory can be leveraged to overcome deficits in episodic memory in the context of visual exploration remains an open question for future studies to address (Nakhla, Banuelos, Pagán, Gavarrete Olvera, & Razani, 2022).

2.5.3 Limitations

To the best of my knowledge, the present study is the first to investigate the relationship between episodic and semantic memory performance and active vision in neurodegeneration. As such, a number of methodological and theoretical limitations warrant discussion, not least my relatively small sample size. Future studies comprising larger groups will be required to replicate my results. Due to the rarity of the SD syndrome, I aggregated left and right-sided cases into an overall SD group to increase study power. While no significant differences in task performance were found between the SD subgroups, it is plausible that the lateralisation of temporal lobe atrophy may influence behavioural and oculomotor behaviour during visual exploration and memory retrieval. Finally, future studies should address the underlying neural substrates supporting object detection and recollection during the unconstrained exploration of naturalistic scenes. Studies incorporating electrophysiological recordings via EEG have recently started to emerge in this context, and represent a promising avenue to explore the neural mechanisms supporting the intersection of memory and active vision (Coco, Nuthmann, & Dimigen, 2020).

2.5.4 Conclusions

The findings of the present study suggest the employment of different behavioural strategies to support visual search and memory performance based on the cognitive profile of each participant group. My analyses further reveal the emergence of distinct patterns of oculomotor behaviour in each dementia syndrome, which may reflect underlying neural mechanisms driven by the progressive deterioration of episodic or semantic memory. Deconstructing the precise interaction between oculomotor behaviour and different expressions of memory is necessary to deepen our understanding of how imagery-rich cognitive mechanisms unfold, and potentially break down, in both healthy ageing and neurodegeneration. As previously mentioned, the dynamic interplay between memory and active vision plays a pivotal role in supporting not only memory encoding, consolidation, and retrieval, but also many other memory-laden, construction-based processes such as episodic future thinking and atemporal scene construction. While several experimental studies over the past few decades have investigated memory deficits in both ageing and clinical populations, age-related alterations during scene construction mechanisms and their extension to neurodegenerative conditions remain largely unexplored. To address this gap in the literature, in the next two chapters I will focus on atemporal and future-oriented mental construction in healthy younger and older populations. In doing so, I will explore how age-related alterations in mental imagery capacities relate to cognitive performance, subjective experience, and oculomotor behaviour.

Chapter 3

Atemporal scene construction in healthy ageing

3.1 Introduction

Chapter 2 revealed important differences in the way younger and older adults sample the visual world and how they subsequently deploy this information to support memory formation and retrieval (Açık, Sarwary, Schultze-Kraft, Onat, & König, 2010; Firestone, Turk-Browne, & Ryan, 2007; Wynn, Amer, et al., 2020). As we have seen, older adults appear to rely to a greater extent on prior knowledge or expectations to guide memory-related behaviours (Umanath & Marsh, 2014). During visual search tasks, this reliance on prior knowledge leads to preferential and repeated visual sampling of semantically congruent areas (e.g., searching for a toaster on the kitchen counter) but decreased memory accuracy and increased search time when items are displayed in semantically incongruent locations (e.g. a toaster displayed somewhere on the floor, Wynn, Ryan, et al., 2020). Further, mounting evidence suggests that older adults are more likely to direct their attention towards externally salient cues, even when explicitly instructed to ignore them or previously warned of their imminent appearance (Erel & Levy, 2016). Compared to younger adults, older adults have been found to produce more gaze fixations when exposed to novel stimuli during visual exploration, (Z. X. Liu, Shen, Olsen, and Ryan (2018). While some of these changes may reflect age-related deficits in cognitive function, evidence suggests that alterations in oculomotor behaviour may sometimes serve a compensatory function to offset cognitive decline as we age and to potentially augment cognitive performance in response to increasing task demands (Wynn et al., 2018; Wynn et al., 2019).

To date, eye tracking studies of memory-related processes in healthy ageing have tended to focus on experimental tasks involving the explicit presentation and subsequent recollection of visual stimuli. As such, it remains unclear how age-related changes in oculomotor behaviour manifest in the absence of visual cues, that is on tasks relying on the endogenous generation and maintenance of complex mental constructions. Scene construction refers to the capacity by which humans mentally construct and envisage richly detailed and spatially integrated three-dimensional representations in the mind's eye (Hassabis & Maguire, 2007, 2009) and is suggested to underpin a range of complex cognitive endeavours, including episodic retrieval, future thinking, and spatial navigation (Mullally & Maguire, 2014). Given its complexity, the construction of three-dimensional spatially integrated scenes invariably draws upon several underlying cognitive processes, including the retrieval and reinstatement of episodic and semantic representations, their flexible recombination, as well as their active maintenance in the mind's eye. Functional neuroimaging and clinical lesion studies converge to reveal the importance of a distributed brain network, centred on the hippocampus, for the construction of spatially contiguous scenes (Hassabis, Kumaran, Vann, & Maguire, 2007; Irish et al., 2017; Mullally, Hassabis, & Maguire, 2012; Wilson et al., 2020).

Empirical research exploring age-related changes in scene construction capacity is scarce, although two studies warrant discussion in this context. First, Rendell et al. (2012) demonstrated that the overall capacity to construct atemporal scenes is significantly reduced in older compared to younger adults. The scenes generated by older adults contained significantly less contextual detail and were subjectively perceived as less salient and less vivid relative to their younger counterparts (Rendell et al., 2012). Along the same lines, a separate study using visually presented verbal cues assessed age-related changes in relational processing during scene construction (Romero & Moscovitch, 2012). Results indicated that older adults generated fewer inter-item associations and displayed an increased propensity to omit item words when presented with larger item sets (i.e., six elements, as opposed to three, four or five). This reduced capacity for multimodal integration was associated with poorer performance on a subsequent cued recall test in the older group (Romero & Moscovitch, 2012). As such, the authors suggested that while constructive deficits in older adults largely reflect age-related changes in associative processing, the capacity to maintain a coherent mental representation of items in long-term memory may also moderate task performance (see also De Beni, Pazzaglia, & Gardini, 2007; Romero & Moscovitch, 2012).

In summary, the limited, yet compelling evidence presented above points to age-related changes in the construction of mental scenes relying on internally generated imagery. No study to our knowledge, however, has explored the intersection between oculomotor behaviour and scene construction in healthy ageing. Given the considerable functional interplay between the reinstatement of visual imagery and the dynamic construction of events described in Chapter 1 (Conti & Irish, 2021; Kinjo, Fooken, & Spering, 2020; Wynn, Van Genugten, Sheldon, & Schacter, 2022), this gap in the literature is quite surprising. Furthermore, recent neuroimaging studies in young adults indicate that unrestricted eye movements strengthen effective connectivity between hippocampal and oculomotor regions during scene construction, while constraining oculomotor behaviour significantly reduces the perceived vividness of the resulting scene imagery (Ladyka-Wojcik, Liu, & Ryan, 2022). Whether and to what extent such dynamics shift in healthy ageing remains an open question. While age-related changes in the integrity of the episodic memory system have been shown to influence the efficiency of the oculomotor system and related visual exploration patterns (Ryan, Shen, & Liu, 2020; Ryan et al., 2022), concerted research efforts are needed to better understand the intersection between these systems.

To address these issues, I adapted a novel paradigm developed by Summerfield and Maguire (2010) to track how scene construction performance and concurrent eye movement behaviour varies as a function of task complexity in older and younger healthy adults. I hypothesised that, irrespective of age group, when task demands are low, eye movements would support the visuospatial processing required to yield a coherent scene representation in the mind's eye. In contrast, when task demands increase above a certain threshold, I predicted a concomitant reduction in oculomotor behaviour due to the higher cognitive demands placed on working memory while maintaining a more densely populated and spatially coherent scenario in the mind's eye. I also predicted that such oculomotor response would be observed to a much greater extent in the older compared to the younger group, reflecting a potential compensatory mechanism to support task performance in response to age-related deficits in visual encoding, spatial processing and attentional mechanisms (Segen, Avraamides, Slattery, & Wiener, 2021).

3.2 Methods

3.2.1 Participants

Thirty-two participants, comprising 16 younger adults and 16 cognitively healthy older adults, were recruited between March and July 2022. Younger adults (18-26 years) were undergraduate students at the University of Sydney and participated in the study in exchange for course credit through the Sydney University Psychology SONAPSYCH Research Participation System. Older adults (62-78 years) were recruited through the volunteer research pool at FRONTIER, the frontotemporal dementia research clinic based at the Brain and Mind Centre, University of Sydney, Australia.

Prior to the experimental session, older adults were required to score >88/100 on the Addenbrooke's Cognitive Examination-III (ACE-III; Hsieh et al., 2013; So et al., 2018), a broad assessment of cognitive function covering domains of attention, memory, fluency, language, and visuospatial function. Exclusion criteria for both younger and older participants included concurrent psychiatric diagnosis, presence of other neurological syndrome, traumatic brain injury, or history of alcohol or substance abuse. All participants had normal or corrected-to-normal vision.

3.2.2. Eye-tracking apparatus

The eye-tracking equipment and setup for this study was the same as presented in Chapter 2. Please refer to section 2.2.2 for all details.

3.2.3. Task stimuli

In keeping with the Summerfield et al. (2010) study, stimuli comprised 360 audio recordings, divided into 180 construction elements and 180 control elements. Construction elements were short descriptions of objects commonly found in indoor settings, such as pieces of furniture (e.g., “A blue sofa with cushions”; “A large round table”), everyday and/or decorative items (e.g., “A green leafy plant”; “A small grey radio”; “A pair of woolly gloves”), or background features (e.g., “A pink patterned wall”; “A cream stone floor”). In contrast, control elements were short phrases whose combination of words was carefully designed to elicit minimal imagery or memory representations (e.g., “A single unit of quanta”; “A principle of matter”; “An important type”; see Summerfield et al. (2010) for full task description). Given that the original audio stimuli were recorded by an English speaker for use in a UK population, we re-recorded the audio stimuli by an Australian-English speaker to avoid attentional disruptions due to unfamiliar pronunciations.

Regardless of the experimental condition (construction or control), each trial presented between three and six elements, whose order of presentation was randomised across subjects. Participants performed a total of 80 trials (40 construction trials, 40 control trials), randomly intermixed and divided into 8 blocks of 10. Participants also conducted a practice test to familiarise themselves with the task and, if needed, to request clarification on the experimental procedure. The practice test comprised 4 trials (2 construction trials and 2 control trials) whose elements were randomly selected from a separate list. As in the main task, each practice trial presented between three and six elements. These elements were not counterbalanced across subjects and were not used in the main experiment.

3.2.4. Procedure

Figure 3.1. presents a schematic of the testing protocol, adapted from Summerfield and Maguire (2010). Testing proceeded largely in keeping with the original study design. Each trial began with the text “Clear your imagination” at the centre of the screen against a black background (2s), prompting participants to prepare for the upcoming trial. This was followed by a cue indicating the current experimental condition, i.e., “Construct” for construction trials and “Attend” for control trials (1s), and finally a fixation cross, displayed in the middle of the screen (1s). At this point, the screen would turn black, and participants heard a series of audio stimuli (i.e., elements), ranging between three and six elements. Each stimulus was followed by a short visualisation interval whose duration increased as the number of elements increased (i.e., 1s after the first stimulus, 1.5s after the second stimulus, 2s after the third, fourth and fifth stimulus, and finally 2.5s after the sixth stimulus). The duration of each visualisation interval was informed by the original Summerfield & Maguire (2010) experimental protocol. Importantly, participants did not know beforehand how many elements would be presented in any given trial.

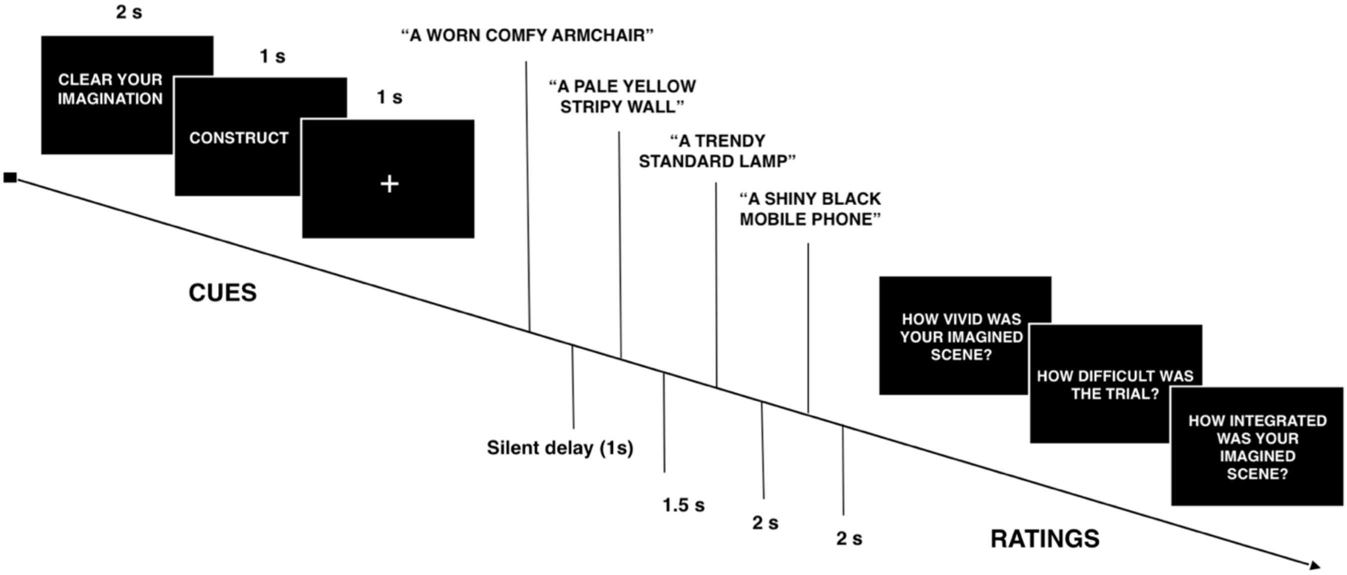

Figure 3.1 Scene construction task design.

Notes: Representative timeline of a construction trial in which four elements must be integrated into a coherent scene representation. Adapted from Summerfield & Maguire (2010).

Subjective ratings

Following the construction of each scene, participants were prompted to provide ratings about specific aspects of each trial using the keyboard. For construction trials, participants were asked to rate the vividness of the imagined scene (1= not vivid, .. , 5 = very vivid), the overall difficulty of the current trial (1 = easy, .. , 5 = difficult), as well as the level of integration of the imagined scene (1 = not integrated, .. , 5 = very integrated)[2]. For control trials, participants were asked whether a particular word was present or absent in the trial and to rate the overall difficulty of the current trial. No time limit was imposed when answering these questions to accommodate slower search times in older participants. Participants were allowed to move their eyes as desired, provided their gaze was directed towards the screen. Participants were

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[2] Participants were asked to provide subjective ratings on key phenomenological dimensions using a scale from 1 to 5. In keeping with the protocol implemented by Summerfield & Maguire (2010), only the upper and lower limits were explicitly stated (i.e., for vividness ratings the scale was displayed as "1 = not vivid, .., 5 = very vivid").

also instructed to keep their eyes open at all times and were only permitted to look away from the screen to locate the appropriate button on the keyboard when prompted to provide subjective ratings.

Post-experiment debriefing

Once the experimental task was completed, participants completed a short questionnaire to provide ratings (ranging from 1 to 5) on different aspects of the task. For construction trials, ratings were collected regarding the overall ease of visualisation and spatial integration of the different elements within the scene, the degree of familiarity, plausibility, coherence, and emotional salience of the imagined scene, as well as the viewer's perspective, the involvement of the self, and the level of adherence to the narrative description. For control trials, ratings included the imageability of phrases and the extent to which they elicited any memory representation.

3.2.5. Statistical analyses

Behavioural performance on the scene construction task was analysed using R (R Core Team, 2012, version 4.2.0) and MATLAB (The MathWorks Inc, 2017). Wilcoxon and Kruskal-Wallis rank sum tests, as well as post-hoc tests using the Benjamini-Hochberg procedure (Groppe, 2023), were performed to explore potential group differences between younger and older adults in terms of subjective ratings (i.e., vividness, difficulty, integration) and all behavioural variables included in the post-experiment questionnaire. Group differences on oculomotor measures of interest (i.e., number and duration of fixations, number of saccades, and total scan paths) were investigated using linear mixed-effect models (LME) and Sidak post-hoc tests (R function afex, Singmann et al., 2022). For each oculomotor variable, scaled with respect to the duration of each gap interval, I defined a separate linear mixed model with "Group" as fixed effect and “Subject Number”, “Condition” (i.e., Construction or Control) and “Complexity” (i.e., the number of trial elements, ranging from 3 to 6), as random effects. Post-hoc power calculations on sample size for eye-tracking data were conducted using G*Power (Faul et al., 2007). Results from these calculations revealed that a sample size of 32 participants was sufficient to detect a significant main effect of size $f = 0.5$ with 88% power and an alpha level of 0.05, as well as a significant interaction of size $f = 0.25$ with 78% power and an alpha level of 0.05. Finally, Spearman correlation analyses were run to explore potential associations between key oculomotor measures of interest and subjective ratings provided by participants.

3.3. Behavioural Results

3.3.1 Post-experiment questionnaire

Table 3.1. presents the subjective ratings provided by participants for construction and control trials on the post-experiment questionnaire. Overall, for construction trials, younger and older adults found it relatively easy to clear their mind in preparation for the upcoming audio stimulus presentation. Once the narrative had begun, both groups tended to find it easy to imagine a single acontextual item, and moderately easy to integrate subsequent elements into the scene. Constructed scenes were typically imagined from a first-person visual perspective although participants did not subjectively feel immersed in the scene. Constructed scenes were rated by participants as emotionally neutral, primarily novel, highly plausible, and spatially coherent. Participants found it moderately easy to maintain all the presented elements within the scene and reported adhering to the task instructions by keeping to the narrative description. These patterns are in keeping with previous behavioural findings using the same task in healthy young participants (Summerfield & Maguire, 2010).

Wilcoxon rank sum tests revealed no significant differences between younger and older adults across the post-experiment ratings (all *p* values > .05 Benjamini-Hochberg adjusted). For control trials, the audio stimuli did not elicit rich mental imagery or detailed memory representations in either group.

Table 3.1 Mean overall task ratings for construction and control trials provided by younger and older participants in the post-experiment questionnaire.

		Younger (n=16)	**Older (n=16)**	**Group differences**
Construction trials (N = 40)	Ease of clearing one's mind	2.00 (0.82)	1.56 (0.73)	*p* = .322
	Ease of imagining first item	1.36 (0.50)	1.19 (0.54)	*p* = .334
	Ease of integration	2.94 (1.00)	2.38 (0.89)	*p* = .282
	1st person perspective	2.44 (1.46)	2.81 (1.91)	*p* = .735
	Absence from the scene	4.25 (1.24)	3.63 (1.75)	*p* = .641
	Emotional salience	1.88 (1.02)	1.94 (1.00)	*p* = .840
	Novelty	2.31 (1.08)	3.00 (0.97)	*p* = .282
	Plausibility	3.88 (0.81)	3.64 (1.02)	*p* = .655
	Coherence	3.44 (0.81)	3.64 (0.62)	*p* = .641
	Ease of maintaining all scene elements	3.25 (1.13)	2.69 (1.40)	*p* = .520
	Adherence to task narrative	2.68 (1.40)	1.63 (1.15)	*p* = .112
Control trials (N = 40)	Mental imagery	2.07 (1.06)	1.25 (0.45)	*p* = .112
	Memory representation	1.56 (0.72)	1.44 (0.73)	*p* = .655

Notes: Values represent mean subjective ratings across all construction or control trials, with corresponding standard deviation provided in brackets. Ratings ranged from 1 to 5 and were coded as follows: difficulty: 1 = easy, 5 = difficult; perspective: 1 = 1st person, 5 = 3rd person; personal involvement: 1 = involved, 5 = absent; emotional salience: 1 = neutral, 5 = emotional; novelty: 1 = novel, 5 = familiar; coherence/plausibility: 1 = low, 5 = high; adherence to task narrative: 1 = kept to the narrative description, 5 = added new elements or context. For control trials, ratings also ranged from 1 to 5 and were coded for both mental imagery and memory representation as follows: 1 = low, 5 = high. Group differences were explored using Wilcoxon rank sum tests and Benjamini-Hochberg corrections.

3.3.2 Subjective ratings

Table 3.2. displays the average vividness, integration, and difficulty ratings according to level of scene complexity for younger and older adults. Wilcoxon rank sum tests revealed that older participants subjectively rated their constructions as more vivid and more integrated than the younger group (all *p*-values < .01). Older adults also tended to rate construction trials as less difficult compared to younger adults (*p* = .07 for trials containing 3 elements, then all *p*-values < .02 for trials containing 4, 5 or 6 elements; see Table 3.2.). Finally, Kruskal-Wallis rank sum tests revealed that, irrespective of age group, self-reported vividness, and level of integration of constructed scenes significantly decreased as the number of scene elements increased (both *p*-values < .001) and difficulty ratings significantly increased as a function of scene complexity (*p* < .001).

Table 3.2 Subjective ratings for construction trials by scene complexity for younger and older participants.

Variable	Number of elements[a]	Younger (n = 16)	Older (n = 16)	Group differences
VIVIDNESS	3	4.09 (1.03)	4.46 (0.86)	***
	4	3.69 (1.19)	4.22 (0.98)	***
	5	3.69 (1.16)	3.98 (1.10)	*
	6	3.28 (1.25)	3.88 (1.10)	***
INTEGRATION	3	3.73 (1.17)	4.19 (1.10)	**
	4	3.44 (1.27)	3.9 (1.19)	**
	5	3.32 (1.19)	3.74 (1.09)	**
	6	3.17 (1.27)	3.59 (1.21)	**
DIFFICULTY	3	1.81 (1.04)	1.61 (0.91)	(*p* = .07)
	4	2.34 (1.19)	2.02 (1.10)	*
	5	2.51(1.20)	2.18 (1.21)	*
	6	2.94 (1.24)	2.44 (1.21)	**

Notes: [a]Ratings based on 40 total construction trials per participant, with 10 trials per level of complexity. Subjective ratings were provided on a scale from 1 (lowest score) to 5 (highest score). Group differences were determined using Wilcoxon rank sum tests and Benjamini-Hochberg corrections where * $p < .05$; ** $p < .01$; *** $p < .001$.

3.3.3 Control trial performance

For control trials, participants were prompted to pay attention and try to remember the stimuli that had been auditorily presented and indicate whether a particular word was present or absent in the trial. Accordingly, trials with more elements placed greater demands on working memory. Participants were also asked to score the overall difficulty of each trial. Wilcoxon rank sum tests revealed that, in trials comprising a smaller number of elements (i.e., 3 and 4) performance accuracy was higher in the older compared to the younger group, while the opposite was true in trials comprising a greater number of elements (i.e., 6, see Table 3.3). In contrast, no significant group differences could be found in terms of the perceived difficulty across all control trials (all *p*-values > .05, see Table 3.3.).

Table 3.3 Difficulty ratings for control trials by scene complexity for study participants.

Variable	Number of elements[a]	Younger (n = 16)	Older (n = 16)	Group differences
ACCURACY	3	70.00%	84.38%	**
	4	65.63%	75.63%	($p = .05$)
	5	68.75%	68.13%	($p = .91$)
	6	68.13%	44.38%	***
DIFFICULTY	3	2.11 (1.22)	2.36 (1.41)	($p = 1$)
	4	2.41 (1.30)	2.57 (1.46)	($p = 1$)
	5	2.43(1.26)	2.73 (1.55)	($p = 1$)
	6	2.87 (1.33)	2.92 (1.49)	($p = 1$)

Notes: [a]Performance accuracy scores and difficulty ratings based on 40 total control trials per participant, with 10 trials per level of complexity. Subjective ratings were provided on a scale from 1 (lowest score, i.e. easy) to 5 (highest score, i.e. difficulty). Group differences were determined using Wilcoxon rank sum tests and Benjamini-Hochberg corrections where * $p < .05$; ** $p < .01$; *** $p < .001$.

3.4 Oculomotor Results

I next analysed the eye movements produced in the gap intervals following each stimulus presentation. The oculomotor variables of interest were the number of fixations, the average fixation duration, the number of saccades and the total scan paths. In keeping with the experimental protocol of the original study, the duration of the gap intervals between stimuli increased as the number of elements presented increased to accommodate for the heightened working memory demands and overall complexity of the task. As a result, all oculomotor measures were calculated with respect to the duration of the corresponding trial (cf. Section 3.2.4). Furthermore, given that the distributions of the above-mentioned variables were skewed and heavy-tailed, I applied either a logarithmic (number of fixations, number of saccades and total scan paths) or an n^{th} root transformation (fixation durations: n = 5) of the data prior to performing linear mixed model analyses.

3.4.1 Number and duration of fixations

A linear mixed model analysis revealed no significant main effect of Group ($F(1,30) = 0.93$; p =.34), Condition ($F(1,30) = 2.04$; p =.16), or Complexity ($F(2.71,81.40) = 2.20$; p =.10) in terms of the number of fixations participants produced. Nonetheless, a significant Group x Condition interaction emerged ($F(1,30) = 4.88$; p =.035), whereby older adults were found to produce more fixations in control versus construction trials compared to younger adults.

Considering the duration of fixations, no significant main effect of Group ($F(1,30) = 0.47$, p = .49) was found. However, a significant main effect of Condition emerged ($F(1, 30) = 28.78$; p <.001), whereby average fixation durations were significantly longer in control compared to construction trials, irrespective of group ($p < .0001$). Linear mixed model analyses also revealed a significant main effect of Complexity ($F(2.61, 70.46) = 223.70$; p <.001). Post-hoc tests further indicated that fixation durations steadily decreased as the number of elements increased (Estimated marginal means[3]: 3 elements: 0.52; 4 elements: 0.49; 5 elements: 0.47; 6 elements: 0.45; all *p-values* < .0001). On the other hand, no significant interactions emerged in terms of the average duration of the fixations produced by participants (all *p*-values > .4).

3.4.2 Number of saccades

A linear mixed model analysis revealed no significant main effect of Group (*F*(1,30) = 0.97; *p* =.33), Condition (*F*(1,30) = 1.90; *p* =.18), or Complexity (*F*(2.72,81.56) = 1.78; *p* =.16) in terms of the number of saccades participants produced. Nonetheless, a significant Group x Condition interaction emerged (*F*(1,30) = 5.32; *p* =.028), whereby older adults were found to produce more saccades in control versus construction trials compared to younger adults.

3.4.3 Total scan path

I calculated the total scan paths produced by participants after each stimulus presentation as a function of the duration of the corresponding gap interval (see Figure 3.2.). A linear mixed model analysis revealed no significant main effect of Group (*F*(1,30) = 0.35; *p* =.56). Nonetheless, a significant main effect of Condition was found (*F*(1,30) = 4.11; *p* =.05), whereby the amount of eye movements (AEM) participants produced was higher in control compared to construction trials (Estimated marginal mean in logarithmic scale: Construction – Control = -0.336). Furthermore, a significant main effect of Complexity was found (*F*(2.06,61.68) = 7.97; *p* <.001), indicating that the total AEM participants produced was higher in trials comprising 5 and 6 elements, compared to trials comprising 3 elements only (3 versus

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[3] Estimated marginal means are given on the n^{th} root scale (n = 5).

5 elements: $p = .01$; 3 versus 6 elements: $p = .006$; for all other post-hoc pairwise comparisons adjusted p-values >.1). No significant interactions were found (all p-values > .2).

In summary, the linear mixed model analyses failed to reveal significant group differences in the total scan paths participants produced over the course of the experimental task, although they point to a significant increase in the AEM as the number of stimuli increased from 3 to 6. Nonetheless, given that auditory stimuli were presented in a sequential manner, it remains unclear whether the production of eye movements differed across groups in the early stages of the scene construction process (i.e., while participants were required to visualise and integrate the first 1 to 3 elements). To determine whether this was the case and how the presentation of a new element affected participants' oculomotor response as the number of task stimuli gradually increased, I focused on pairwise differences between the scan paths participants produced in the gap intervals following the presentation of adjacent stimuli (see Figure 3.2). I then built a separate linear mixed model for each variable. Given that the distributions of the resulting variables were skewed and heavy-tailed, we applied an n^{th} root transformation of the data ($n = 3$) prior to performing linear mixed model analyses.

Interestingly, the linear mixed model analyses yielded significant results exclusively when comparing the difference in the AEM participants produced following the presentation of the first and the second stimulus (all p-values for models focusing on subsequent comparisons > .05). More precisely, I found a significant main effect of Group ($F(1,30) = 10.29$, $p = .003$), whereby after the presentation of the second stimulus the AEM effectively decreased in older but not younger participants (Estimated marginal means of the difference in AEM between 1st and 2nd stimulus in the n^{th} root scale, $n = 6$: Younger adults: -0.58; Older adults: 13.94; Group difference: 14.5, $p = .003$). In contrast, no significant main effect of Condition could be found

(*F*(1,30) = 0.37, *p* = .55). Similarly, the Group x Condition interaction was not significant (*F*(1,30) = 0.93, *p* = .34). No significant main effects or interactions were found in the difference in AEM past the presentation of the third stimulus (all *p*-values >.1).

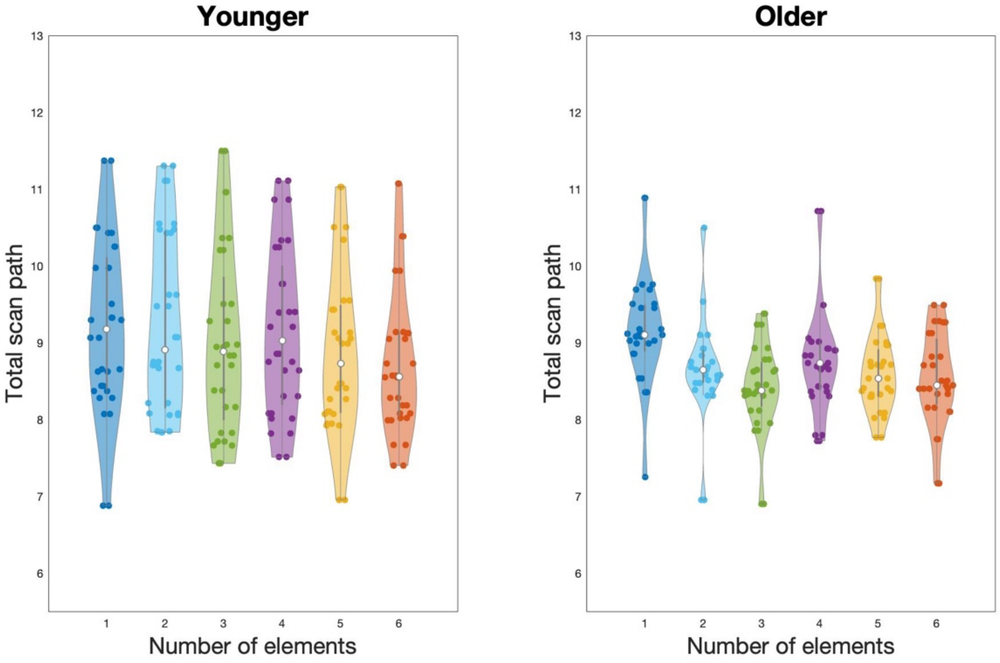

Figure 3.2 Participants' total scan paths in the scene construction task.

Notes: Total scan paths produced by younger (left) and older (right) participants in the experimental task following the sequential presentation of each auditory stimulus. Data are shown in the nth root scale (n = 6). Violin plots were obtained using the *violinplot* function for Matlab (Bechtold, 2016).

3.5 Correlation analyses

Spearman correlation analyses with Benjamini-Hochberg corrections for multiple comparisons were run to explore potential associations between behavioural and oculomotor measures of interest on construction trials for each level of complexity. Given that the linear mixed model analyses presented in the previous section failed to reveal a significant main effect of group, I aggregated data from our two participant groups prior to conducting the correlation analyses.

No significant correlations emerged between the number of fixations and saccades participants produced or their total scan paths and the perceived vividness, integration, and difficulty of constructed scenes (all adjusted *p*-values >.05). On the other hand, in trials comprising 3 and 4 elements, the average fixation duration was found to be positively correlated with both the subjective vividness (3 elements: $r = 0.14$, $p = .03$; 4 elements: $r = 0.12$, $p = .05$) and the subjective integration of the mental constructions (3 elements: $r = 0.20$, $p = .0006$; 4 elements: $r = 0.23$, $p = .0001$), but not their perceived difficulty (3 elements: $r = -0.04$, $p = .68$; 4 elements: $r = -0.11$, $p = .24$; see 3.4). Similarly, no significant associations were found between the average fixation duration and subjective ratings in trials comprising a higher number of elements (i.e., 5 or 6 elements, all adjusted *p*-values >.05).

Table 3.4 Correlation analyses between participants' average fixation duration and subjective ratings of vividness, integration, and difficulty in construction trials.

Variable	Number of elements [a]	Correlation	*p*-value
VIVIDNESS	**3**	***r* = 0.14**	*
	4	***r* = 0.12**	*
	5	*r* = - 0.003	(*p* = .95)
	6	*r* = 0.07	(*p* =.26)
INTEGRATION	**3**	***r* = 0.20**	***
	4	***r* = 0.23**	***
	5	*r* = 0.07	(*p* = .17)
	6	*r* = 0.09	(*p* = .13)
DIFFICULTY	3	*r* = - 0.04	(*p* = .68)
	4	*r* = - 0.11	(*p* = .24)
	5	*r* = 0.003	(*p* = .96)
	6	*r* = - 0.09	(*p* = .25)

Notes: [a] Ratings based on 40 total construction trials per participant, with 10 trials per level of complexity. Subjective ratings for construction trials were provided on a scale from 1 (lowest score) to 5 (highest score). Statistically significant Spearman correlation values post Benjamini-Hochberg corrections for multiple comparisons are highlighted in bold, with * $p < .05$; ** $p < .01$; *** $p < .001$.

These results suggest that, on trials comprising a smaller number of elements, maintaining fixation may have facilitated the elaboration and maintenance of the constructed scenarios in participants' mind's eye, enhancing the phenomenological experience of the mental endeavour.

3.6 Discussion

The objective of this study was to understand how oculomotor behaviour unfolds during scene construction performance in younger versus cognitively healthy older adults in the absence of externally cued visual stimuli, and to explore the impact of increasing task complexity on this relationship. Using an adapted version of the scene construction task developed by Summerfield & Maguire (2010), I demonstrated significant age-related changes in patterns of visual exploration during the endogenous generation and maintenance of complex scene imagery. Notably, profiles of oculomotor behaviour in the early stages of scene construction differed in younger and older adults, suggesting an age-related recalibration of cognitive resources in response to task demands. My findings resonate with recent theoretical frameworks proposing that visuo-oculomotor behaviour depends on available cognitive resources and is therefore susceptible to task influences in older age (reviewed by Conti & Irish, 2021; Ryan et al., 2022; Wynn et al., 2019).

3.6.1 Age differences in oculomotor behaviour

The key finding from the present study is that oculomotor behaviour during the endogenous construction of scene representations appears to be influenced by task complexity. In fact, irrespective of age group, participants were found to produce a greater amount of eye movements in control versus construction trials and as the number of task elements increased. Along the same lines, my analyses indicate that the durations of participants' fixations were longest in trials comprising a smaller number of elements (i.e., 3 or 4), while also being positively correlated with the subjective vividness and integration of the corresponding scenes.

Given that longer fixations have been previously shown to index greater cognitive effort and focused attention (Dewhurst et al., 2018; Henderson & Hollingworth, 2003; Hollingworth, 2006), a possible explanation for these findings is that, during the initial phase of the scene construction process, when only a few elements are presented and a vivid and spatially contiguous semantic scaffold must first be generated, cognitive demands are particularly heightened. As a result, maintaining fixation rather than engaging in visual exploration may have been beneficial, or indeed required, to support task performance. On the other hand, once a coherent spatial backdrop for the mental simulation has been established, the integration of an increasing number of elements into the scene can be more easily achieved. By this view, in the later stages of scene construction, more cognitive resources can be allocated to the production of eye movements, which in turn resulted in shorter fixations.

Interestingly, when looking at changes in participants' scan paths in the early phase of scene construction, in older adults the production of eye movements was found to decrease immediately after the presentation of the second auditory stimulus. This attenuation of oculomotor behaviour may reflect the dynamic redeployment of cognitive resources as task demands exceed memory capacity to better support the construction and maintenance of complex scenes in the mind's eye (Engelhard, van den Hout, Janssen, & van der Beek, 2010). If this is the case, such shifts in oculomotor behaviour would be most relevant in situations where external visual cues are not available, as in the current task, thus placing increased demands on working memory capacity to maintain scene representations.

3.6.2 Age differences in phenomenological indices

Interestingly, the age-related shift in oculomotor behaviour observed in healthy ageing was not borne out on the phenomenological level as older adults perceived their mental constructions as more vivid and integrated than their younger counterparts, suggesting that the quality of the resultant scenes was not compromised. Recent studies on autobiographical memory and episodic future thinking incorporating eye-tracking may help reconcile these findings as they demonstrate that the vividness and emotionality of past and future recollections is significantly reduced when voluntary eye movements are concomitantly executed (Engelhard et al., 2010; Kavanagh, Freese, Andrade, & May, 2001; Kemps & Tiggemann, 2007; van den Hout, Muris, Salemink, & Kindt, 2001). As it has been argued, this may occur because eye movements selectively disrupt visuospatial working memory (Andrade, Kavanagh, & Baddeley, 1997). Accordingly, the quantitative reduction in eye movements displayed by the older group may have facilitated the recruitment of available cognitive resources to support scene construction, which in turn enhanced the phenomenological experience of the mental simulations.

Another counterintuitive finding of the present study is that older adults generated significantly more fixations and saccades relative to younger adults exclusively on control trials, where visual imagery generation was not explicitly cued. As recent work demonstrated, it appears that the production of eye movements may be guided by both visual and semantic representations (De Groot, Huettig, & Olivers, 2016), and that the activation of these representations occurs simultaneously when task stimuli are introduced verbally rather than visually (Huettig & McQueen, 2007). As a result, it is possible that the distinct profiles of oculomotor behaviour I observed in control trials reflected participants' tendency to prioritize visual or semantic representations to support their constructive endeavour. It is now well-established that, as we age, domain-specific knowledge assumes an increasingly prominent role in driving how we perceive, process, and recall external stimuli (Umanath & Marsh, 2014). Therefore, this tendency to rely on semantic information to a greater extent may explain why older participants generated more fixations and saccades than younger adults in control compared to construction trials, where stimuli were specifically designed to be abstract in nature. While further research is needed to confirm this hypothesis, my findings provide an initial hint that patterns of oculomotor behaviour might diverge in healthy ageing in response to alterations in underlying cognitive mechanisms, particularly in the absence of externally cued visual stimuli.

The results presented in this Chapter stand somewhat in contrast to those of the study by Rendell et al. (2012) in which older adults rated their imagined scenarios as less salient and less spatially coherent than their younger counterparts. Task differences likely account for the above-mentioned discrepancies in subjective ratings. Notably, in the Rendell et al. (2012) study, participants were asked to generate novel atemporal scenarios in familiar settings such as a beach, museum, and a pub, in keeping with the Hassabis et al. (2007) scene construction task (e.g., "*Imagine you're lying on a deserted white sandy beach in a beautiful tropical bay*", "*Imagine you're sitting, having a drink in a pub*"). In contrast, I used a more highly structured and carefully controlled experimental paradigm with well-defined cues to ensure participants adhered to the narrative description as much as possible, a methodological choice that may have supported task performance in older adults (see also Sheldon & Levine, 2016). Importantly, while previous studies have interrogated the provision of contextual details as the main outcome measure on mental construction tasks, I constrained my focus to key oculomotor and phenomenological indices. This approach allowed me to explore the process of scene construction while avoiding potential confounds driven by age-related differences in narrative style, as well as measurement errors that need to be addressed when scoring participants' narratives. For example, the extant literature suggests that verbal descriptions do not necessarily capture the subjective experience of mental constructions and that their objective assessment by external examiners may diverge from participants' assessments of their own thoughts (Miloyan & McFarlane, 2019).

3.6.3 Current theories of neural and oculomotor dynamics in ageing

Mounting evidence supports the proposal that older adults may leverage oculomotor behaviour as a compensatory mechanism to support task performance (Ryan et al., 2022; Wynn et al., 2019). Studies using multi-modal and multivariate approaches on memory-based tasks indicate that age-related changes in the activity and structure of the hippocampus and broader medial temporal lobe (MTL) may lead to moment-to-moment alterations in the amount and patterns of visual exploration in an effort to upregulate the encoding and successful retrieval of information (Z. X. Liu et al., 2018). For instance, oculomotor mechanisms such as gaze reinstatement may be preferentially recruited in older populations to help recapitulate the spatiotemporal context of previously encountered stimuli, particularly in the early stages of visual exploration and at lower levels of cognitive demands compared to younger adults (Ryan et al., 2022). Nonetheless, in the absence of externally cued visual stimuli, the findings of the present study point to distinct age-dependent oculomotor dynamics that may better support the mental construction. Specifically, when task demands increase beyond a critical threshold, it may become more efficient to conserve available cognitive resources by attenuating the production of eye movements and increasing efforts towards the construction and maintenance of a spatially coherent scene representation in working memory, particularly in the older population. Such dynamic reduction in oculomotor behaviour is likely to result from the increasing demands placed on working memory capacity to maintain scene representation when external visual cues are not available. While the precise cognitive mechanisms enhancing or inhibiting the production of eye movements and its relationship to memory performance remain unclear, my results contribute to the current body of evidence in suggesting that age-related declines in the integrity of the memory system influence active vision (see Ryan et al., 2022 for a comprehensive review).

3.6.4 Limitations

A number of methodological considerations warrant attention. Firstly, I did not include an objective index of the contextual details generated during scene construction. As previously mentioned, this was intentional as the focus of this study was to explore oculomotor dynamics as a function of task complexity using a carefully controlled paradigm. It is becoming increasingly clear that currently available verbal tasks assessing complex expressions of memory fail to capture adaptive neural and cognitive changes that naturally occur in older age, such as a shift from detail- to gist-based memory representations (see Andrews-Hanna et al., 2019; Grilli & Sheldon, 2022). This finding suggests that narrative-based tasks designed to elicit the provision of specific detail are not always suitable in the context of ageing research (discussed by Miloyan, McFarlane, & Suddendorf, 2019). On the other hand, oculomotor signatures of visual exploration provide an objective measure to gain insight into the cognitive mechanisms supporting performance in construction-based tasks, particularly age-related deficits in visuospatial processing and working memory (Van der Stigchel & Hollingworth, 2018). Secondly, it should be noted that the stimuli used in the current study may be more familiar or meaningful to older adults and may have enabled them to harness schemas or gist-based representations rather than constructing scenes *de novo* (Irish, 2020). The novelty ratings provided by participants at the end of the experimental task suggest that older adults generated scenes that were more familiar compared to younger adults, which may also explain why they rated construction trials as less difficult and experienced their imagined scenarios as more vivid and integrated. As a result, it may be that the richer repository of semantic and general conceptual world knowledge of older adults affords the necessary scaffold to generate familiar scenarios, in line with the semantic scaffolding hypothesis (Irish, 2016; Irish & Piguet, 2013).

Furthermore, this idea resonates with the experimental findings presented in Chapter 2, suggesting that older adults tend to evoke their semantic knowledge to a greater extent compared to their younger counterparts when performing a variety of cognitive endeavours. Finally, given that my experimental paradigm focused exclusively on the endogenous generation of visual mental imagery, future studies directly comparing endogenously generated versus externally cued visual imagery will be crucial to deepen our understanding of how atemporal scene construction mechanisms may change in healthy ageing.

3.6.5 Conclusions

This study is the first to explore the intersection between age-related changes in scene construction and visuo-oculomotor behaviour in the context of internally generated mental imagery. My findings suggest a compensatory shift away from the endogenous production of eye movements in older adults as a function of increasing task complexity. Future studies will be required to clarify the neural mechanisms driving the dynamic recalibration of resources in response to variations in task demands, and how such processes might be leveraged to predict cognitive outcomes in older age. As previously discussed, contributions from semantic and conceptual knowledge may have facilitated performance in the older group. Therefore, it remains unclear how older adults might fare on experimental tasks that disproportionately tax the construction of novel or implausible scenarios where traditional semantic associations are violated (discussed by Renoult et al., 2019). To address this issue, in the next chapter I will investigate age-related changes in cognitive performance and concurrent oculomotor behaviour during prospection, while manipulating both the temporal scale and the level of plausibility of the constructed scenarios.

Chapter 4

Seeing into the future: Episodic future thinking in healthy ageing

4.1 Introduction

In the previous Chapter, I explored age-related differences in atemporal scene construction and related visuo-oculomotor behaviour in the context of internally generated mental imagery. By employing a carefully controlled experimental paradigm, I was able to assess how gradual increases in task complexity affect scene construction mechanisms in younger and cognitively healthy older adults and how these dynamics translate to the subjective phenomenological experience of the mental endeavour. Results from this study point to changes in oculomotor profiles during the endogenous generation and maintenance of complex scenes. More precisely, both participant groups were found to engage in the production of eye movements to a greater extent in control versus construction trials and as the number of task elements progressively increased, irrespective of experimental condition. To explain these findings, I hypothesised that higher cognitive demands in the initial phase of the scene construction process may dampen visual exploration to support the establishing of a coherent and spatially contiguous representation in the mind's eye. Importantly, older adults experienced a significant reduction in oculomotor behaviour as soon as a second auditory element was introduced, suggesting an age-related, dynamic redeployment of cognitive resources as task demands exceed memory capacity to maintain scene representation. Under these circumstances, the production of eye movements may stand in competition for available cognitive resources and may therefore be attenuated to facilitate task performance.

4.1.1 The prospective brain: a human bias towards prospection

The findings summarised above provide novel insights into scene construction mechanisms in healthy ageing in the absence of externally cued visual stimuli. By incorporating an eye-tracking component, I was able to uncover some of the potential cognitive processes at play, make predictions about their possible age-related dynamic recalibration, and include an objective measure of the cognitive effort deployed in response to increasing task complexity. Most importantly, these results may inform further enquiries into similar mental feats such as episodic future thinking, where considerable demands are placed on both visual mental imagery and working memory capacities (Hill & Emery, 2013; Zavagnin, De Beni, Borella, & Carretti, 2016). When we construct and visualise spatially contiguous scenes in our mind's eye, we often project ourselves into the future, either in anticipation of what lies ahead or to foresee how hypothetical alternative scenarios may play out. This natural predisposition towards prospection has rapidly drawn attention within the scientific community (Conti & Irish, 2021; Schacter et al., 2012). Over the past two decades, neuroimaging studies comparing autobiographical memory and episodic future thinking performance have consistently demonstrated that these construction-based processes are strongly intertwined (Mullally & Maguire, 2014). In fact, not only are they believed to rely upon the flexible recombination of episodic content retrieved from long-term memory (Schacter & Addis, 2007), but they also appear to be underpinned by the same neural substrate, known as the core episodic network (Addis et al., 2007; Szpunar, Watson, & McDermott, 2007).

4.1.2 Alterations in future thinking capacities in healthy ageing

The discovery of considerable overlap in the cortical systems supporting memory retrieval and episodic future thinking strongly suggests that comparable disturbances may arise in populations where episodic memory is compromised. This parallel impairment across past and future contexts has been demonstrated in healthy ageing (Addis, Musicaro, Pan, & Schacter, 2010). Mounting evidence indicates that older adults' ability to engage in complex cognitive tasks is affected due to declines in working memory capacities, reduced efficacy of executive processes and poor inhibitory mechanisms (Craik & Salthouse, 2011; Hasher, Lustig, & Zacks, 2007). While deficits in episodic memory have traditionally been proposed as the primary mechanism driving alterations in future thinking capacities, the progressive degradation of visual imagery processes may also be a contributing factor. A growing body of literature converges to suggest that when visuospatial functions are affected, performance in imagery-laden and future thinking tasks is disproportionately compromised in older adults (Castellano et al., 2015; Gaesser et al., 2011). Accordingly, age-related degradation of stored visual percepts, coupled with impaired access to these representations, may impact the ability to recruit the content necessary for future simulations (Conti & Irish, 2021).

4.1.3 Investigating oculomotor behaviour to understand prospection

Valuable insights into future thinking mechanisms can be gleaned from the anatomical and functional overlap evident between oculomotor behaviour and prospection. To date, however, only a handful of studies have investigated oculomotor metrics in the context of future thinking. Interestingly, preliminary evidence suggests that the execution of voluntary, but guided eye movements selectively interferes with spatial imagery, one of the underlying processes commonly implicated in future thinking (de Vito, Buonocore, Bonnefon, & Della Sala, 2014; Wiebels et al., 2020). Future thinking performance during guided eye movement production appears to be significantly disrupted, in that participants generate fewer episodic, and more external or semantic details relative to unconstrained, freely moving conditions (de Vito et al., 2015). As such, guided eye movements may trigger a compensatory mechanism whereby participants recruit accessible yet tangential details to 'fill in the blanks' (Irish et al., 2012b).

On the other hand, whether spontaneous oculomotor behaviour facilitates the elaboration of future simulations remains unclear. For example, El Haj and Lenoble (2018) explored common oculomotor metrics in young adults during past and future thinking and reported that past experiences were rated as more vivid than future events and elicited more fixations and saccades relative to future simulations. This oculomotor response was interpreted by the authors as reflecting the specific operations of the visual system in the curation (via saccades) and subsequent activation (via fixations) of the appropriate sensory-perceptual information to populate the recollected mental scene during retrieval (El Haj & Lenoble, 2018). In contrast, a significant reduction in the production of eye movements was evident during prospection. Given that future thinking often requires a more effortful and dynamic manipulation of episodic content (Buckner & Carroll, 2007; Hassabis & Maguire, 2007; Schacter, 2012)[4], the authors suggested that the additional cognitive effort imposed by the associative demands of future simulations is associated with a quantitative reduction in oculomotor behaviour (El Haj & Lenoble, 2018).

4.1.4 Temporal context and plausibility contributions to episodic future thinking

The oculomotor findings presented so far resonate well with theoretical accounts attempting to understand how constructive processes change with increasing task demands. One such account is in relation to the construction of events set to take place in the distant future or the construction of events that are perceived as highly implausible (D'Argembeau & Van der

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[4] The assumption that future thinking is a constructive and effortful process, particularly when compared to memory retrieval, has recently been questioned on the basis of research findings showing that prospective thoughts can be experienced with the same phenomenological richness as past memories. To address this apparent paradox, Cole and Kvavilashvili (2021) put forward a *dual process account* of future thinking, postulating that episodic future thoughts may be elaborated via two distinct "routes" which are associated with separable cognitive processes and functions: (a) a slow, more effortful, voluntary route that involves the controlled and deliberate construction of a hypothetical future scenario and (b) a rapid, spontaneous route whereby episodic future simulations are simply a re-iteration of a previously constructed future event and therefore do not necessarily require the engagement of cognitively effortful processes.

Linden, 2004). Converging lines of research suggest that temporal distance from the present negatively affects the provision of episodic detail, the specificity of such detail, and the overall subjective experience associated with the future thinking process, whereby representations of temporally distant events tend to be more abstract and decontextualized (Trope & Liberman, 2003). In contrast, plausible scenarios (e.g., enjoying a family dinner during the upcoming Christmas holidays) are found to be qualitatively richer than implausible scenarios (e.g., a day trip to Juno) in terms of sensory-perceptual and semantic information (Pezdek, Blandon-Gitlin, & Gabbay, 2006). A possible explanation for these findings is that scenarios expected to happen in the near future may be perceived as easier to visualise and construct since they map more closely onto recently experienced events or may be more connected to the individual's current purposes, goals, and motives (D'Argembeau & Van der Linden, 2004). As a result, participants may have a clearer representation of how such events unfold drawing on their past experience, and can therefore envisage themselves as primary actors in such scenarios (see Libby & Eibach, 2002; Nigro & Neisser, 1983; Robinson & Swanson, 1993 for similar findings and arguments with respect to past events). In contrast, the elaboration of temporally distant and/or highly implausible events may disproportionately tax the semantic memory system, whereby participants must first generate an appropriate semantic scaffold into which event details can be assimilated (Irish, 2020). Therefore, the ambiguity imposed by the lack of a well-defined and coherent spatiotemporal backdrop may increase the generative demands of the constructive endeavour (Addis, 2018; Van Mulukom, 2013). For the same reason, such demands may require a greater allocation of cognitive resources. Where spontaneous oculomotor behaviour is concerned, under such circumstances we may predict a concomitant degradation of the subjective experience of the mental simulation, in terms of its perceived vividness and self-referential quality (Conti & Irish, 2021). Disentangling these complex dynamics in healthy ageing will be particularly relevant, where the production of eye movements during scene construction appears to be especially vulnerable to increasing task demands.

4.3.5 Study objectives

To address some of the questions outlined above, I implemented in the present study a novel experimental paradigm to examine the provision of episodic detail during prospection and its relationship with key oculomotor metrics, as well as participants' subjective experience. More precisely, I investigated age-related differences in behavioural and oculomotor variables of interest by manipulating the temporal distance of the constructed scenarios (near versus far future) and their objective plausibility (low versus high). Building on the extant literature, I hypothesised that, irrespective of age group, events that are temporally distant and implausible would be significantly less vivid, and accompanied by significantly fewer eye movements, due to their inherently higher constructive demands. Given the results presented in Chapter 3, I did not expect to observe significant between-group differences in participants' subjective ratings. However, I anticipated that distinct patterns of visual exploration may arise in each age group contingent on the generative demands imposed by each experimental condition and that older participants in particular would experience reductions in oculomotor behaviour as the perceived difficulty of the constructive endeavour increases.

4.2 Methods

4.2.1 Participants

Forty participants, comprising 22 younger adults and 18 cognitively healthy older adults, were recruited between October 2022 and September 2023. Younger adults (18-24 years, 15 females) were undergraduate students at the University of Sydney and participated in the study in exchange for course credit through the Sydney University Psychology SONAPSYCH Research

Participation System. Older adults (62-76 years, 12 females) were recruited through the volunteer research pool at FRONTIER, the frontotemporal dementia research clinic based at the Brain and Mind Centre, University of Sydney, Australia.

Prior to the experimental session, older adults were required to score >88/100 on the Addenbrooke's Cognitive Examination-III (ACE-III; Hsieh et al., 2013; So et al., 2018), a broad assessment of cognitive function covering domains of attention, memory, fluency, language, and visuospatial function. Exclusion criteria for both younger and older participants included concurrent psychiatric diagnosis, presence of other neurological syndrome, traumatic brain injury, or history of alcohol or substance abuse. All participants had normal or corrected-to-normal vision.

A posteriori power calculations on sample sizes were performed using G*Power (Faul et al., 2007). The results of these analyses are presented in the corresponding sections based on the statistical tests employed therein.

4.2.2. Eye-tracking apparatus

The eye-tracking equipment and setup for this study was the same as in Chapters 2 and 3. Please refer to section 2.2.2 for all details.

4.2.3. Task stimuli

Participants were required to elaborate and verbally describe hypothetical future scenarios in response to auditory cues while looking at a blank screen. Auditory cues for this study were 9 short audio recordings (8 event cues and 1 control cue, see Table 4.1) providing the initial framework of an event including key details about the "what", "where" and "when" of the to-be-constructed scenario. A 2 x 2 design was used to explore whether behavioural and oculomotor outcomes of the future thinking process were affected by (i) Temporal Context (Near, i.e., one year from the day of testing, vs Far, i.e., 10 years from the day of testing), and (ii) Plausibility (Low vs High). Over the course of the task, participants were required to generate two events per experimental condition (*near future – low plausibility; near future – high plausibility; far future – low plausibility; far future – high plausibility*).

Event cues were designed in discussion with my primary supervisor, Prof. Muireann Irish, to maximise the dimensions of plausibility/implausibility. Furthermore, to ascertain that the choice of scenarios effectively allowed the manipulation of my variables of interest, prior to data collection a group of 12 healthy young adults provided ratings on the plausibility and difficulty of each stimulus on a scale from 1 to 5 (1 = low plausibility or low difficulty, .., 5 = high plausibility or high difficulty, see Table 4.1). Statistical analyses using paired t-tests pointed to significant differences in the ratings provided between plausible and implausible scenarios for both temporal conditions (near future: $t = 12.87$; $p < .001$; far future: $t = 5.71$; $p < .001$). In addition, and in agreement with the current literature, scenarios set in the near future were perceived as less difficult to envisage relative to scenarios set in the far future (low plausibility: $t = -3.82$, $p < .001$; high plausibility: $t = -5.13$; $p < .001$). Importantly, paired t-tests also indicated that events within the same plausibility and temporal context were matched across conditions (all p-values >.2), with the only exception that one low plausibility scenario in the far future (i.e. a trip to the local medical centre, now run by robots, see Table 4.1) was perceived as more plausible than the other ($t = -5.74$; $p = .001$).

As part of the experimental protocol, the order of presentation of event cues was first counterbalanced by temporal distance and secondly by plausibility. In other words, half of the sample completed the near future condition first, followed by the far future, and vice versa for the remainder of the sample, and event cues within each temporal condition were further randomised across subjects. The control cue presented an atemporal and commonplace scenario and was always performed at the end of the experimental session. The control trial was used to control for participants' verbal narration, generativity, fluency, and the ability to structure a coherent narrative from beginning to end.

Table 4.1 Event and control cues for the future thinking task alongside mean plausibility and difficulty ratings provided by a piloting group of 12 healthy young adults.

	Plausibility	**Scenario**	**Plausibility Ratings Mean (SD)**	**Difficulty Ratings Mean (SD)**
Near Future	**Low**	Imagine yourself one year from now. You are sitting with your family watching television and you receive a call to inform you that you have just won the Nobel Prize. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	1.58 (0.90)	2.08 (0.90)
		Imagine yourself one year from now. You are going on a morning walk to the nearby park with your pet tiger. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	2.17 (1.47)	1.83 (0.72)
	High	Imagine yourself one year from now. You are going on holiday for one week to your favourite destination and you have just arrived at your hotel. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	4.67 (0.49)	1.17 (0.58)
		Imagine yourself one year from now. You are going to the cinema with a friend to watch the premiere of your favourite actor's new movie. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	4.58 (0.67)	1.42 (0.67)

Far Future	**Low**	Imagine yourself 10 years from now. You are celebrating your birthday with your family and friends at your underwater home, located right at the bottom of the Pacific Ocean. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	2 (1.28)	2.92 (0.79)
		Imagine yourself 10 years from now. You are going to your local medical centre for a check-up. The clinic is now run by robots with full-body scanners that tell you what's wrong and provide medical advice. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	3.25 (0.97)	2.33 (1.07)
	High	Imagine yourself 10 years from now. You are going to the supermarket and it's your first time in your brand-new self-driving car. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	4.08 (0.67)	1.75 (0.75)
		Imagine yourself 10 years from now. You are going to visit the USA. You are about to embark on a zero-emission plane taking only 8 hours to reach your destination. Describe this experience in as much detail as possible, including what you can see, hear, and feel.	3.67 (1.07)	1.92 (0.67)
Control condition		Describe your morning routine in as much detail as possible, from the moment you wake up to the moment you step out of the door, ready for the day.	N/A	N/A

Notes: All cues were audio recorded and presented to participants at the beginning of each trial. Subjective ratings were provided on a scale from 1 (lowest) to 5 (highest). Mean ratings for Plausibility and Difficulty are shown, with standard deviations (SD) provided in brackets.

4.2.4. Procedure

Figure 4.1 presents a schematic of the testing protocol for this study. Each trial began with the text "Clear your imagination" displayed at the centre of the screen for 2 seconds, prompting participants to clear their mind in preparation for the upcoming trial. This was followed by the audio presentation of the event cue providing the framework for the hypothetical future scenario to be constructed (cf. Section 4.2.3). A fixation cross then appeared at the centre of the screen (1s), followed by the text "Press the space bar when ready to describe" (2s). At this point the screen turned completely black, and participants could take as much time as they needed to develop the scenario in their mind's eye. Participants then pressed the space bar when they were ready to provide a detailed verbal description of their imagined scene. The descriptive phase of the trial had a fixed duration of 2 minutes. A beep sound (1s) immediately following the keyboard press indicated when to begin the verbal description of the constructed event. Once 2 minutes had elapsed, a beep sound (1s) indicated that the trial was now over. Importantly, at the beginning of the experiment, participants were informed about how much time they would have to describe their scenarios and were encouraged to provide as many details as possible until the allocated description time had elapsed. Participants were also instructed to always keep their eyes open during both the elaboration and the description phase of each trial. They were allowed to move their eyes as desired, as long as their gaze was directed towards the screen. Verbal narratives were recorded using a Philips DVT1160 Voice Tracer, and later transcribed using the machine learning-based software Otter.ai (Angeli, 2016).

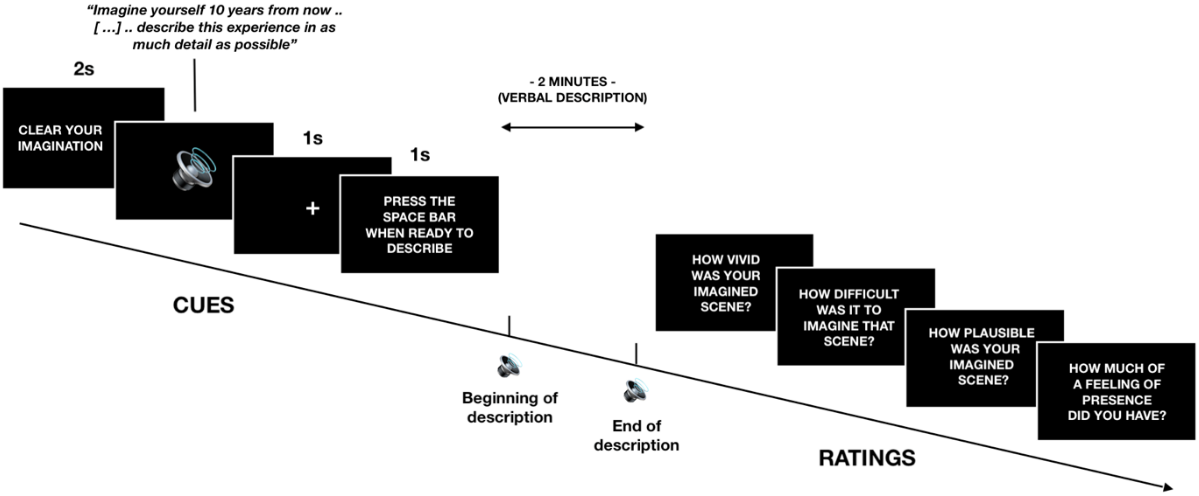

Figure 4.1 Episodic future thinking task design.

Notes: Representative timeline of a construction trial set in the far future (i.e., 10 years from the time of testing).

Subjective ratings

Following the narrative description of each event, participants were prompted to provide ratings about specific aspects of each constructed scenario using the keyboard. For construction trials, participants were asked to rate the vividness of their imagined scene (1= not vivid, .. , 5 = very vivid), the overall difficulty of the current trial (1 = easy, .. , 5 = difficult), the plausibility of their imagined scene (1 = low plausibility, .., 5 = high plausibility), as well as their sense of presence in the imagined scene (1 = not at all, .. , 5 = very strong). For the final control trial, participants were only asked to rate the vividness and the overall difficulty of the current trial using the same rating scales presented above. No time limit was imposed when answering these questions to accommodate slower search times in older participants when using the keyboard. For this phase of the study, participants were permitted to look away from the screen to provide their subjective ratings. The experimental task was completed in a single session, taking approximately 30 minutes.

4.2.5. Scoring

The content of participants' narrative descriptions was analysed using the scene construction scoring protocol developed by Hassabis et al. (2007). Each scenario was segmented into a set of content statements and every statement was classified as belonging to one of the following four categories: (i) Entities Present, (ii) Spatial References, (iii) Sensory Descriptions, and (iv) Thoughts/Emotions/Actions. The Entities Present category was a simple count of any unique items or people that were mentioned in the scenario description (e.g., "there is plenty of coral"). The Spatial References category comprised statements describing the relative position of entities within the scene (e.g., "behind the reception desk", "around the tiger's neck"). The Sensory Description category consisted of statements describing the property of an entity (e.g., "the windows are made of glass"), as well as general descriptions of the scene environment (e.g., “it’s all white and clean”) and its weather conditions (e.g., “it is a warm sunny day”). The Thoughts/Emotions/Actions category covered any introspective thoughts or emotional feelings (e.g., “I feel very excited to be going on vacation”), as well as the thoughts, intentions or actions of other entities in the scene (e.g., “my whole family is awestruck”, “the stewardess offers me a drink”). Repeated statements, irrelevant details, or other tangential information that could not be classified into one of the four categories were discarded. One point was awarded for each separable statement, up to a maximum of 7 points for each of the four categories. The total possible content score for each imagined experience was therefore 28, in keeping with the original scoring protocol (Hassabis et al., 2007).

Interrater Reliability Analysis

Myself and a second independent rater (MI) blind to group and condition scored 20% of the dataset. This subset corresponds to the narratives for 8 participants in the study (i.e., 72 events) randomly selected from the full sample. I then conducted an inter-rater reliability analysis using the R function *icc* (Wolak, Fairbairn, & Paulsen, 2012) to obtain Intraclass Correlation Coefficients (ICC) and confidence intervals. Results from this analysis indicated strong convergence of scores for all detail categories between the raters (all ICC > 0.7, all *p-values* < .001; see Table 4.2). As a result, the remaining 80% of the dataset was scored by one rater only, i.e., myself.

Table 4.2 Inter-rater reliability analysis for the scoring procedure.

	ICC (reliability coefficient)	**Confidence interval**	***p*-value**
Total content [28]	0.891	[0.789 - 0.940]	***
Entities present [7]	0.756	[0.636 - 0.840]	***
Sensory descriptions [7]	0.872	[0.802 - 0.918]	***
Spatial References [7]	0.801	[0.609 - 0.891]	***
Thoughts/Emotions/Actions [7]	0.731	[0.601 - 0.823]	***

Notes: Intraclass Correlation Coefficients (ICC) and confidence intervals were obtained using the R function *icc* with * $p < .05$; ** $p < .01$; *** $p < .001$.

4.2.6. Statistical analyses

Behavioural performance on the future thinking task was analysed using R (R Core Team, 2012, version 4.2.0) and MATLAB (The MathWorks Inc, 2017). Prior to analyses, the number of episodic details, subjective ratings and oculomotor data in each experimental condition were averaged across the 2 corresponding trials. For continuous variables, normality of distributions and homogeneity of variances were examined using Kolmogorov–Smirnov tests and Levene tests, respectively. Group differences in Total Episodic Content were assessed via a 2 x 2 x 2 mixed ANOVA with Group (Younger, Older) as the between-subject factor, and Temporal Context (Near, Far) and Plausibility (Low, High) as the within-subject factors. For ease of interpretation, and due to no significant main effect of Group being found, four 2 x 2 mixed ANOVAs with Temporal Context and Plausibility as the within-subject factors were performed on the whole dataset for each detail subcategory separately (Entities Present, Sensory Descriptions, Spatial References and Thoughts, Emotions and Actions). The alpha level to determine statistical significance was set at $p < .05$. Partial eta-squared values (η^2_p) were assessed as a measure of effect size for ANOVA statistics. Post hoc comparisons were adjusted using Bonferroni correction.

Oculomotor measures of interest (i.e., number and duration of fixations, and total scan paths) were investigated using linear mixed-effect models (LME) and Sidak post-hoc tests (R function afex, Singmann et al., 2022) with Group (Younger, Older) as fixed effect, and Temporal Context and Plausibility as random effects. Appropriate continuous transformations were applied as required when assumptions of normality distributions were violated, or due to the presence of a few outlier datapoints (cf. Section 4.5).

Differences in participants' subjective ratings (i.e., vividness, difficulty, plausibility, and sense of presence) were examined using non-parametric Kruskal-Wallis tests for independent samples, and Wilcoxon signed-rank tests for related samples. Post hoc comparisons were adjusted using Benjamini-Hochberg corrections (Groppe, 2023).

Finally, one-tailed Spearman correlation analyses with Benjamini-Hochberg corrections were performed to explore potential associations between behavioural and oculomotor measures of interest. I constrained my focus to a single experimental condition (*near future – low plausibility*) based on the results presented in the sections preceding the correlation analyses (cf. Section 4.6). This enabled me to reduce the number of overall correlations and to make predictions on the specific direction of potential associations between behavioural and oculomotor measures using one-tailed Spearman correlation analyses.

4.3 Results

4.3.1 Total content

First, I considered the total number of details participants generated in construction trials (i.e., Total Content, max score: 28). I performed a 2 x 2 x 2 mixed ANOVA with Group (Younger, Older) as the between-subject factor, and Temporal Context (Near, Far) and Plausibility (Low, High) as the within-subject factors. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample size of 40 participants was sufficient to detect a significant main effect of size $f = 0.4$ with 87% power and an alpha level of 0.05, and a significant two-way interaction of size $f = 0.23$, corresponding to $\eta^2_p = 0.05$, with 94% power and an alpha level of 0.05.

Results from the mixed model ANOVA failed to reveal a significant main effect of Group ($F(1,38) = 1.37$, $p = .25$, $\eta^2_p = 0.04$), indicating that the overall provision of contextual detail did not differ between the groups. However, a significant main effect of Temporal Context was found ($F(1,38) = 6.93$, $p = .01$, $\eta^2_p = 0.15$) indicating that, irrespective of group, participants generated more content for scenarios in the far vs near future ($p = .01$). Similarly, a significant main effect of Plausibility was found ($F(1,38) = 13.18$, $p <.001$, $\eta^2_p = 0.26$) whereby, irrespective of group, participants generated more content when event plausibility was high vs low ($p = .008$). Finally, the Temporal Context x Plausibility interaction was significant ($F(1,38) = 7.98$, $p = .008$, $\eta^2_p = 0.17$). Post-hoc analyses on this interaction term revealed that, for near future scenarios, participants generated more contextual details when plausibility was high compared to low ($p <.001$ see Figure 4.2, left side panel). Furthermore, when event plausibility was low (i.e., implausible), participants generated more contextual details in the far compared to near future ($p <.001$; see Figure 4.2, right side panel).

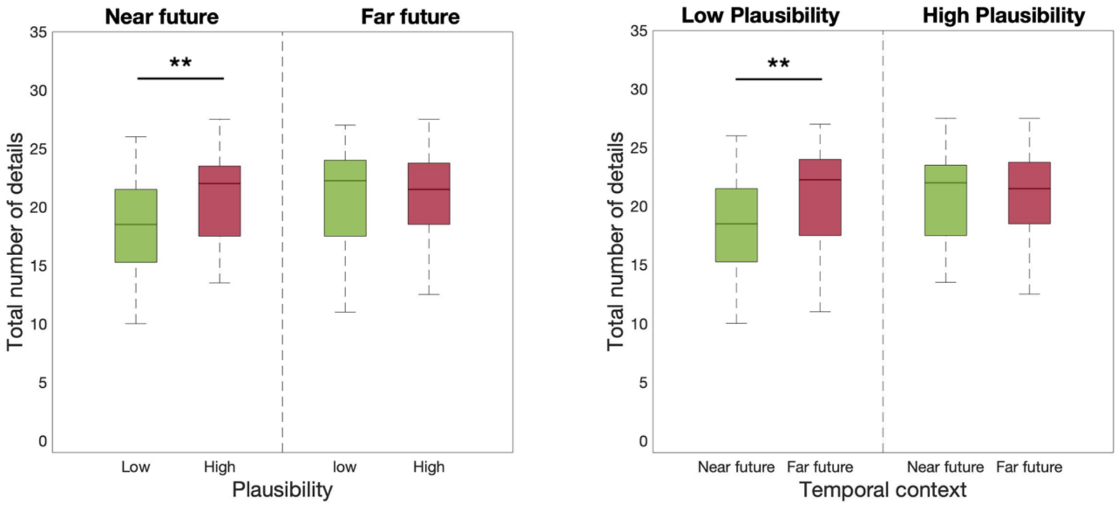

Figure 4.2 Total content generated by participants for each experimental condition.

Notes: Temporal Context x Plausibility interaction on the Total Content generated by participants during the episodic future thinking task. Statistically significant results from post-hoc analyses are shown with * $p < .05$; ** $p < .01$; *** $p < .001$.

4.3.2 Contextual detail profile

Figure 4.3 shows the breakdown of Total Content according to the four content subcategories on the scene construction task. Given there was no significant main effect of Group (cf. Section 4.3.1), I aggregated the data from the younger and older participant groups (n = 40). Then, I performed four separate 2 x 2 mixed ANOVAs, one for each detail subcategory (Entities Present, Sensory Descriptions, Spatial References, and Thoughts, Emotions and Actions), with Temporal Context (Near, Far) and Plausibility (Low, High) as the within-subject factors. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample size of 40 participants was sufficient to detect a significant main effect, as well as a significant two-way interaction, of size $f = 0.23$, corresponding to $\eta^2_p = 0.05$, with 94% power and an alpha level of 0.05.

Entities Present

A significant main effect of Temporal Context was found ($F(1,39) = 3.99$, $p = .05$, $\eta^2_p = 0.09$), indicating that participants generated more unique entities in the far compared to near future (mean difference: 0.256, $p = .05$). No significant main effect of Plausibility ($F(1,39) = 3.37$, $p = .07$, $\eta^2_p = 0.08$) was found. The Temporal Context x Plausibility interaction was significant ($F(1,39) = 20.81$, $p <.001$, $\eta^2_p = 0.35$). Post-hoc analyses on this interaction term indicated that, for scenarios in the near, but not far future, participants provided significantly more entities present for plausible relative to implausible events (mean difference: 0.9, $p <.0001$). Conversely, for implausible, but not plausible events, the number of entities present was significantly higher in the far versus near future (mean difference: 0.89, $p <.001$, see Table 4.3).

Sensory Descriptions

A significant main effect of Temporal Context ($F(1,39) = 9.41$, $p = .004$, $\eta^2_p = 0.19$) was found, indicating that participants generated more sensory description details in the far compared to near future (mean difference: 0.72, $p = .004$). Similarly, a significant main effect of Plausibility was found ($F(1,39) = 12.31$, $p = .001$, $\eta^2_p = 0.24$), whereby participants generated more sensory description details for plausible relative to implausible events (mean difference: 0.66, $p = .001$). The Temporal Context x Plausibility interaction was also significant ($F(1,39) = 15.19$, $p < .001$, $\eta^2_p = 0.28$). Post-hoc analyses on this interaction term indicated that participants provided more sensory description details for scenarios in the near, but not far future, when event plausibility was high compared to low (mean difference: 1.39, $p < .0001$). Conversely, when event plausibility was low, the number of sensory descriptions was significantly higher in scenarios set to take place in the far versus near future (mean difference: 1.45, $p < .0001$, see Table 4.3). No significant differences emerged when event plausibility was high ($p > .05$).

Spatial References

No significant main effect of Temporal Context ($F(1,39) = 0.79$, $p = .004$, $\eta^2_p = 0.002$) was present for spatial references. However, a significant main effect of Plausibility was found ($F(1,39) = 7.43$, $p = .01$, $\eta^2_p = 0.16$), indicating that participants generated more spatial references for plausible relative to implausible events (mean difference: 0.45, $p = .01$). The Temporal Context x Plausibility interaction was not significant ($F(1,39) = 1.17$, $p = .29$, $\eta^2_p = 0.03$, see Table 4.3).

Thoughts, Emotions and Actions

No significant main effects were found for Temporal Context ($F(1,39) = 0.00$, $p > .99$, $\eta^2_p < .001$) or Plausibility ($F(1,39) = 0.97$, $p = .33$, $\eta^2_p = 0.002$) in relation to the Thoughts/Emotions/Actions subcategory. However, the Temporal Context x Plausibility interaction was significant ($F(1,39) = 10.63$, $p = .002$, $\eta^2_p = 0.21$). Post-hoc analyses on this interaction term indicated that for the near future, participants generated significantly more thoughts, emotions and actions details for implausible relative to plausible events (mean difference: 0.44, $p = .01$). In contrast, for far future scenarios, participants generated significantly more thoughts, emotions and actions details when event plausibility was high compared to low (mean difference: -0.26, $p = .05$). Regarding the other side of the interaction, when event plausibility was low, participants generated more thoughts, emotions and actions details in the near versus far future (mean difference: 0.35, $p = .01$). No significant differences emerged when event plausibility was high ($p > .05$).

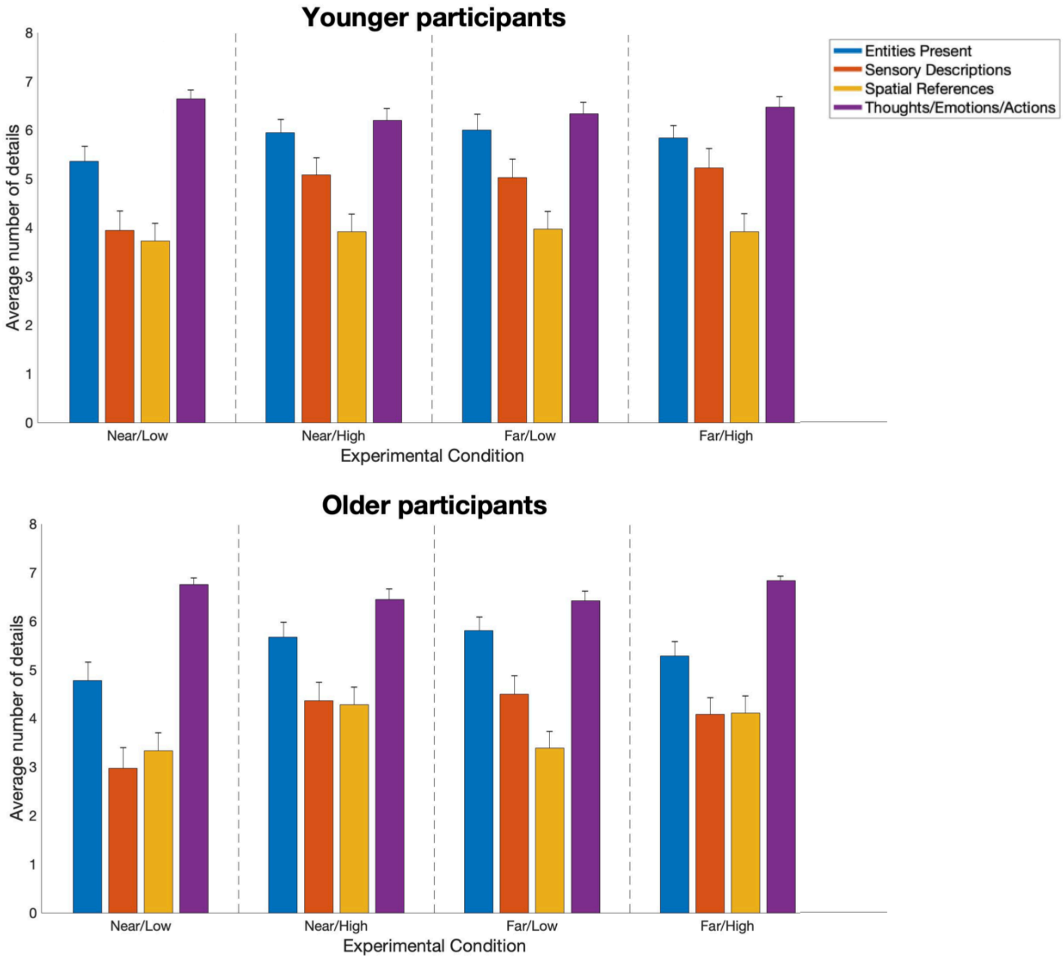

Figure 4.3 Contextual detail profile by experimental condition and participant group.

Notes: Contextual detail profile by experimental condition for younger (top bar plots) and older participants (bottom bar plots). Scores are based on 8 construction trials per participant with 2 trials per experimental condition. Participants' scores in each experimental condition were averaged across the 2 corresponding trials. Error bars correspond to one standard error.

Table 4.3 Temporal Context x Plausibility interaction for details generated during the future thinking task.

	Plausibility		**Temporal Context**	
Experimental Condition	**Low**	**High**	**Near**	**Far**
Total Content	Far > Near	Far = Near	High > Low	High = Low
Entities Present	Far > Near	Far = Near	High > Low	High = Low
Sensory Descriptions	Far > Near	Far = Near	High > Low	High = Low
Spatial References	n.s.	n.s.	n.s.	n.s.
Thoughts/Emotions/Actions	Near > Far	n.s.	Low > High	High > Low

Notes: The Temporal Context x Plausibility interaction is shown for the whole data sample combining younger and lder participants. n.s. = Temporal Context x Plausibility interaction not significant.

As summarised in Table 4.3, for implausible events, participants generated more contextual details overall, and particularly more unique entities, sensory descriptions, and spatial references, for scenarios in the far (e.g., Celebrating one's birthday at the bottom of the Pacific Ocean in 10 years' time), versus near future (e.g., Going on a morning walk with a pet tiger). However, participants generated more thoughts, emotions, and action details for implausible events in the near versus far future (see Table 4.3, left side panel - *Plausibility*). Similarly, for events in the near future, participants generated more contextual details overall, and particularly more unique entities, sensory descriptions, and spatial references, when event plausibility was high (e.g., Going to the cinema with a friend) versus low (e.g., Winning the

Nobel prize). However, events in the near future contained higher levels of thoughts, emotions, and action details when event plausibility was low versus high (see Table 4.3. right side panel – *Temporal Context*).

4.4 Subjective ratings

Between group differences

Table 4.4. displays the average vividness, integration, plausibility, and presence ratings according to the experimental condition for younger and older adults. Non-parametric Kruskal-Wallis tests with Benjamini-Hochberg corrections for multiple comparisons failed to reveal significant group differences in any of these ratings (all p values >.1). These results indicate that, overall, the phenomenological experience associated with future thinking did not differ between younger and older adults.

Table 4.4 Mean subjective ratings for construction trials by experimental condition for younger and older participants.

Variable	**Condition**		**Younger (n = 22)**	**Older (n = 18)**	**Group differences**
VIVIDNESS	Low Plausibility	Near Future	3.16 (0.75)	3.58 (0.97)	(p = .30)
		Far Future	3.27 (0.83)	3.58 (0.77)	(p = .36)
	High Plausibility	Near Future	3.70 (0.67)	4.08 (0.94)	(p = .11)
		Far Future	3.23 (0.64)	3.69 (0.84)	(p = .11)
DIFFICULTY	Low Plausibility	Near Future	2.80 (0.84)	2.81 (1.82)	(p = .85)
		Far Future	2.80 (0.97)	2.61 (0.88)	(p = .66)
	High Plausibility	Near Future	2.37 (1.01)	2.03 (1.05)	(p = .49)
		Far Future	2.43 (0.70)	2.00 (0.89)	(p = .28)

PLAUSIBILITY	Low Plausibility	Near Future	1.41 (0.61)	1.47 (0.76)	(*p* = .98)
		Far Future	1.73 (0.75)	1.72 (0.66)	(*p* = .98)
	High Plausibility	Near Future	3.91 (1.92)	4.00 (0.99)	(*p* = .98)
		Far Future	3.09 (1.05)	2.94 (0.86)	(*p* = .98)
PRESENCE	Low Plausibility	Near Future	2.95 (0.86)	3.14 (1.10)	(*p* = .49)
		Far Future	2.75 (0.84)	3.14 (0.66)	(*p* = .28)
	High Plausibility	Near Future	3.30 (0.77)	3.86 (0.92)	(*p* = .10)
		Far Future	3.07 (0.60)	3.28 (0.86)	(*p* = .49)

Notes: Ratings based on 8 construction trials per participant, with 2 trials per experimental condition. Subjective ratings were provided on a scale from 1 (lowest) to 5 (highest). Participants' ratings in each experimental condition were averaged across the 2 corresponding trials. Mean values are shown, with standard deviation provided in brackets. Group differences were explored using non-parametric Kruskal-Wallis tests with Benjamini-Hochberg corrections.

Within group differences

Wilcoxon signed-rank tests with Benjamini-Hochberg corrections were used to explore phenomenological differences across experimental conditions within each participant group.

For younger adults, constructed scenarios were perceived as more vivid when plausibility was high compared to low in the near future (Z = -2.00; p =.05) but not the far future (p =.77). Furthermore, plausible scenarios were rated as more both more vivid and more plausible when set in the near compared to far future (vividness: Z = -2.00; p =.05, plausibility: Z = -2.50, p =.01), while no such difference was found for implausible scenarios (both *p-values* >.07). Ratings of perceived difficulty and subjective sense of presence were comparable across all experimental conditions (all *p-values* >.3). Finally, Spearman correlation analyses failed to reveal significant associations between any of the subjective ratings and the total content generated by younger adults in any of the experimental conditions (all adjusted *p-values* >.05).

For older adults, no significant within-group differences were found for ratings of subjective vividness, difficulty, or sense of presence based on the experimental condition (all adjusted *p-values* >.05). Plausible scenarios were perceived as more plausible, irrespective of temporal context (near future: Z = - 4.52, p <.001; far future: Z = -3.67, p <.001). Furthermore, when event plausibility was high, subjective ratings of plausibility were significantly higher for scenarios set in the near vs far future (Z = -3.07, p =.002). In contrast, when event plausibility was low, subjective ratings of plausibility were comparable across temporal contexts (Z = -1.41, p = .16). Finally, Spearman correlation analyses failed to reveal significant associations between any of the subjective ratings and the total content generated by older adults (all adjusted *p-values* >.05).

4.4.2 Control trial performance

In control trials, participants were asked to describe their morning routine in as much detail as possible and to rate the vividness and difficulty of the trial. This trial was included to control for participants' verbal narration, generativity, fluency, and the ability to structure a coherent narrative from beginning to end. Kruskal-Wallis tests revealed that older participants rated their imagined scenario as more vivid compared to their younger counterparts (p = .05), while no significant differences emerged in terms of subjective difficulty or total content generated (both p-values > .4; see Table 4.5). These results indicate that general constructive and narrative endeavours were not perceived as more cognitively demanding in one age group compared to the other.

Table 4.5 Performance on control trials for younger and older participants.

Variable	Younger (n = 22)	Older (n = 18)	Group differences

Total Content [28]	20.73 (3.78)	19.61 (5.14)	($p = .70$)
Vividness	**4.50 (0.67)**	**4.89 (0.47)**	*
Difficulty	1.00 (0.00)	1.05 (0.23)	($p = .43$)

Notes: Subjective ratings were provided on a scale from 1 (i.e. not very vivid/easy) to 5 (i.e. extremely vivid/difficult). Mean values are shown, with standard deviation provided in brackets. Group differences were determined using non-parametric Kruskal-Wallis tests and Benjamini-Hochberg corrections. Statistically significant group differences are highlighted in bold, with * $p < .05$; ** $p < .01$; *** $p < .001$.

4.5 Oculomotor Results

Next, I analysed the eye movements produced while participants were describing their imagined scenarios. The oculomotor variables of interest were the number of fixations participants produced, the duration of each fixation, and the amount of eye movements (AEM) participants produced in the descriptive phase of the experimental task, measured as the total distance (i.e., total scan path) their eyes travelled in the allocated 2 minutes. Due to the presence of a few outlier datapoints in the number of fixations and given that the distributions of participants' scan paths and the durations of fixations were skewed and heavy-tailed, I applied a logarithmic transformation prior to performing linear mixed model analyses on the oculomotor variables. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample size of 40 participants was sufficient to detect a significant main effect of size $f = 0.4$, with 87% power and an alpha level of 0.05, and a significant two-way interaction of size $f = 0.2$ with 85% power and an alpha level of 0.05.

4.5.1 Number of fixations

A linear mixed model analysis revealed no significant main effect of Group ($F(1,38) = 0.59$; $p = .45$), Temporal Context ($F(1,38) = 0.09$; $p = .76$) or Plausibility ($F(1,38) = 0.86$; $p = .36$) in terms of the number of fixations participants produced. Similarly, no significant interactions were found (all *p-values* > .1).

4.5.2 Duration of fixations

The linear mixed model analysis failed to reveal a significant main effect of Group (*F*(1,38) = 0.09; *p* =.77), Temporal Context (*F*(1,38) = 0.17; *p* =.68) or Plausibility (*F*(1,38) = 3.26; *p* =.08), on the duration of fixations during future thinking. Similarly, no significant interactions were found (all *p-values* > .1).

4.5.3 Total scan path

I calculated the amount of eye movements (AEM) participants produced while describing their imagined scenarios as the total distance their eyes travelled during this time (i.e., total scan path, see Figure 4.4). The linear mixed model analyses failed to reveal a significant main effect of Group (*F*(1,38) = 0.05, *p* = .82), Temporal Context (*F*(1,38) = 0.95, *p* = .34) or Plausibility (*F*(1,38) = 0.22, *p* = .64). No significant interactions were found (all *p-values* > .08).

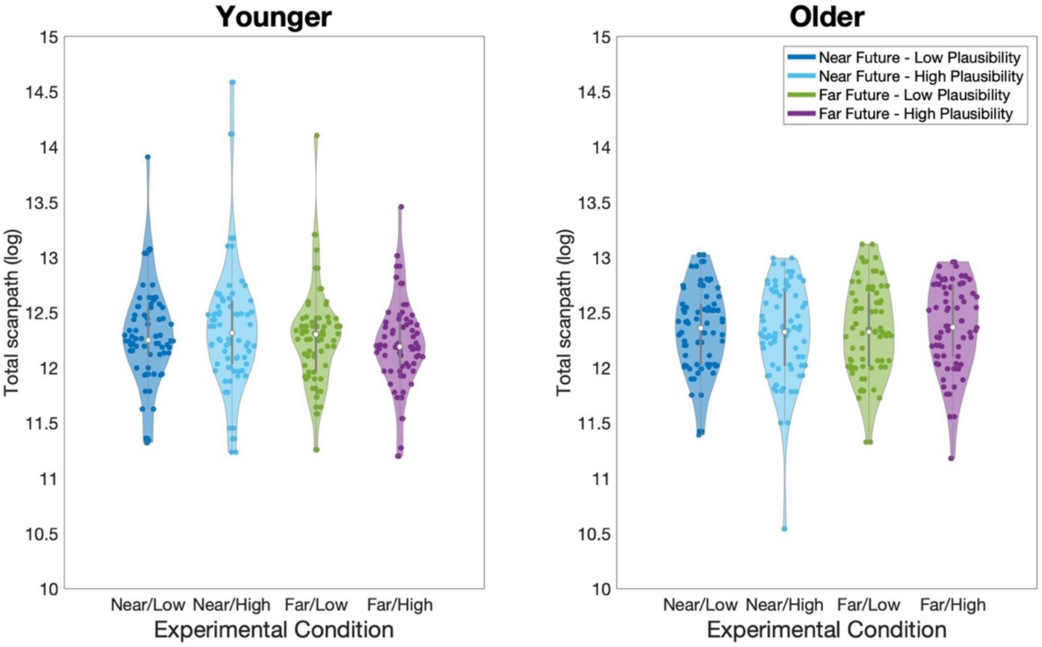

Figure 4.4 Participants' scan paths by experimental condition.

Notes: Mean scan paths produced by younger (left) and older (right) participants in the descriptive phase of the experimental task based on the temporal context (Near vs Far) and plausibility (Low vs High) of the constructed scenarios. Data are shown in logarithmic scale. Violin plots were obtained using the *violinplot* function for Matlab (Bechtold, 2016).

4.6 Correlation analyses

Spearman correlation analyses were performed to explore potential associations between behavioural and oculomotor measures of interest on test trials in a selected experimental condition (see Table 4.6). Given that no statistically significant main effect of Group emerged from the LME analyses on the oculomotor measures, correlations were run across the entire sample of 40 participants. Post-hoc power calculations using G*Power (Faul et al., 2007) indicated that a total sample size of 40 participants was sufficient to detect a significant correlation of size $r = 0.3$, with 60% power and an alpha level of 0.05.

Table 4.6 Correlation analyses between oculomotor measures of interests and subjective ratings of vividness, difficulty, and presence in near future, low plausibility scenarios.

Oculomotor variable	**Subjective rating (n = 40)**	**Correlation**	***p-value***
Number of fixations	Vividness	**$r = -0.39$**	*
	Difficulty	$r = 0.24$	($p = .07$)
	Sense of presence	$r = -0.27$	($p = .07$)
Mean fixation duration	Vividness	**$r = 0.34$**	*
	Difficulty	**$r = -0.30$**	*
	Sense of presence	**$r = 0.35$**	*
Total scan path	Vividness	**$r = -0.35$**	*
	Difficulty	**$r = 0.32$**	*
	Sense of presence	$r = -0.22$	($p = .08$)

Notes: Number of fixations, average fixation duration, total scan path and subjective ratings based on 2 test trials per participant. Subjective ratings were provided on a scale from 1 (lowest score) to 5 (highest score). Both participants' ratings and oculomotor data in the selected experimental condition were averaged across the 2 corresponding trials. Correlation values were obtained using one-tailed Spearman correlations and Benjamini-Hochberg corrections for multiple comparisons. Statistically significant correlations are highlighted in bold, with * $p < .05$; ** $p < .01$; *** $p < .001$.

As indicated in Section 4.4, both participant groups perceived implausible scenarios in the near future as being the least vivid and the least plausible, the most difficult to imagine, and evoking the weakest sense of presence (cf. Table 4.3). In such scenarios, participants were also found to generate the smallest number of contextual details overall (cf. Section 4.3.1), particularly unique entities, sensory descriptions, and spatial references. Interestingly, the number of thoughts, emotions, and actions generated in this condition was significantly higher compared to high plausibility trials (cf. Section 4.3.2). Accordingly, I examined potential correlations between oculomotor data and phenomenological experience (i.e., vividness, difficulty, and presence) for *implausible near future events*.

Spearman correlation analyses revealed that fewer but longer fixations were associated with greater vividness (0.34 ≦.|r| ≦.0.39, all *p-values* ≦.03), greater ease of construction (0.24 ≦.|r| ≦.0.32, all *p-values* ≦.07), and a stronger sense of presence (0.22 ≦.|r| ≦.0.35, all *p-values* ≦.08; see Table 4.6).

4.7 Discussion

Much of human daily life consists of anticipating and preparing for what lies ahead. This so-called prospective bias is evident in our everyday choices, whether imposed by immediate needs (e.g., thinking about our next meal) or more long-term decisions (e.g., choosing a career path or romantic partner). Despite this proclivity for prospection, our capacity to introspect and report reliably upon the visual contents of future thoughts is difficult to probe. The precise contribution of visual mental imagery to future thinking is not well-characterised and the extent to which temporal distance from the current moment and the perceived plausibility of simulated events influences the vividness of the constructed scenarios remains unclear. In the present study, I sought to address some of these questions by exploring oculomotor dynamics in younger and cognitively healthy older adults during the construction of hypothetical future scenarios and to determine how these dynamics relate to participants' subjective experience of constructed future events. I designed event cues to investigate how the specific temporal context (near versus far future) and plausibility of each scenario (low versus high) would affect the provision of contextual details, as well as the concomitant production of eye movements.

4.7.1 Variations in episodic content based on temporal context and plausibility

Analyses on the total episodic content generated during prospection revealed interesting dynamics at both ends of the temporal and plausibility spectrum (i.e., *near future plausible*, and *far future implausible*). More precisely, participants were found to generate more overall content, including more unique entities, sensory descriptions and spatial references, in these experimental conditions compared to the others. A potential explanation for these findings in relation to the near future comes from *construal level theory* (Liberman, Sagristano, & Trope, 2002). This theoretical account proposes that, by forming abstract mental construals of distal objects or events, we enable ourselves to make predictions about the future, remember the past, imagine other people's reactions, and speculate about what never occurred but might have been (Trope & Liberman, 2010). Furthermore, where near future events are concerned (e.g., going on vacation during the upcoming summer holidays), this theory proposes that the inclusion of a higher number of low-level construals, including more circumstantial, subordinate, and incidental details, yields more concrete, temporally close representations with a higher level of detail specificity (Cantor & Mischel, 1979; Rosch & Lloyd, 1978; Trope & Liberman, 2000). In contrast, the construction of far future events (e.g., going to the local clinical centre for a medical check-up in 10 years' time) would primarily invoke more abstract schemas or higher level construals, including more general, stereotypical and superordinate features of objects or events (Cantor & Mischel, 1979; Rosch & Lloyd, 1978; Trope & Liberman, 2000). In addition, a parallel line of research proposes that people may find it easier to elaborate detail-rich, temporally close events because these typically involve self-concepts that are perceived as more similar to the present self-concept (D'Argembeau & Van der Linden, 2004). As a result, people are more likely to represent and describe their narratives of near future events from a first-person rather than a third-person perspective (Libby & Eibach, 2002). By these views, I suggest that in near future plausible scenarios, participants in the present study were more likely to position themselves as actors in those scenarios, while also being able to draw from a larger autobiographical repository to furnish their mental simulations.

In contrast, when events were temporally distant from the present time (i.e., 10 years from the time of testing) and perceived as implausible (i.e., hosting a birthday party at the bottom of the Pacific Ocean), participants could not draw on personal memories or past experiences to enrich their narrative descriptions. Nonetheless, the significant Temporal Context x Plausibility interaction for Total Content indicates that participants did succeed in constructing and describing detail-rich far future, implausible events, meaning that the provision of contextual detail in these scenarios was not compromised. While future events presenting a strong contextual relationship with prior experience have often been found to contain more sensory details and clarity (Szpunar & McDermott, 2008), my results suggest that this is not always the case. For example, converging evidence from a large body of cognitive studies strongly suggests that increasing the temporal distance of future events from the present moment promotes creative thinking (Chen, Zhang, & Qi, 2020; Chiu, 2012; Förster, Friedman, & Liberman, 2004), which in turn may facilitate detail generation (Addis, Pan, Musicaro, & Schacter, 2016). Furthermore, a compelling future thinking study by Anderson (2012) suggests that the ability to elaborate implausible future scenarios results from the dynamic recombination of relevant content derived from a variety of sources, including not only autobiographical memories, but also self-unrelated experiences, as well as media-sourced information. In other words, irrespective of event plausibility or whether the individual has previously experienced similar events, information about past experiences is harnessed from a variety of sources. For instance, when personal memories are not immediately available to help populate the mental scene, participants may defer to conceptual knowledge and semantic information to support their constructions (Irish, 2016, 2020). Such content can then be flexibly integrated to yield a vivid and detail-rich future-oriented simulation (Anderson, 2012). Therefore, I tentatively suggest that these cognitive mechanisms may provide a potential explanation for the greater number of contextual details generated by participants in far future implausible scenarios.

4.7.2 An inverse relationship between oculomotor behaviour and subjective experience

Analyses of oculomotor responses in this study revealed that neither the temporal context nor the level of plausibility of the simulated scenarios seemed to impact the quantity, or quality, of the eye movements participants produced. These findings deviate from my initial predictions, in that I anticipated to see an attenuation of oculomotor behaviour during the construction of temporally distant and highly implausible scenarios. Interestingly, however, correlation analyses suggested that the production of eye movements was negatively associated with the phenomenological experience of the future thinking process, specifically in near future, implausible scenarios. In this context, when maintaining fixation rather than engaging in visual exploration, both participant groups rated their simulated events as more vivid and evoking a stronger sense of presence. These findings are not entirely unexpected, in that the constructive demands of episodic future thinking are particularly heightened when event plausibility is low, as novel associations between disparate details must be generated (Wiebels et al., 2020). From a neural standpoint, this idea is supported by compelling evidence of increased brain activity in cortical areas involved in the processing and relational binding of event details where no pre-existing associative links exist, particularly the right anterior hippocampus (Weiler, Suchan, & Daum, 2010). As the cognitive effort associated with the mental simulation increases, concomitant engagement in oculomotor behaviour may be disadvantageous.

Therefore, in the absence of externally cued visual stimuli that may otherwise be leveraged to support the provision of content, I tentatively suggest that the inverse relationship I observed between behavioural indices and oculomotor metrics may result from the necessity to redirect available cognitive resources, particularly working memory capacities and attention, to achieve task completion.

4.7.3 Absence of age-related differences in behavioural and oculomotor measures

Another unexpected finding in the present study was the lack of significant differences in both behavioural and oculomotor measures between younger and older adults. While oculomotor contributions to episodic future thinking remain largely unexplored, and even more so in the context of healthy ageing, a large body of cognitive research indicates age-related changes in complex constructive endeavours. Neuropsychological studies exploring past and future thinking consistently report narrative descriptions comprising a disproportionate number of external details, thoughts and references to separate events, as opposed to internal details, in older compared to younger adults (Addis et al., 2010; Levine et al., 2002). These changes have been suggested to reflect greater difficulty in accessing episodic details and/or age-related shifts toward conceptual and reflective processes (Andrews-Hanna et al., 2019). Nonetheless, my finding of comparable performance between younger and older adults on behavioural measures of past and future thinking is not entirely unseen. For example, studies suggest that in more naturalistic, everyday life settings, the nature and frequency of spontaneous past and future thoughts is not necessarily affected by the ageing process and that older adults may even experience an increase in prospective thoughts when compared to their younger counterparts (Berntsen, Rasmussen, Miles, Nielsen, & Ramsgaard, 2017; Gardner & Ascoli, 2015; Kvavilashvili & Fisher, 2007). This sharp contrast between findings of age-related decline and no effect, or even positive age effects in future thinking tasks conducted in laboratory-based and naturalistic contexts, respectively, has been termed the *age - prospective memory paradox* (Aberle, Rendell, Rose, McDaniel, & Kliegel, 2010; Kvavilashvili, Cockburn, & Kornbrot, 2013; Niedźwieńska & Barzykowski, 2012). More precisely, such paradox arises from converging evidence that task performance is significantly impoverished in older adults in laboratory-based (Maillet & Schacter, 2016; Schacter et al., 2013) but not naturalistic forms (Henry, MacLeod, Phillips, & Crawford, 2004; Phillips, Henry, & Martin, 2008; Rendell & Craik, 2000) of mental time travel. Although no clear understanding of this striking phenomenon currently exists, it has been suggested that a combination of variables such as perceived task difficulty, motivation and the specific methodological procedures typically employed in laboratory-based cognitive studies may influence these mixed findings (Warden, Plimpton, & Kvavilashvili, 2019). In relation to the present study, it is worth pointing out that participants were not interrupted and did not receive any general probes while constructing and describing their imagined scenarios. This means that they could freely elaborate on their spontaneous thoughts and enrich their narrative reports with as many details and associations that may have come to mind within the allocated two minutes. By contrast, in most behavioural studies of episodic future thinking, participants typically receive frequent cues to encourage the provision of additional contextual details as they elaborate on their accounts, and the individual nature of such details is inevitably constrained by the well-defined queries raised by the experimenter (Cole, Staugaard, & Berntsen, 2016; Schlagman & Kvavilashvili, 2008). Additionally, most future thinking studies have made use of the cue-word method, whereby participants are asked to come up with a specific event in the immediate or distant future starting from an arbitrary cue word providing minimal contextual support. Instead, in the present study event cues comprised a few well-defined elements to help participants set the scene. Accordingly, it may be argued that the generative demands of the constructive task used in this study are markedly reduced given that the semantic scaffold against which participants were required to elaborate their mental simulations was provided in full (see also Irish, 2020). As such, we tentatively suggest that the specific testing protocol may have circumvented potential age-related differences in the initial construction of events, however future research on cognitive ageing and prospection will be required to test this proposal. Finally, other methodological discrepancies may also explain the unusual findings presented in this chapter. First, in previous research on episodic future thinking, the temporal distance of event cues rarely exceeded three to five years (see for example Addis et al., 2010; Liberman et al., 2002; Terrett et al., 2016). As a result, the extent to which my behavioural results may be comparable to this body of evidence may be questioned. Furthermore, in cognitive tasks where future thinking capacities are explored by means of verbal reports, the reproducibility and validation of the corresponding results may be influenced by differences in the specific measures chosen to assess episodic foresight (Miloyan & McFarlane, 2019), particularly scoring criteria and whether or not a cap on the number of details participants generated was applied to control for variations in verbal fluency. As it has been argued, the majority of currently available measures to investigate prospection have not been appropriately validated and, if nothing else, my conflicting results indicate that considerable efforts are still needed to demonstrate the fitness of such instruments for the measurement of episodic foresight (Miloyan & McFarlane, 2019).

4.7.4 Theoretical implications

The findings presented in this chapter suggest that the cognitive effort required during episodic future thinking may not necessarily manifest in distinct profiles of oculomotor and behavioural responses in healthy ageing. It has become increasingly clear that an individual's capacity to mental time travel across past and future contexts hinges not only on the retrieval and autonoetic re-experiencing of episodic memories, but also the semantic continuity in terms of one's own narrative (Conway, 2005). Converging evidence from both cognitive and neuroimaging studies strongly suggests that, with the passage of time, autobiographical memories tend to become more abstract in nature (Moscovitch et al., 2005; Piolino, Desgranges, & Eustache, 2009), providing a semantic scaffold against which sensory-perceptual details from recent personal events can be extracted and/or flexibly recombined into novel simulations (Irish & Piguet, 2013). In this light, semantic information that is personally relevant should pay an important role in supporting the episodic simulation of future experiences, and particularly temporally distant events due to their higher generative demands (D’Argembeau & Van der Linden, 2004). This idea is further corroborated by evidence that, when constructing a hypothetical future scenario, people typically access general personal knowledge before generating episodic details (D'Argembeau & Mathy, 2011), and they tend to organise episodic future thoughts into event clusters that reflect the influence of higher-order conceptual information (Demblon, Bahri, & D'Argembeau, 2016; Schacter et al., 2017). Furthermore, mounting evidence indicates that the phenomenology and quality of prospective thoughts is modulated by temporal distance (Arnold, McDermott, & Szpunar, 2011). As mentioned in the introduction of this chapter, hypothetical future events that are temporally distant from the present time tend to incorporate more decontextualised and abstract features, while also evoking little mental imagery and feeling of pre-experiencing (D’Argembeau & Van der Linden, 2004). Building on these observations, La Corte and Piolino (2016) proposed a *Temporal Distance in Future Thinking* (TEDIFT) neurocognitive model postulating that personal semantics (semantic aspects of autobiographical memory, i.e., concept-based knowledge about the self, including personality traits, personal beliefs and generic autobiographical facts; Grilli & Verfaellie, 2014; Martinelli, Sperduti, & Piolino, 2013) assume an increasingly prominent role in future thinking as a function of temporal distance. In other words, the more distant the temporal context of the mental simulation, the greater the narrative shift from episodic to semantic forms of personal future representations (La Corte & Piolino, 2016). Importantly, over reliance on semantic knowledge and narrative shifts towards conceptual information are well-documented in the older population (Levine et al., 2002; Umanath & Marsh, 2014). As a result, older adults may be expected to generate an abundance of semantic details when imagining temporally distant future scenarios, although the specificity of such details may be relatively poor and the self-perspective accompanying the mental endeavour may lean towards that of an observer rather than an actor (Irish, Lawlor, et al., 2011; Piolino et al., 2006). In the present study, Future enquiries examining changes in viewer perspective as a function of temporal distance will be required to confirm or disprove these predictions in the context of healthy ageing.

4.7.5 Limitations and outstanding questions for future research

Given the exploratory nature of the current study and its novel combination of behavioural and oculomotor metrics, a number of methodological issues warrant consideration. First, to guard against fatigue in the older participant group and allow for the experimental task to be conducted in a single, relatively short session, I designed my study to comprise only 2 trials per condition, thus reducing overall study power. Similarly, I based my experimental protocol on a shortened version of the scene construction task and omitted the Spatial Coherence Index (SCI) from the original study. The Spatial Coherence Index is a measure of the contiguousness and spatial integrity of the constructed scenarios and is based on participants' selection of appropriate statements from a small set of options providing a possible qualitative description of the imagined experience (e.g., "I could see the whole scene in my mind's eye", "It was a collection of separate images"; cf. Hassabis et al., 2007). Inclusion of this index would enable me to further investigate how manipulations of both temporal context and plausibility influence the spatial cohesion of the resulting scenes, as well as how they relate to the provision of contextual detail. This would be especially insightful in far future, implausible scenarios, to better understand whether participants approached the construction of these events in a different way compared to the other experimental conditions. For example, they may have been inclined to seek out and elaborate more creative or divergent associations between items to circumvent the lack of an appropriate conceptual framework to draw upon.

Secondly, unlike previous studies my experimental protocol focused exclusively on future thinking and did not include a past condition. Comparing behavioural and oculomotor responses during past and future event simulation may help to characterise potential cognitive mechanisms that are unique to future thinking endeavours and the extent to which participants in each age group rely on prior experiences as opposed to constructing hypothetical future scenarios *ex novo*.

Finally, post-hoc power calculations on correlation analyses between oculomotor metrics and phenomenological indices suggested that a larger sample size might have facilitated a deeper comprehension of the interplay between these variables during prospection. Future studies in a larger sample of participants, with a greater number of experimental trials will therefore be required to replicate the current findings. Given that my analyses failed to reveal a statistically significant main effect of group in all behavioural and oculomotor measures of interest, it will be important to understand whether this would also be the case in neurodegenerative populations where imagery and memory-based abilities are compromised (Irish, Lawlor, et al., 2011; Wilson et al., 2020). Deficits in episodic and/or semantic memory are often observed in conjunction with alterations in future thinking capacities (Addis et al., 2009; Irish et al., 2012a). Therefore, exploring the interaction between the provision of episodic detail during prospection and potential changes in the production of eye movements in these clinical populations may provide a unique opportunity to help characterise cognitive impairment in all of its complexity.

4.7.6 Conclusions

To my knowledge, the present study is the first to employ an eye-tracking paradigm to explore age-related differences in future thinking performance while simultaneously manipulating the temporal context and the level of plausibility of the simulated scenarios. My results indicate that the provision of content is significantly affected by the temporal distance and the plausibility of the constructed events, yet I did not find any age-related differences in the total content or amount of eye movements produced. Further, correlation analyses suggest an inverse association between the production of spontaneous eye movements and the subjective experience of the future thinking process in selected contexts. These findings provide valuable insights into the relationship between oculomotor behaviour and future thinking and warrant further investigation in clinical populations.

Chapter 5

General discussion

This thesis sought to explore how eye movement metrics may be harnessed to gain insight into the cognitive mechanisms involved in imagery-driven constructive tasks. Overall, the findings from this thesis illustrate the strong interplay between oculomotor behaviour and construction-based processes in both healthy ageing and dementia syndromes. These findings offer a novel perspective on the complex mechanisms supporting constructive endeavours and how they may shift in response to task contingencies as well as age-related changes across the lifespan. Here, I will summarise the main results from my experimental work and place them in context with current research on healthy ageing and neurodegeneration. Further implications in terms of clinical applications and future directions are also discussed.

5.1 Visual exploration, semantic knowledge, and memory performance

Consistent with previous research, the findings from this thesis reveal a bi-directional relationship between oculomotor behaviour and episodic and semantic forms of memory during visual exploration (Ryan, Shen, & Liu, 2020). As we have seen in Chapter 2, repeated exposure to the same set of visual stimuli helps consolidate newly acquired memories for relevant item-location associations, as demonstrated by increasingly shorter reaction times across multiple search blocks. At the same time, reliance on conceptual knowledge strongly influences visual search strategies by preferentially directing gaze and attention towards stimuli and features that are consistent with prior expectations (Wynn, Ryan, et al., 2020). This behavioural response is particularly pronounced in the older population, whose rich repository of semantic information tends to be accessed and harnessed more readily than perceptual details to achieve task completion. Accordingly, in contexts where greater cognitive flexibility is required in response to unexpected occurrences (e.g., target objects being displayed in semantically incongruent locations), performance is compromised in healthy older adults (cf. Chapter 2.3).

Building on these findings, I wanted to investigate to what extent these oculomotor and cognitive mechanisms are compromised in the presence of deficits in the episodic and/or semantic memory systems. Distinct alterations in oculomotor signatures may help characterise cognitive impairment in neurodegenerative syndromes by providing a unique opportunity to explore potentially adaptive and compensatory processes as they dynamically unfold. The results from the experimental study presented in Chapter 2 highlight distinct oculomotor patterns for each patient group (i.e., Alzheimer's disease and semantic dementia) that may be related to the well-documented cognitive changes typically encountered in these clinical populations (Alescio-Lautier et al., 2007; Merck et al., 2020; Tales et al., 2005; Viskontas et al., 2011). More precisely, patients with Alzheimer's disease (AD) were found to spend a disproportionate amount of time exploring target congruent areas when target objects had been displayed in semantically incongruent locations. This repeated behaviour was suggested to reflect an impaired capacity to encode and consolidate new memories, whereby patients with AD likely defaulted to existing, semantic knowledge to support task performance (Strikwerda-Brown et al., 2019). Not surprisingly, such compensatory strategy inevitably led to slower reaction times and reduced task accuracy. In contrast, patients with semantic dementia (SD) scored in line with controls in the visual search task, exclusively in the incongruent condition. As previously discussed, performance in congruent trials was dependent upon semantic-driven expectations, which in this group could either be degraded or not effectively utilised to inform visual exploration. By contrast, incongruent trials could be completed relatively free from the constraints imposed by semantic associations and by relying to a greater extent on salient, perceptual details (Itti & Koch, 2000). These proposed mechanisms were further supported by findings of similar oculomotor behaviour in SD and controls, suggesting that both groups could leverage sensory features of task stimuli to guide visual exploration to a comparable degree. Since visuospatial processing, attentional mechanisms and episodic memory function have been found to remain relatively intact in SD (Irish et al., 2016a; Salimi et al., 2018b), my findings converge with the extant literature in demonstrating that performance in cognitive tasks not involving the extraction and manipulation of conceptual information is not necessarily compromised in SD and that oculomotor signatures of visual exploration do reflect some of the cognitive mechanisms supporting these endeavours.

Nonetheless, it will be important to understand at which point in the progressive deterioration of the semantic knowledge base these behavioural and oculomotor dynamics begin to shift towards more perceptually based forms of visual exploration and whether concurrent alterations in eye movement patterns may be utilised to define a clear biomarker for the onset of the disease or its progression into a more advanced stage. Future enquiries investigating visual exploration and memory consolidation and retrieval at different levels of disease severity will likely provide compelling insights to address these outstanding questions.

5.2 Cognitive effort modulates oculomotor behaviour in construction-based tasks

In Chapters 2 and 3 of this thesis, I focused on constructive endeavours based solely on internally generated mental imagery, namely atemporal scene construction and episodic future thinking. The rationale behind both studies was to characterise the type of oculomotor behaviour accompanying these cognitive efforts in the absence of externally cued visual stimuli, and whether age-related differences in concomitant eye movement patterns could also be detected. Finally, I wanted to establish whether participants' oculomotor signatures correlated with the provision of episodic detail (specifically in the future thinking task) as well as the perceived phenomenology of the mental simulations, either in the positive or in the negative direction.

Results from the scene construction task indicated that, irrespective of group, the production of eye movements was greater in control versus construction trials and as the number of task elements progressively increased. A proposed explanation for these findings is that, during the initial phase of the scene construction process, when only a few elements are presented and a vivid and spatially contiguous semantic scaffold must first be generated, cognitive demands are particularly heightened. As a result, maintaining fixation rather than engaging in visual exploration may have been beneficial, or indeed required, to support task performance. In contrast, once a coherent spatial backdrop for the mental simulation had been established, the integration of an increasing number of elements into the scene could be more easily achieved, freeing up cognitive resources that could be allocated to the production of eye movements. In other words, there may be a critical threshold beyond which it becomes more efficient to conserve available cognitive resources by attenuating the production of eye movements and increasing efforts towards the construction and maintenance of a spatially coherent scene in working memory (Engelhard et al., 2010). Furthermore, I tentatively suggested that such cognitive thresholds may be age-related, as demonstrated by the different profiles of oculomotor behaviour I observed in younger and older adults in the early stages of scene construction. These profiles may reflect an age-related recalibration of cognitive resources in response to task demands and will be important to study in more detail in future studies.

Interestingly, these age-specific oculomotor dynamics were not found to impact participants' subjective experience of the mental simulation, whereby older adults rated their constructed scenes as more vivid, more integrated, and less difficult to elaborate than their younger counterparts. This disconnect between oculomotor and behavioural outcomes suggests that younger and older adults may have been equally able to achieve task completion by relying on distinct underlying cognitive mechanisms to support their constructive endeavours, such as the preferential activation of visual versus semantic representations as task stimuli were sequentially introduced (De Groot et al., 2016). In fact, our stimuli were auditorily presented and, by design, devoid of any perceptual features that might have otherwise been leveraged to furnish the mental simulation. Consequently, to visualise and integrate each item into a coherent scene representation, participants likely had to access and search through their mental repository of semantic information. Given that semantic memory assumes an increasingly prominent role in guiding the way we perceive, process, and recall external stimuli as we age (Umanath & Marsh, 2014), such age-related shift towards domain-specific knowledge may have facilitated scene construction performance in the older group.

In contrast, and quite surprisingly at first, analyses on the episodic future thinking task presented in Chapter 4 failed to reveal significant age-related differences in either oculomotor or behavioural metrics of interest. While I would have expected the provision of episodic detail and the perceived phenomenology of the future simulations to be lower in the older compared to the younger group, compelling evidence suggests that in naturalistic, as opposed to laboratory-based, settings, the nature and frequency of spontaneous future thoughts is not necessarily negatively affected as we age (Kvavilashvili et al., 2013; Warden et al., 2019). It is therefore possible that the experimental protocol I designed for this task, whereby no additional prompts or cues were provided and the experimenter did not interrupt the narrative descriptions, encouraged participants to follow a somewhat unconstrained train of thoughts, thus mitigating some of the age-related deficits typically observed in the literature. Moreover, in keeping with the original scoring protocol by Hassabis et al. (2007), the number of contextual details participants provided in their narrative descriptions was capped to a maximum of 7 for each of the four category of interest (i.e., Entities present, Sensory descriptions, Spatial references and Thoughts, emotions and actions) to control for differences in verbal fluency. As a result, potential discrepancies in methodological practices may explain why the findings from the present study stand somewhat in conflict with prior research where uncapped scoring systems may have been employed.

Interestingly, irrespective of age group, participants were found to generate more overall content, including more unique entities, sensory descriptions, and spatial references, in two experimental conditions, namely near future, plausible scenarios and far future, implausible scenarios. I drew on the *construal level theory* (Liberman et al., 2002) to propose that participants may have harnessed autobiographical experiences to populate their mental simulations and thereby establish a detail-rich vivid representation of temporally close, plausible events. By contrast, in the case of temporally distant, implausible events where personal memories may not be immediately available or indeed relevant to the mental construction, I suggested that participants may defer to conceptual knowledge and semantic information to support their constructive endeavours (Irish, 2016, 2020). Drawing on either source of information (e.g., autobiographical versus semantic) seemed sufficient for older and younger adults to construct contextually rich accounts of implausible and plausible future events.

Finally, analyses of oculomotor responses indicated that neither the temporal context nor the level of plausibility of the simulated scenarios seemed to impact the quantity, or quality, of the eye movements participants produced. In the near future condition, however, strong negative correlations emerged between key oculomotor metrics and phenomenological indices exclusively for implausible scenarios. Accordingly, when maintaining fixation rather than engaging in visual exploration, both participant groups rated their simulated events as more vivid and evoking a stronger sense of presence. As I argued, this inverse relationship may result from the higher generative demands of the future thinking task in this specific experimental condition (Weiler et al., 2010; Wiebels et al., 2020). These results corroborate my findings from the previous study in suggesting that, when task demands increase beyond a certain threshold, available cognitive resources may need to be redirected and drawn away from the production of eye movements to achieve task completion. Along these lines, recent studies investigating pupil dilation during prospection, an oculomotor signature previously shown to reliably index cognitive load (Hess & Polt, 1964; Kahneman & Beatty, 1966), have revealed increased pupil size during future compared to past thinking (El Haj & Moustafa, 2021). While episodic future thinking is more cognitively effortful compared to other construction-based tasks, it remains unclear how the temporal distance and plausibility of hypothetical future scenarios impact the cognitive resources required to support task performance. Similarly, the neural substrates supporting these endeavours remain unclear. Accordingly, future studies incorporating both eye-tracking and brain imaging techniques will provide converging evidence regarding how such complex mechanisms unfold and interact in both young and older adults.

5.3 Theoretical implications

From a theoretical standpoint, the findings from this thesis confirm that oculomotor behaviour may be employed to explore cognitive mechanisms driving performance in imagery laden, construction-based tasks in both healthy ageing and dementia populations. The first mechanism that unequivocally stood out throughout my research work is the contribution of semantic memory to constructive endeavours. As postulated by recent accounts, episodic and semantic memory constitute complementary, yet strongly interconnected systems (Lane, Ryan, Nadel, & Greenberg, 2015; Renoult et al., 2019), and this inherent interdependency allows us to avail of, and integrate both perceptual and conceptual details into vivid, spatially coherent past and future simulations (Irish & Piguet, 2013). In the presence of cognitive deficits that disrupt access to or engagement from either memory system, the other steps in to support task performance (Craver, Kwan, Steindam, & Rosenbaum, 2014; Irish, 2020). As we age, the remarkable flexibility of this interactive process allows us to continue to navigate through life's complexities by harnessing and optimising the information that is most readily accessible to guide our choices and behaviour. As a result, the relative weight of episodic and semantic memory in the process of constructive simulation is likely to shift based on task demands, prior experience, and the integrity of the underpinning neural systems (Irish, 2020). This dynamic is most evident in the presence of neurodegeneration, whereby cortical atrophy and functional impairment likely necessitate a shift towards the system least affected (Irish et al., 2012a; Steinvorth, Levine, & Corkin, 2005). Converging evidence from neuroimaging and neuropsychological studies of memory and episodic future thinking in dementia syndromes and other brain disorders indicates that the capacity to engage in mental time travel is selectively affected based on the specific profile of the disease. For example, amnesic patients with medial temporal lobe lesions are largely unable to remember previously experienced events or project themselves forward in time to envisage possible future scenarios but can retrieve impersonal and knowledge-based information or elaborate on non-episodic future issues (Race, Keane, & Verfaellie, 2013). At the other end of the spectrum, patients diagnosed with SD can remember and describe episodic events from their recent past in rich contextual detail. However, given that the mental construction of novel events heavily taxes the semantic memory system, and that the conceptual knowledge base progressively deteriorates in these patients, future simulations are often entirely recapitulated from previous experiences, reflecting an over-reliance on relatively intact episodic memory stores (Irish, 2020). Furthermore, as discussed in Chapter 4, the contribution of semantic memory to episodic future thinking appears to be modulated by temporal distance (Arnold et al., 2011), whereby the recruitment of conceptual knowledge is particularly critical to the elaboration of scenarios taking place in the distant future (D'Argembeau & Van der Linden, 2004; La Corte & Piolino, 2016). As a result, if episodic and semantic representations can be positioned along a continuum (Irish & Vatansever, 2020) and leveraged more prominently in the context of near future and distant future projections respectively, it is possible that cognitive impairments in future thinking capacities traditionally observed in Alzheimer's disease and SD may be bounded to the temporal context of the mental simulation. Accordingly, AD patients may display significant performance deficits specifically in the near future dimension, and vice versa distant future scenarios may prove to be more challenging to elaborate in the presence of semantic dementia. Undoubtedly, further studies investigating prospection in neurodegenerative syndromes are required to better understand how the temporal distance of hypothetical future events relates to cognitive mechanisms involved in episodic future thinking and I predict that they will provide a compelling testbed to explore episodic-semantic interactions in the context of construction-based processes.

The second mechanism that I have repeatedly invoked to explain some of the unexpected findings presented in this thesis is the dynamic (re-)allocation of available cognitive resources in response to increasing task demands, as well as its relationship to specific profiles of oculomotor behaviour. As previously argued, this proposed adaptive response is thought to facilitate performance by focusing attention onto what is most relevant to the task at hand. Moreover, the cognitive flexibility conferred by this functionally-driven shift may be especially advantageous in the absence of externally cued visually stimuli, where higher working memory efforts are required to establish and maintain a spatially contiguous scene representation in the mind's eye. As a result, disruptive mechanisms such as voluntary and spontaneous oculomotor behaviour are impeded, as often demonstrated by increases in both fixation durations and pupil size (El Haj & Moustafa, 2021). Furthermore, my findings reveal important age-related differences based on the nature and temporal dimension of the mental simulation. More precisely, in the context of atemporal scene construction, older adults were found to cross their presumed cognitive threshold earlier than their younger counterparts, meaning that the capacity to successfully integrate multiple task stimuli into a coherent scene and simultaneously engage in visual exploration was found to diminish at an earlier time point in the constructive process. On the other hand, as far as episodic future thinking is concerned, no statistically significant age effects could be detected. Consequently, the additional generative demands imposed by the novelty of future simulations may have closed the gap in terms of the proposed cognitive threshold, bringing older and younger adults to comparable levels. While speculative, the theoretical implications discussed in this thesis call for future investigations to understand how different neural networks interact with one another to support overall performance in complex cognitive tasks and how such processes potentially diverge with age.

5.5 Concluding remarks

The experimental findings presented in this thesis draw attention to some of the dynamic mechanisms supporting imagery-rich and memory-laden constructive endeavours. As the content and subjective experience of past and future mental simulations may not always be accurately captured or amenable to verbal report, objective assays to tap these processes are needed. Oculomotor variables extracted from eye-tracking paradigms represent one such promising avenue for further research, enabling us to derive surrogate markers of past and future thinking and their respective phenomenology. As the field moves progressively towards more nuanced and integrative positions, I envision that the inclusion of objective indices of this nature will help further characterise these complex cognitive mechanisms and how they might adaptively shift or break down in both healthy ageing and neurodegeneration.

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