BRAIN RHYTHMS AND WORKING MEMORY IN HEALTHY AGEING

A thesis submitted for the Degree of

DOCTOR OF PHILOSOPHY

By

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Abstract

Working memory (WM), the ability to maintain and manipulate information to guide immediate cognitive processing, is vulnerable to age-related decline. Compared with younger adults, older adults demonstrate smaller WM capacities, a decrease in the ability to manipulate items held in WM, and a greater susceptibility to interference from distracting information. However, the neural underpinnings of WM decline in normal ageing are unclear. One technique that can be used to investigate the neurophysiological processes underlying cognition is electroencephalography (EEG), which non-invasively records activity from the awake human brain. The research described in this thesis uses EEG to investigate the neurophysiology of WM in healthy younger and older adults, with a particular focus on neural oscillatory activity in the alpha frequency range (8-12 Hz). As such, Chapter 1 consists of a review of the literature relevant to use of EEG to investigate the neurophysiology of WM performance in younger and older adults.

WM performance deficits in older adults are particularly salient under increasing WM loads. Alpha oscillations have been shown to support verbal WM performance under high loads in younger adults, so the aim of Chapter 2 was to investigate the load-dependent modulation of alpha oscillatory power and frequency in younger and older adults during verbal WM. No age differences in verbal WM performance were found, and alpha power and alpha peak frequency were modulated in a similar task- and load-dependent manner in both younger and older adults.

Another factor influencing WM performance in older adults is a decline in selective attention. Older adults perform worse on and are less able to modulate alpha power than younger adults in tasks involving cues about ‘where’ or ‘when’ a memory set will appear. The study described in Chapter 3 investigated whether providing cues towards memory set presentation time led to enhanced selective attention before the onset of the memory set, as indexed by alpha oscillatory activity. Predictive cues led to improved WM performance in both age groups, but alpha power in preparation of the memory set did not influence task performance.

In Chapter 3, there were no age differences in WM performance when manipulating memory set presentation time. However, processing speed may not only limit the speed at

which items are encoded into WM, but also the speed at which stimuli are transformed into a stable memory representation (i.e., WM consolidation). Therefore, the study contained in Chapter 4 investigated age differences in the ability to consolidate items into visual WM. In this study, older adults demonstrated poorer WM performance and slower consolidation at low WM loads, providing evidence for altered visual WM consolidation with age.

Finally, visual WM is severely limited in capacity, highlighting the importance of encoding task-relevant information while ignoring distractors. The modulation of alpha oscillatory power has been implicated in the inhibition of distractors during WM in younger adults, but it is unclear if alpha power modulation also supports distractor inhibition in older adults. The study described in Chapter 5 investigated age differences in alpha oscillatory power before the onset of distractors during the visual WM retention period. Although there were no age differences in WM performance, younger adults demonstrated functionally relevant increases in alpha power before distractors, while older adults showed decreases in alpha power. Therefore, younger and older adults likely use different neural strategies to inhibit distractors during WM performance.

Taken together, the results of the studies contained in this thesis provide further evidence for age-related changes to neural oscillatory activity, particularly in the alpha frequency band, even when age differences in WM performance are not present. These findings may have important implications for providing novel targets for detecting or preventing age-related cognitive decline.

Table of Contents

List of Figures

List of Tables

Declaration

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General Introduction

In Australia, the proportion of older adults (those aged 65 years and over) in society is expected to double by 2057. Although an ageing population is largely a positive outcome, reflecting increased standards of living and advancements in medicine, normal ageing continues to be associated with a progressive decline in cognitive performance, even in the absence of dementia-causing illnesses such as Alzheimer's disease.

Age-related cognitive decline is most prominently seen in domains such as processing speed, memory, and executive function. Of particular vulnerability to age-related decline is working memory (WM), which refers to the ability to maintain and manipulate items in mind to guide immediate cognitive processing. On average, older adults can hold fewer items in WM, are less able to manipulate those items, and more vulnerable to interference from distracting information compared with younger adults. Importantly, WM supports many aspects of higher cognition, goal-directed behaviour, and activities of daily living, so deficits in WM can have a profound impact on quality of life for older adults. While several theories have attempted to explain age-related declines in WM performance, the neural mechanisms underlying such deficits are not well understood.

One method that can be used to non-invasively measure the neurophysiological processes underlying cognitive performance is electroencephalography (EEG). Rhythmic brain activity or 'neural oscillations' have been implicated in supporting cognition across a range of domains, with a vast body of research linking neural oscillatory activity to WM performance in younger adults. Although rhythmic brain activity undergoes a range of age-related changes, much less research has investigated the role of neural oscillations during WM performance in older adults. Therefore, the aim of the research presented in this thesis was to use EEG to investigate age-related changes in neural oscillatory activity during WM performance in younger and older adults.

Following a review of the literature in Chapter 1, the experimental chapters in this thesis explore age-related changes in WM performance across a range of tasks. Chapters 2, 3 and 5 consist of experimental studies that investigate age differences in neural oscillatory activity during WM using EEG, while Chapter 4 contains a behavioural-only study that explores age-related changes in visual WM performance. Specifically, Chapter 2 examines the role of alpha oscillatory activity in supporting verbal WM performance under varying loads in younger and older adults, Chapter 3 investigates age-differences in neural oscillatory activity in response to varying memory set presentation times and predictive cues during visual WM, Chapter 4 explores age-related changes in visual WM consolidation, and Chapter 5 investigates age-related changes in alpha oscillatory activity for distractor inhibition during visual WM. Finally, this thesis will close with a general discussion of the main findings, with a focus on methodological implications and future directions for exploring the neurophysiological underpinnings of age-related WM decline.

Chapter 1: A review of the literature

1.1 AGEING AND SOCIETY

Worldwide, the proportion of older adults in the population is rapidly growing (Beard et al., 2016). In 2017, there were 3.8 million Australians aged 65 and over (15% of the total population), increasing from 5% of the population in 1927 and 9% of the population in 1977. The proportion of older adults in the Australian population is projected to grow to 22% in 2057, and 25% by 2097 (ABS, 2014). Population ageing is largely a positive outcome, reflecting improved life expectancy due to increased standards of living, advancements in medicine and education (Gerstorf et al., 2015). However, advancing age continues to be associated with higher rates of disability, with 49.6% of people aged over 65 reporting a disability in 2018 (ABS, 2018).

The second leading cause of death in Australia and a major source of age-related disability is dementia (ABS, 2020). In 2020, it was estimated that there were between 400,000 and 459,000 Australians living with dementia, with Alzheimer's disease accounting for approximately 70% of diagnosed cases (Australian Institute of Health and Welfare, 2020). Advanced age is a major risk factor for dementia, and without a significant breakthrough in treatment, the number of people with dementia is expected to double by 2050 (Australian Institute of Health and Welfare, 2020), placing a greater demand on the Australian healthcare system.

Despite the level of importance placed upon research into dementia-causing illnesses such as Alzheimer's disease, an overlooked population in Australian society are older adults who experience declines in cognitive function, even in the absence of neuropathology. Normal ageing is associated with a progressive decline in cognitive performance, most prominently seen in domains such as processing speed, memory, and executive function. However, the neural mechanisms of normal age-related cognitive decline are unclear. Understanding the neural underpinnings of normal cognitive ageing will not only help distinguish between healthy and pathological states, but may also provide targets for dementia prevention and therapeutic interventions to ensure that adults can maintain health and independence into old age. Ultimately, increasing the quality of life and health of older adults ensures that Australia, and the world, can continue to benefit from the experience, knowledge, and wisdom that an ageing population can bring to society.

In this review, an overview of the cognitive changes seen with age and the theories that attempt to explain these changes will be provided, with specific reference to working memory (WM) deficits. Age-related brain changes, and how these changes influence WM performance will then be discussed. Finally, the technique of electroencephalography (EEG), and how it can be used to investigate the neurophysiological mechanisms underlying WM decline with age, will be described.

1.2 NORMAL COGNITIVE AGEING

Cognitive ageing is a largely heterogeneous process, both between individuals and in the variability of cognitive domains affected. For example, cross-sectional and longitudinal studies report robust declines in WM, processing speed, visuospatial and executive function abilities with age (Harada et al., 2013; Hedden & Gabrieli, 2004). In contrast, autobiographical memory, procedural memory, vocabulary and language abilities remain stable and even improve with age (Hedden & Gabrieli, 2004; Nyberg et al., 2012). Behavioural research has suggested that there are three main patterns of changes in cognition: lifelong declines, late life declines and stability across life (Hedden & Gabrieli, 2004).

Lifelong declines are present in basic cognitive functions such as processing speed and working memory, and begin as early as early adulthood (Craik & Bialystok, 2006). A cross-sectional study involving individuals in each decade between 20 and 80 years demonstrated that processing speed, WM and episodic memory underwent linear, lifelong declines when participants were matched for education, health, and other demographic variables (Park et al., 1996). Likewise, cross sectional data from the Seattle Longitudinal Study of Adult Cognitive Development found linear declines in processing speed, spatial reasoning and episodic memory as age progressed (Schaie & Willis, 2010).

Late life declines in some cognitive processes have been identified in longitudinal studies. Longitudinal analyses from the Seattle Longitudinal Study demonstrated little to no decline in domains such as verbal memory, and verbal and numerical abilities until later life (after 60 years), in which decline in these domains accelerated in the 3-6 years before death (Schaie & Willis, 2010). Likewise, well learned tasks or tasks that rely on knowledge and experience show little performance decrement until late life (Hedden & Gabrieli, 2004). For example, digit span (i.e., number of repeated digits after hearing an ordered series) tends to decline slightly with age, before taking a sharper decline after the age of 70 (GrÉGoire & Van Der Linden, 1997).

Finally, certain cognitive domains demonstrate stability across the lifespan. Autobiographical memory (Fromholt et al., 2003) and certain social cognitive processes such as theory of mind (Happé et al., 1998), as well as implicit memory, such as procedural and unconscious memory, tend to remain stable with age (Ward & Shanks, 2018).

1.3 WORKING MEMORY

Working memory, the ability to maintain and manipulate information over a short period of time (Baddeley, 1992), is one of the cognitive processes most vulnerable to age-related decline (Grady & Craik, 2000). WM is a requirement for many higher-order cognitive processes such as problem solving and multitasking (Conway et al., 2002), and is essential to the organisation of mental processes that support goal-directed behaviour in everyday life (Shallice & Burgess, 1991). As such, WM deficits may underlie a reduced ability for older adults to maintain quality of life with advancing age (Davis et al., 2010). In this section, the theoretical models that describe WM, the ways in which WM performance can be assessed, and the changes in WM in late life will be discussed.

1.3.1 Models of WM

There have been multiple theoretical models proposed to describe the concept of WM. For example, the term ‘working memory’ was first used by Miller (1956), who discussed the limitation in the number of items that can be held in immediate memory. The limits of this memory system were tested by asking participants to recall a list, verbatim, that they had seen or heard immediately prior (Miller, 1956). The ability to repeat the list was said to be limited to approximately seven ‘chunks’ of meaningful information, in which ‘chunking’ refers to the recoding of smaller units of information into larger, more familiar units. In situations where chunking of information is unable to occur, adults can typically retain only 3 to 4 items at a given time (Cowan, 2001).

The most prominent theoretical model of WM is the multicomponent model proposed by Baddeley and Hitch (1974). The multicomponent model suggests that WM not only functions to store information in mind but also acts as a system that allows for the manipulation of information for use in complex cognitive processes. The three subcomponents involved in the system are the phonological loop, visuo-spatial sketchpad, and central executive (Baddeley, 1992). A fourth component, the episodic buffer, was added to the model in 2000 (Baddeley, 2000).

The phonological loop is the most well characterised component of the WM model. It comprises a temporary phonological store where memory for verbal information decays over a period of a few seconds unless the memory trace is refreshed by articulatory rehearsal (Baddeley, 1992). Similarly, the visuo-spatial sketchpad is assumed to involve the maintenance and manipulation of visual and spatial information, such as colour, form, and spatial location of objects. The central executive has been defined as a general pool of processing resources which has control over the other systems and is involved in the manipulation of information in WM and attentional control over the contents of the WM store. Finally, the episodic buffer is described as a temporary storage system that integrates information from a range of sources. Like the concept of episodic memory (Tulving, 1989), the episodic buffer stores episodes of information that are integrated across space and time to bring information to conscious awareness, and allow reflection, manipulation and modification of that information (Baddeley, 2000).

1.3.2 Measuring WM

WM is thought to consist of three stages: encoding, retention, and retrieval. In a typical WM task, participants must process and encode the items of the memory set (encoding) and then maintain those items throughout a period in which no information is present (retention). A probe array is then presented, and participants retrieve the relevant items from the WM store (retrieval). As a note, the phrase ‘retention period’ will be used throughout this thesis, but the terms ‘maintenance’ and ‘delay’ period are used synonymously with ‘retention’ in the literature.

Historically, span tasks were the most commonly used method to measure WM (Shah & Miyake, 1996). Span measures involve presenting a sequence of items to a participant (e.g., letters, digits) and asking them to recall the items. Span tasks can involve recalling the items in the order they were heard (forward span), in reverse order (backward span), in ascending/descending order (sequence span) or in no order. Testing in these tasks usually begins with a list length of two stimuli and increases by one after two trials. Testing ends when the participant is incorrect on two trials of the same list length. Span can be calculated in a range of ways, including the total number of stimuli recalled or the longest series recalled (Bopp & Verhaeghen, 2005).

Memory for verbal content is often measured using classic or modified versions of the Sternberg task (Sternberg, 1966). In the classic Sternberg task, letters or digits are presented sequentially in an encoding phase. Participants then hold the verbal information in mind during a retention period, before indicating whether a probe item was present in the memory set. There have been many modifications to the Sternberg task, one of which involves presenting all stimuli of the memory set simultaneously in the encoding phase, allowing for clear temporal delineation between encoding, retention, and retrieval phases. *N*-back tasks are also commonly used to assess verbal WM. *N*-back tasks are a continuous performance measure in which participants are presented with a sequence of stimuli (usually letters), and then are required to respond when the current stimulus matches the one from *n* steps earlier in the sequence (Kirchner, 1958). The load, or *n* factor can be adjusted to increase the difficulty of the task. Due to the continuous nature of the task, *N*-back paradigms involve simultaneous encoding, retention, and retrieval periods.

Delayed match-to-sample tasks are commonly used to assess WM for visual stimuli. In delayed match-to-sample tasks, participants are presented with stimuli (e.g., coloured squares, oriented bars, spatial location) in an encoding period, followed by a retention period where the stimuli disappear from the screen and participants hold the items in mind. At the end of a trial, a probe is presented, and participants must recall the stimuli or some feature of the stimuli. Paradigms differ in the way participants are tested on the items. In full report change detection tasks, participants are presented with an entire probe/test array which might be the same or different from the memory set (e.g., one colour in the probe array has changed). In partial report change detection tasks, participants are shown a single probe stimulus and must indicate whether the item or a feature of the item was or was not present in the memory set (e.g., location or colour). In spatial WM tasks, participants may be asked to report the orientation of a bar by rotating a probe bar clockwise or counter-clockwise to match a bar from the memory set using the mouse. In colour WM tasks using a precision report, participants may be asked to recall the colour of a probe square by indicating the exact colour on a colour wheel.

In this thesis, a modified Sternberg task and a range of delayed match-to-sample tasks of the change detection format are used to investigate verbal and visual WM, respectively.

1.3.3 Age-related decline in WM

Studies comparing WM performance between young and older adults have generally found that older adults demonstrate WM deficits for both verbal and visuospatial information

(Grady & Craik, 2000; Park et al., 2002). While age differences are not reliable for simple storage tasks such as forward digit span, WM tasks that require executive functions such as inhibitory control or manipulation of items lead to pronounced age deficits (Bopp & Verhaeghen, 2005). For example, in a study investigating WM across the adult lifespan (30-99 years), age differences were negligible in forward and backward digit span tasks, but older adults aged 60 years and over performed significantly worse in a WM task involving the manipulation of digits held in mind (Dobbs & Rule, 1989).

WM declines with age have also been documented using delay match-to-sample tasks. Change detection tasks have identified two main components of age-related decline in WM: a decrease in the number of objects held in memory, and a failure to maintain associations that bind visual features to objects (Cowan et al., 2006). Feature binding is the process in which individual characteristics of stimuli (e.g., colour, shape, location) are integrated to create objects or conjunctions (e.g., blue square on the left of the screen). In a study employing a delayed match-to-sample task where the probe array could differ from the memory set by either the addition of a new colour (feature change) or a change in which colour appeared at a certain location (conjunction change), a performance cost was present for older adults in the conjunction condition, suggesting that age-related visual WM decline could be due to a lack of ability to maintain object binding information (Cowan et al., 2006). However, studies using similar paradigms have failed to find a binding deficit in older adults, but rather demonstrated that older adults performed worse than younger adults in memory for both features and conjunctions (Brockmole et al., 2008).

Age-related WM deficits have also been demonstrated in precision tasks. In a study where participants reported both the orientation and colour of bars during the probe stage, older adults demonstrated poorer precision recall than younger adults, and were more likely to incorrectly report a distractor item being present, demonstrating evidence of feature binding issues (Peich et al., 2013). In contrast, it has been suggested that WM for verbal content is more resistant to age-related decline than WM for visual content (Hale et al., 2011).

1.4 COGNITIVE THEORIES OF AGE-RELATED WM DECLINE

There is no single account that completely captures the mechanisms underlying WM decline with age. However, there have been multiple suggestions that mainly encompass the fact that processing speed, inhibition, and cognitive control show varying degrees of vulnerability to decline. In the following section, the two prevailing cognitive and behavioural mechanisms that have been proposed to explain age-related WM deficits will be outlined.

1.4.1 Inhibitory deficit hypothesis

The ‘Inhibitory Deficit Hypothesis’ proposed by Hasher and Zacks (1988) suggests that age-related deficits in WM performance are due to age-related declines in inhibitory control. The hypothesis assumes that attentional regulation underlies cognitive functioning across a range of domains, including WM, selective attention, language comprehension and decision making (Hasher & Zacks, 1988). Though many theoretical perspectives suggest that larger workspaces that maintain more WM representations at any given time leads to better cognitive performance (Baddeley, 2000), the work of Hasher and Zacks focuses on the executive control processes that keep mental representation packages small and goal relevant, leading to more efficient information processing.

According to this theory, inhibition consists of 3 functions: access, deletion, and restraint (Hasher et al., 2008; Hasher & Zacks, 1988). Initial activations of memory representations are largely automatic and occur in response to stimuli that either occur in the external environment or in mind. The ‘access’ function then acts to determine which activated representations enter the focus of attention, depending on one’s goals (Cowan, 1993). If this process is working efficiently, task-irrelevant information can be suppressed, and the contents of the WM store will be tied to behavioural goals. Evidence for impairment in the access function in older adults comes from visual search tasks, in which older adults are slower to detect targets when distractors are present (Ben-David et al., 2014; West, 1999). During WM performance, older adults perform worse than younger adults on tasks showing distractors during the encoding phase, suggesting that older adults are less able to access the task-relevant mental representations when there is task-irrelevant information present (McNab et al., 2015).

The ‘deletion’ function serves to remove task-irrelevant information from the focus of attention, allowing for efficient processing of information relevant to task goals. Older adults are more likely to allow distractions to enter the memory store compared with younger adults, and then fail to delete the distractions even when they are aware that the information is irrelevant (Hasher & Zacks, 1988). Hasher and colleagues suggest that failure to delete irrelevant information is a key component of WM span decline with age, as older adults are prone to proactive interference, which occurs when information that has been previously remembered (e.g., in previous lists in span tasks, or previous trials in change detection tasks) interferes with memory for a new task goal (Lustig et al., 2001). In a study testing age-effects in proactive interference in an *n*-back task, older adults demonstrated greater susceptibility to 'lure' items providing information about prior trials, even when the lure item was shown up to 10 trials prior (Samrani et al., 2017). These results suggest that older adults demonstrate an inability to delete information from their WM store, potentially underlying age-related deficits in WM performance.

Finally, the 'restraint' function refers to the ability to control strong behavioural responses. For example, in the Stroop task where participants name the colour of a word stimulus but ignore the word itself, older adults perform worse in incongruent trials where the word spells out the name of a colour different to the word's colour (i.e., 'red' printed in blue) (Uttl & Graf, 1997).

To summarise, Hasher and Zacks (1988) proposed that inhibitory mechanisms serve the information processing system of WM by preventing irrelevant information from entering the WM store, deactivating irrelevant information already in the WM store and preventing attention from returning to irrelevant information once it has been suppressed. Within this framework, WM serves as the focus of attentional resources, while inhibitory processes act as a central control mechanism to monitor the contents of the WM store (Hasher, 2015). Each of these processes decline with age and may be responsible for age-related decline in WM performance.

1.4.2 Processing speed hypothesis

Several decades ago, it was noted that slowing of many types of behaviours was a robust phenomenon of human ageing (Birren, 1965). It was then observed that deficits in many cognitive functions, including WM, executive functions and selective attention in healthy older adults were closely correlated with a slowing of perceptual processing speed (Salthouse, 2000).

Processing speed follows a regular lifespan trajectory in which speed increases throughout childhood and adolescence, reaches a peak in young adulthood, and then progressively declines with increasing age thereafter (Kail & Salthouse, 1994). The assumption in the processing speed hypothesis is that a major factor contributing to age-related differences in cognitive performanceis a reduction in the speed of which cognitive functions can be executed (Salthouse, 2000). If less computational processing can be completed in a set amount of time, then less information is available for higher-order functions such as WM (Kail & Salthouse, 1994).

There are two possible mechanisms suggested to underlie the relationship between processing speed and cognition: the limited time mechanism and the simultaneity mechanism (Salthouse & Babcock, 1991). The limited time mechanism suggests that processing speed may constrain performance if cognitive operations are executed too slowly to be completed in the time available for task performance (Kail & Salthouse, 1994). The simultaneity mechanism suggests that slower processing speed may constrain cognitive performance if products of early processing are lost by the time that later processing is completed (Salthouse, 2000). There are two ways this might occur: the quality or quantity of information could become less available over time due to decay, or information could become obsolete for the task at hand by the time it is available for use. The simultaneity mechanism is particularly relevant to WM performance given that WM is often conceptualised as consisting of information that is currently available for maintenance, manipulation, or both, before being retrieved for goal-directed behaviour.

In order to investigate which of the two possibilities best explained age-related declines in WM performance, Salthouse and colleagues (1994) employed a continuous paired associates task. In this task, the stimulus and response pairs continuously change, requiring the participant to monitor and update new information while actively maintaining prior information. The variables manipulated were presentation time per pair (i.e., rate to encode), and the number of pairs between the presentation and test of a given stimulus-response pair (i.e., rate of information loss). It was found that older adults required considerably longer presentation times to achieve a similar level of accuracy to younger adults, but the decrease in accuracy with the number of intervening pairs was similar between age groups. Therefore, processing speed likely limits WM performance in older adults as they are slower to encode information or to achieve a stable, internal representation of the items, not because they lose information more quickly over time (Kail & Salthouse, 1994). In this thesis, age-differences in the time course of developing stable WM representations (i.e., WM consolidation) will be investigated in Chapter 4.

1.4.3 Summary

Advancing age is associated with a progressive decrease in cognitive performance, with WM being particularly vulnerable to age related decline. Theories such as the inhibitory deficit and processing speed hypotheses attempt to explain the cognitive and behavioural mechanisms underlying such declines, but it is crucial to consider age-related brain changes also. In the next section, brain changes associated with normal ageing and theories that attempt to bridge age-related brain changes and age-related cognitive decline will be discussed.

1.5 NORMAL BRAIN AGEING

Post-mortem and in vivo studies have demonstrated that a hallmark of normal brain ageing is cerebral atrophy, which involves the shrinkage of grey and white matter volumes and enlargement of the cerebrospinal fluid spaces. The volume of the brain declines at a rate of approximately 5% per decade after age 40, with the rate of decline accelerating after age 70 (Scahill et al., 2003). The decline in brain volume is likely a result of lower synaptic densities in older adults, rather than neuronal death (Terry, 2000).

Structural magnetic resonance imaging (MRI) is a key technique used to determine age differences in volume of brain areas across the lifespan. An early cross-sectional volumetric study that measured the brain structure of participants both at a baseline and after 5 years demonstrated that the greatest age-related shrinkage occurred in prefrontal areas, the hippocampus, cerebellum and caudate (Raz et al., 2005). It is well documented that grey matter volume also declines with age, with some reports of shrinkage occurring in periods as short as 2 years in healthy older adults aged over 60 (Resnick et al., 2003). Frontal and parietal cortices are most prone to grey and white matter shrinkage with age, followed by temporal and occipital cortices (Good et al., 2001; Raz et al., 2005; Resnick et al., 2003; Salat et al., 2004).

Age-related changes to frontal regions are proposed to be a significant contributor to cognitive decline in healthy ageing (Gabrieli, 1996; West, 1996) (see section 1.6.1). Structures of the prefrontal cortex (PFC) undergo significant age-related reductions in volume that are likely due to decreased synaptic density (Haug and Eggers, 1991; Resnick et al., 2003), with an estimated linear decline of approximately 5% of volume per decade after age 20 (Raz et al., 2004). Similarly, diffusion tensor imaging studies have demonstrated that age-related white matter changes are greatest in the PFC and anterior corpus callosum (Head et al., 2004).

There are also various changes in neurotransmitters that may contribute to age-related cognitive decline. The dopaminergic system undergoes age-related changes, with human positron emission tomography and autopsy studies reporting decreases in frontal, striatal and hippocampal D1 and D2 receptor densities throughout the lifespan (Bäckman et al., 2010; Suhara et al., 1991), with the fastest rate of decline and lower glucose metabolism found in the frontal cortex (Kaasinen et al., 2000). Likewise, dopamine synthesis in the dorsolateral prefrontal cortex (DLPFC) has also been reported to decrease with age (Ota et al., 2006). Serotonin receptor availability in the frontal cortex also declines with age, but this decline is most prominent in mid, relative to late life (Sheline et al., 2002). Finally, a cross-sectional study of adults aged 20-76 years demonstrated an approximate 5% decrease in frontal cortex GABA concentration per decade of age (Gao et al., 2013).

1.6 COGNITIVE NEUROSCIENCE THEORIES OF COGNITIVE AGEING

Understanding the brain mechanisms underlying the age differences in cognitive performance is a key objective in cognitive neuroscience. There are several theories that have been suggested to explain age differences in brain activity both at rest and during cognitive tasks. In the following section, evidence for the frontal lobe, top-down modulation, compensation, neural noise, and cognitive reserve theories will be detailed, with a focus on how each of these theories attempt to describe age-related WM deficits.

1.6.1 Frontal lobe hypothesis

The frontal lobes of the brain are particularly vulnerable to both functional and anatomical age-related deterioration that is thought to be responsible for cognitive decline (West, 1996). The frontal lobe hypothesis of ageing is supported by several lines of evidence including: 1) executive control abilities are thought to be mediated by PFC, and age-related cognitive deficits are most pronounced in abilities requiring executive control, such as WM (Braver & Barch, 2002; West, 1996); 2) PFC undergoes pronounced age-related atrophy; and 3) white matter deterioration with age is most pronounced in frontal brain regions, including PFC (Raz et al., 2005).

Early evidence for the role of PFC in age-related cognitive decline arose from comparisons between the cognitive changes seen in older adults and those seen in patients with prefrontal lesions. Prefrontal lesions are associated with disruptions to attention and WM processes, particularly when maintaining items in WM for goal-directed behaviour and when exerting inhibitory control, such as during the Stroop task (Duncan et al., 1995). Specific to WM, a large body of animal work has tied PFC to the encoding and retention of task relevant information. For example, in macaques, single neuron recordings from PFC have been shown to maintain stimulus information throughout a retention period, even when distracting stimuli are presented during the trial (Miller et al., 1996).

Human neuroimaging studies provided further evidence for the role of PFC in age-related WM decline. Functional magnetic resonance imaging (fMRI) is a commonly used method to investigate age-related functional brain changes, as it measures changes in blood flow that occur with brain activity (measured as blood oxygen level dependent (BOLD) activity). Studies using fMRI have observed reductions in task-related BOLD activity in older, compared with younger adults during WM tasks (Nyberg et al., 2010; Rypma & D'Esposito, 2000). Despite the functional neuroimaging evidence for PFC involvement in WM, some studies have reported that structural changes such as decreases in PFC grey matter volume and white matter hyperintensities do not correlate with WM deficits (Arvanitakis et al., 2016; Gunning-Dixon and Raz, 2003). As an explanation for the differing findings, it has been suggested that structural changes to the PFC may impact selective attention processes that exert top-down control over the contents of WM, rather than directly influence WM performance (Zanto & Gazzaley, 2019).

Additionally, one of the most consistent findings in neuroimaging studies involving visual stimuli is that there is an age-related decrease in occipitotemporal activity coupled with an increase in frontal activity (termed posterior-anterior shift in ageing- PASA) (Davis et al., 2008). PASA was first reported in a positron emission tomography study that investigated face and location perception. In both conditions, older adults showed weaker activity in occipitotemporal regions compared with younger adults, but showed increased activity in anterior areas such as PFC (Grady et al., 1994). It has been suggested that the increased activation in frontal areas during cognitive tasks may represent an age-related increase in top-down control mediated by regions such as PFC to compensate for the age-related PFC changes and a loss of visual processing efficiency (Madden, 2007).

1.6.2 Top-down modulation

There is mounting evidence to suggest that many of the WM deficits experienced by older adults are, in part, due to impaired selective attention processes. One concept thought to underlie both WM and selective attention is top-down modulation, which refers to the ability to enhance neural activity in task-relevant, while suppressing activity in task-irrelevant brain regions (Gazzaley & Nobre, 2012). Aligning with the frontal lobe hypothesis, PFC has long been implicated as a source of top-down control signals that influence activity and processing in downstream brain regions by altering the neural response to stimuli based on task goals (Braver & Barch, 2002).

In a series of fMRI studies, Gazzaley and colleagues reported that older adults demonstrate a deficit in the ability to inhibit task-irrelevant information, as indicated by altered neural markers of top-down modulation throughout various stages of delayed-response WM tasks. In a typical version of their task, each trial involves participants viewing sequences of faces and scenes. Participants are instructed to either remember faces and ignore scenes, remember scenes and ignore faces, or passively view the faces and scenes without attempting to remember them. At the end of a trial, a probe stimulus from the relevant category is shown, and participants indicate whether the stimulus was present during the encoding phase. To test for suppression effects, they contrasted the passive viewing condition with the condition where participants were ignoring stimuli during encoding (e.g., face stimuli when encoding scene stimuli), and vice versa when testing for attentional enhancement effects.

In the studies, fMRI BOLD signal demonstrated that all younger subjects showed greater activity in the regions coding for the relevant stimuli compared with the passive viewing condition (e.g., scene selective region of interest when encoding scenes), and most young participants demonstrated suppressed activity below the passive viewing condition when ignoring the irrelevant condition. In contrast, while most older adults showed greater activity in the scene region of interest when remembering scenes, they were less likely to show suppressed activity when ignoring the relevant category (Gazzaley et al., 2005). The lack of top-down suppression in older adults was paired with poorer behavioural performance in terms of both accuracy and reaction time (RT), implicating top-down suppression deficits in age-related WM decline.

As a follow up study, Gazzaley et al. (2008) had participants complete the same faces/scenes task but measured neural activity with EEG to investigate the precise timing of top-down modulation changes with age. Their results revealed that top-down suppression deficits appeared as early as 100 ms in the visual processing stream, before top-down suppression processes began later during visual processing. However, WM performance deficits still existed in the older adult group, suggesting that suppression ability is not completely abolished with age but rather delayed to later processing stages (Gazzaley et al., 2008). Therefore, top-down suppression deficits support both the inhibitory deficit and processing speed hypotheses of cognitive ageing.

A similar paradigm was used by Bollinger et al. (2011), in which participants were provided with a cue about the stimulus category that would be present in a trial (i.e., faces or scenes). While younger adults demonstrated performance benefits for face stimuli when the face category was expected, older adults did not benefit from the predictive cue. Accordingly, younger adults showed modulation of brain activity in the fusiform face area during the expectation phase of the task when being cued towards faces, while older adults did not. Older adults also demonstrated diminished expectation-related functional connectivity between PFC and fusiform face area relative to younger adults, suggesting that age-related changes to top-down control networks underlie an absence of pre-encoding, visual cortical activity to facilitate WM performance (Bollinger et al., 2011).

In summary, healthy older adults exhibit top-down modulation deficits both when stimuli are present (e.g., during WM encoding) and when stimuli are absent (e.g., WM retention, anticipation), with each of these linked to poorer WM performance.

1.6.3 Compensation and efficiency

There is large variability in the patterns of brain activity seen in neuroimaging studies of cognitive ageing. Some studies report greater brain activity in older adults compared with younger adults, while others report the opposite, with each option being correlated with both better and worse performance.

Several fMRI studies have reported greater BOLD activity in older adults compared to younger adults during WM and attention tasks, particularly in areas of PFC (Cabeza et al., 2004; Grady et al., 2005; Madden, 2007). This overactivation has been associated with both better WM (Cabeza et al., 2004; Grady et al., 2005) and worse visual attention performance (Madden, 2007). Each of these effects are interpreted in the opposite ways. If overactivation of brain areas are associated with better performance, then the activity is compensatory in nature. If it is associated with poorer performance, then it is viewed as evidence of inefficiency due to unnecessary recruitment of neural resources. A specific form of over-activation termed 'hemispheric asymmetry reduction in older adults' (HAROLD) was proposed after findings that suggested older adults recruit resources from the other hemisphere to compensate for age-related deficits in cognitive control (Cabeza, 2002).

One interpretation for the overactivation of brain activity in older compared with younger adults at similar levels of task difficulty is that older adults recruit neural resources at lower loads than younger adults, leading to performance deficits as they have fewer resources remaining for use at higher loads (compensation-related utilisation of neural circuits hypothesis- CRUNCH) (Reuter-Lorenz & Cappell, 2008). A study employing a Sternberg task with memory set sizes ranging from 2 to 6 demonstrated that both younger and older adults with lower WM capacity demonstrated greater brain activation than those with higher WM capacity, providing support for CRUNCH (Schneider-Garces et al., 2009). In contrast, recent work has suggested that CRUNCH does not adequately account for load-dependent changes in WM performance in older adults due to insufficient evidence that explicitly tests the model (Jamadar, 2020).

1.6.4 Neural noise

The neural noise hypothesis of ageing posits that a diminished signal-to-noise ratio in the central nervous system occurs with advancing age, leading to more random and less precise memory representations (Crossman & Szafran, 1956). Signal strength could be decreased because of diffuse neuronal loss, weakened connections between neurons or by a change in inhibitory processes, all of which could contribute to higher levels of spontaneous electrical noise, therefore decreasing the signal-to-noise ratio, and presumably decreasing the efficiency of the ageing brain (Cremer & Zeef, 1987). More recently, it has been suggested that the decreased signal-to-noise ratio may arise as a function of increased baseline neural spiking activity (Hong & Rebec, 2012), which negatively influences neural communication (Voytek & Knight, 2015) and therefore contributes to poorer cognitive performance with age (Voytek et al., 2015).

1.6.5 Cognitive reserve

Late-life cognitive health is thought to be supported by a range of lifestyle factors, with up to a third of Alzheimer's disease cases worldwide related to potentially modifiable risk factors (Norton et al., 2014). Many studies indicate that life experiences such as education and enriching social and leisure activities are associated with reduced risk of developing dementia (Valenzuela et al., 2007) and a slower rate of cognitive decline in normal ageing (Stern, 2009). One theory that aims to describe the heterogeneity of age-related cognitive decline is cognitive reserve, which can be acquired through socially and cognitively enriching activities throughout the lifetime.

Cognitive reserve refers to differences in cognitive processes that explain one's resilience against functional impairment in the presence of age-related neurodegeneration (Stern, 2009). It is an active model of reserve in that the brain attempts to recruit compensatory or pre-existing cognitive processes to cope with age-related brain changes and can be altered based on life experience. Extensive evidence supports the existence of such a reserve, with life experiences such as education, occupation, and engagement in social and leisure activities each being associated with a decreased risk of dementia (Valenzuela & Sachdev, 2006). On the other hand, the concept of brain reserve suggests that structural characteristics of the brain provide an indication of resilience to pathology, for example, having higher brain volumes such that it takes more time for age-related atrophy to reach some critical threshold, beyond which functional impairment is inevitable (Stern, 2017).

There are several ways in which cognitive reserve is thought to be implemented by the brain. ‘Neural reserve’ is a concept that suggests inter-individual variability in the brain networks underlying task performance in a healthy brain will allow some people to cope with the demands imposed by age-related brain changes better than others (Steffener & Stern, 2012). Within the concept of neural reserve, the idea of neural efficiency has been well explored. For example, someone with higher neural reserve may display more efficient cognitive networks (i.e., networks do not require as much activation to successfully perform a task), higher capacity networks (i.e. networks that are able to operate at a greater degree under higher task loads), or greater flexibility in which networks are recruited for task performance, each of which is associated with better WM performance (Barulli & Stern, 2013).

1.7 ELECTROENCEPHALOGRAPHY

Each of the theories discussed above are primarily based around brain changes that are measured using structural and functional MRI. Though MRI allows for excellent spatial resolution, it is limited in temporal resolution and therefore cannot provide insights into brain activity occurring at millisecond time scales, both at rest and during cognitive performance. Neurophysiological methods such as EEG and magnetoencephalography (MEG) can be used to non-invasively capture a range of neurophysiological changes that accompany normal ageing, and importantly, are appropriate in investigating brain activity in real time during WM performance. In this section, the physiology of neurotransmission will be described, before discussing the physiological relevance of neural oscillations.

1.7.1 Neurons and neurotransmission

Brain tissue consists of neurons and glia. Neurons are the functional cells of the nervous system and are highly specialised and well differentiated cells that have four universal properties: 1) they are excitable and respond to environmental changes, 2) they conduct electrical signals, 3) they are secretory in nature, and 4) they do not divide.

The cellular structure of the human cerebral cortex is of specific relevance to EEG. The cerebral cortex forms a complete covering of the cerebral hemispheres. It is composed of grey matter and is estimated to contain approximately 14 to 16 billion neurons. The cortex is between 2-4mm thick and constitutes 40% of the brain’s mass, with the surface area increased considerably due to convolutions of the cortex (gyri) that are separated by fissures (sulci). Approximately 90% of the cerebral cortex consists of the neocortex, while 10% consists of the allocortex. A mixture of neurons, nerve fibres, neuroglia and blood vessels are found in the cortex, with the following, specialised neurons present: pyramidal cells, stellate cells, fusiform cells, horizontal cells of Cajal, and cells of Martinotti. These cells are organised horizontally into six laminae, and vertically into groups of cells that link synaptically across the horizontal layers. The vertical cortical columns consist of neurons with a similar receptive field and are thought to be complex processing units that have both internal and external connectivity (Mountcastle, 1997).

Regardless of the type of neuron, all neurons have a specific morphology consisting of 3 main components: dendrites, a cell body (soma) and an axon. Neurons communicate with one another through connections formed between axons and dendrites, with the number of inputs a neuron receives determined by the complexity of its dendritic network. The cell body is connected to the dendrites and houses the nucleus and organelles. The axon provides a pathway for electrical signalling and terminates at the axon terminal. A synapse is then formed between the axon terminal of the presynaptic neuron and dendrites of the postsynaptic neuron. In most cases, communication at a synapse is performed by the secretion of neurotransmitters. Neurotransmitters are released at the presynaptic terminal, diffuse across the synaptic cleft, and bind to receptors on the postsynaptic neuron. The information received at the postsynaptic neuron travels down the receiving dendrite and is integrated at the origin of the axon of the receiving neuron via an action potential, a self-propagating wave of electrical activity.

An action potential results from a rapid change in membrane potential. All cells contain a plasma membrane consisting of a lipid bilayer. This separates the internal and external cellular environments, acts as an electrical insulator, and controls the movement of substances. Membrane potential refers to the difference in electrical potential between the intracellular and extracellular environments. In a neuron, resting membrane potential is approximately -70 mV, which is maintained by the unequal distribution of Na^+, K^+ and Cl^- ions between the interior and exterior of the membrane. These ions travel both with and against concentration gradients through transmembrane ion channels.

In response to a change in membrane potential beyond a threshold value of approximately -55 mV, voltage gated Na^+ channels will open, leading to Na^+ flooding into the cell. This depolarisation will continue until the membrane potential reaches +40 mV. The neuron will then repolarise, where Na^+ channels close and K^+ channels open. This leads to K^+ ions flooding out of the cell (repolarisation). If too much K^+ leaves the cell, the neuron will enter a refractory period where it can no longer respond to further stimuli (hyperpolarisation).

Once an action potential reaches the axon terminal of the presynaptic neuron, voltage gated Ca^{2+} channels open and Ca^{2+} floods into the cell. The increase in Ca^{2+} stimulates the release of neurotransmitters which diffuse across the synapse and bind to ligand-gated channels on the dendrites of the postsynaptic neuron, creating a graded potential. An excitatory postsynaptic potential occurs when a neurotransmitter binds and ligand-gated Na^+ channels open, leading to an influx of positive ions into the cell which can push the membrane potential towards the action potential threshold of approximately -55 mV. An inhibitory postsynaptic potential occurs when a neurotransmitter binds and ligand gated Cl^- channels open, leading to an influx of negative ions into the cell. The membrane potential becomes more negative, therefore decreasing the chance of the neuron firing an action potential. Postsynaptic potentials undergo summation, in which excitatory and inhibitory postsynaptic potentials in a postsynaptic neuron allow the integration of electrical information provided by all synapses. If the sum of postsynaptic potentials results in an increase in membrane potential towards threshold, the postsynaptic cell will produce an action potential. Conversely, if the sum of postsynaptic potentials results in a decrease in membrane potential, the postsynaptic cell will not produce an action potential.

1.7.2 EEG physiology

The primary source of the EEG signal is synchronised synaptic activity in populations of cortical pyramidal cells organised in cortical columns (Lopes da Silva, 2013). When postsynaptic potentials occur, there are also changes to the electrical charge of the extracellular space. At an excitatory synapse, there is an influx of positive ions intracellularly, leaving the extracellular space more negative than elsewhere along the neuron. Conversely, at an inhibitory synapse, negative ions flow into the cell, leaving the extracellular space more positive than elsewhere along the neuron. The separation of charges creates an electrical dipole, where the region of positive charge is referred to as a source, while the region of negative charge is referred to as a sink. Dipoles from a single neuron are too small to be measured from the scalp, however the summation of dipoles from multiple neurons in an area is measurable as a single dipole (Kandel et al., 2000). As both the negative and positive ends of the dipoles are measurable, neurons must be both synchronously active and arranged in a parallel manner for their signals to summate into a larger signal. If neurons are not arranged in this way, then the individual dipole ends will summate and create a net zero.

The cortical pyramidal cells are the chief output neurons of the cortex and corticospinal tract. Pyramidal cells have a triangular cell body and large apical dendrites that extend out towards the cortical surface, and basal dendrites which extend out horizontally from the cell body. The axons of the pyramidal cells extend from the base of the cell to other cortical areas. Given the proximity of the cortex to the scalp surface, and the parallel arrangements of the dendrites of the pyramidal cells, it is believed that the pyramidal cells are the largest contributor to the EEG signal (Lopes da Silva, 1991).

Volume conduction is responsible for the propagation of the EEG signal within the brain. Volume conduction is defined as the transmission of electric or magnetic fields through biological tissue towards measurement sensors. In the case of the brain, ions in the extracellular space repel ions of the same charge, creating a wave of charge that travels through the extracellular space. However, the electrical signal must travel through the brain, dura, skull layers and scalp before it arrives at an EEG electrode. Once the volume-conducted signal reaches the edge of the volume (i.e., the brain), volume conduction cannot occur as ions cannot leave the volume. For the signal to travel between volumes, capacitive conduction is then responsible for the propagation of the signal. Eventually the signal will reach the EEG sensors on the scalp, allowing for the non-invasive recording of brain activity.

1.7.3 History of EEG

Richard Caton (1842-1926) was the first to explore the electrical activity of the brain by examining the exposed cerebral hemispheres of rabbits and monkeys. To do so, Caton used a galvanometer in which a beam of light directed towards the galvanometer reflected a large scale on the wall. In this visualisation, Caton demonstrated that ‘feeble currents of varying direction pass through the multiplier when the electrodes are placed on two points of the external surface, or one electrode on the grey matter and one on the surface of the skull’. While artefacts may have played a role in the result observed, Caton is credited as discovering the EEG phenomenon, and detailed his experiments on more than 40 rabbits, cats, and monkeys in the British Medical Journal in 1877 (Brazier, 1961).

Hans Berger (1873-1941) discovered human EEG in 1929. Using a galvanometer and non-polarisable pad electrodes, Berger recorded the first human EEG trace on photographic paper. The first report in 1929 features the alpha rhythm and alpha blocking response, with

Berger’s reports on human EEG throughout the 1930’s containing studies of consciousness, the first EEG sleep recordings and the effect of many neurological disorders on the EEG trace (Berger, 1929).

After a range of developments throughout the 1940’s, EEG began to feature in universities, hospitals and private practice, and by the 1970’s the ‘brave new world’ of EEG computerisation had begun to take place. Though the role of clinical EEG has been diminished in modern times (apart from its role in diagnosing and monitoring epilepsy), recent times have seen EEG become a commonly used tool for investigating the neurophysiological underpinnings of cognitive function.

1.7.4 EEG analyses

One of the most significant advances in EEG was the appearance of quantitative EEG measures, specifically, the application of Fourier analyses to EEG recordings (Dietsch, 1932). The Fourier transform involves computing the dot product between the signal (EEG) and kernel (sine waves). Sine waves are defined in terms of magnitude (maximum height of the sine wave peaks/valleys), frequency (number of cycles within a 1 second period, measured in the units of Hertz), and phase (where specific time points fall within a cycle of the sine wave). Therefore, EEG is usually modelled as a series of sine waves of different frequencies overlapping in time and with different phase angles with respect to a stimulus.

The EEG signal can be plotted over time to conduct time-domain analyses but can also be represented in the ‘frequency domain’ by spectral decomposition. As EEG data is a complex signal consisting of many different frequencies, spectral decomposition results in a frequency spectrum, commonly described in a power spectral density plot with frequency on the x-axis and power (magnitude squared) on the y-axis (Figure 1A). However, stationarity is an assumption of the Fourier transform, which assumes that the mean, variance, and frequency of a signal does not change over time. Given that EEG signals are dynamic and change with physiological, perceptual, and cognitive states, time-frequency approaches can be used to analyse the data. There are many time-frequency analysis approaches, but most involve using shorter time windows that slide across the data to capture temporal, as well as frequency information (Figure 1B). Such developments in analyses have made it possible to study multiple indices of neural oscillatory activity, including dominant frequencies and amplitude of frequency bands, as well as how they change across various conditions.

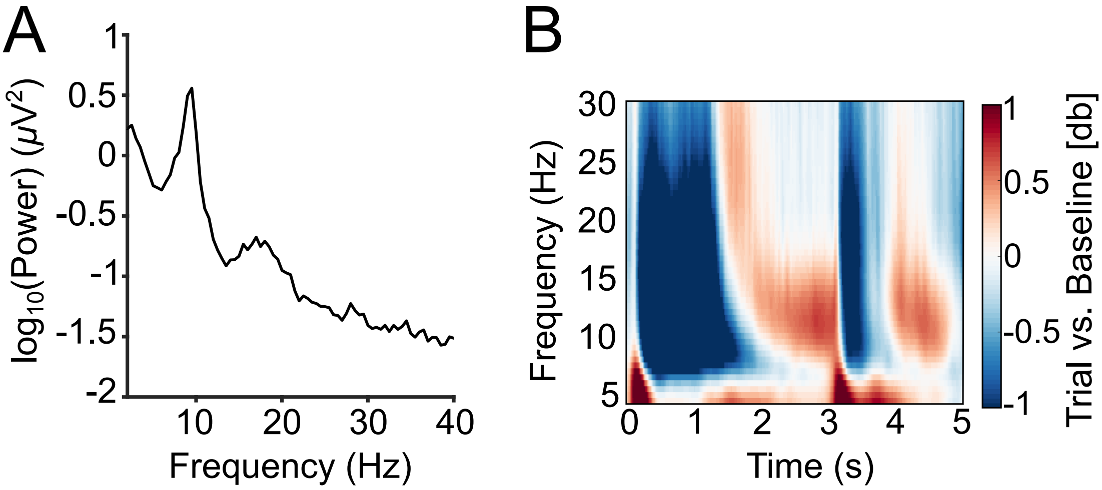

Figure 1.1. Example EEG Analyses. *A) Example of a power spectral density plot with frequency on the x-axis and power on the y-axis (displayed as log10). B) Example of a time-frequency plot with time on the x-axis, frequency on the y-axis, and power relative to a task baseline on the colour bar (adapted from Sghirripa et al. 2020).*

Time frequency approaches will be the main analysis method detailed in the experimental chapters of this thesis, and the next section will describe neural oscillatory activity—the primary outcome of time-frequency analyses.

1.8 NEURAL OSCILLATIONS

Neural oscillations are grouped into 5 frequency bands: delta (~1-4 Hz), theta (~4-7 Hz), alpha (~8-12 Hz), beta (~13-30 Hz) and gamma (~30-80 Hz), although exact ranges vary. As this thesis mainly involves the investigation of alpha oscillatory activity, the delta, theta, beta, and gamma frequency bands will be briefly described, before providing a detailed overview of alpha oscillatory activity and how it changes with age.

1.8.1 Delta oscillations

The delta frequency band involves high amplitude, slow activity in the 0.5-3.5 Hz frequency range. Delta oscillations are most evident during deep sleep, with the prevalence and amplitude of delta oscillations during sleep being highly dependent on the time passed since sleep onset (Lee Kavanau, 2002). Coupling between cortical and reticular delta oscillations have also been linked to functional organisation of the brainstem system, which implements basic autonomic regulation (Lambertz et al., 2000). The exact brain locations where delta oscillations originate from are unclear, but evidence suggests that both waking and sleep delta oscillations likely originate from medial frontal cortical regions, as well as the insula, nucleus accumbens and tegmental brainstem area (Alper et al., 2006; Knyazev, 2012).

The most significant link between delta oscillations and cognition is the correlation between delta and the P3 ERP component, an evoked response to stimuli that are unexpected or infrequent, implying a role for delta activity in attention (Başar-Eroglu et al., 1992). Accordingly, entrainment of cortical delta oscillations has been suggested as a mechanism of selective attention to auditory and visual stimulus streams (Lakatos et al., 2008), highlighting the functional relevance of delta oscillations to basic cognitive functions.

There is currently little general agreement on the modulation of delta activity with age (Hartikainen et al., 1992). While some studies have reported a decrease in resting delta power (Hartikainen et al., 1992), others report increases in delta power in older adults compared with young adults (Breslau et al., 1989). Studies investigating task-related delta oscillatory activity tend to report decreases in event-related delta responses in cognitive tasks such as the go/no-go paradigm in older, compared with younger adults (Schmiedt-Fehr & Basar-Eroglu, 2011).

1.8.2 Theta oscillations

Theta oscillations were first recorded from the hippocampus of rabbits (Jung & Kornmüller, 1938), and have been most extensively studied in the rat hippocampus and surrounding limbic structures, particularly during exploratory movements such as navigating a maze in search of food (Buzsáki, 2002). It should be noted that theta rhythm is used to describe two oscillatory phenomena: 'hippocampal theta' and 'human cortical theta'. Hippocampal theta refers to the aforementioned rhythm discovered in the hippocampus of rats, cats and rabbits (Green & Arduini, 1954), while human cortical theta refers to oscillations in the 4-7 Hz frequency range, as measured by EEG or MEG, regardless of the location it is measured from.

The neural generators of the human cortical theta rhythm are still debated. Original research focusing on local field potential recordings of hippocampal theta in rodents led to the discovery of circuits centred on the medial temporal lobe that generated activity in the 3-8 Hz frequency range (Vinogradova, 1995). It was suggested that in humans, volume conduction and other projections from the medial temporal lobe to cortical areas could entrain other brain regions to the theta rhythm. However, subsequent research identified cortical generators of theta activity, which likely is the main contributor to theta oscillations measured by EEG (Raghavachari et al., 2006).

Early studies linked cortical theta activity to developmental age, pathological conditions, and sleep (Schomer & Lopes da Silva, 2010), with later studies using intracranial electrodes linking theta activity to cognitive performance (Raghavachari et al., 2006, 2001). Specifically during WM performance, theta power appears to be ‘gated’ such that theta power increases with task difficulty (Jensen & Tesche, 2002). Frontal theta has also been implicated in cognitive control (Cavanagh & Frank, 2014), demonstrating that theta activity is associated with a wide range of cognitive functions.

Age-related changes to theta activity have been associated with declines in cognitive performance. Consistent with findings in younger adults, greater resting theta power in healthy older adults correlates with better performance on verbal memory, attention, and executive function assessments (Finnigan & Robertson, 2011). Contrastingly, longitudinal studies have indicated that higher resting theta power is generally associated with subsequent cognitive decline, including the progression of mild cognitive impairment to dementia (Jelic et al., 2000). One explanation for these contrasting reports is that slowing of the alpha rhythm leads to peak resting alpha frequency transitioning from the alpha to the theta band, resulting in higher theta power being measured (Klimesch, 1999). Such slowing has been shown to co-occur with reductions in brain volume and metabolism, as well as the decline in cognitive performance seen in MCI and AD (Jelic et al., 2000). Therefore, age-related changes to the theta rhythm are tightly connected to age-related changes in the alpha rhythm.

1.8.3 Beta oscillations

The beta frequency band includes oscillations in the ~13-30 Hz range. Historically, the discovery of beta activity was closely linked to Berger’s discovery of the alpha rhythm in 1929. When the eyes were open, high frequency ‘beta’ waves were recorded and alpha waves were blocked. Berger (1929) concluded from his findings that beta waves represented a state of wakefulness and attentiveness.

Beta activity is found in nearly every healthy adult and has been traditionally associated with sensorimotor processing (Pfurtscheller & Lopes da Silva, 1999). During the preparation and execution of movement, beta power decreases in the sensorimotor cortex, followed by an increase in power once the movement has been completed (Kilavik et al., 2013). Similar patterns of beta activity exist in the somatosensory system, with beta power suppression occurring in anticipation of, and during sensation, followed by an increase in beta power after stimulus offset (van Ede et al., 2010).

Apart from its role in motor and somatosensory function, beta activity has been implicated in a range of cognitive functions including WM, language processing and visual perception (Engel & Fries, 2010). For example, strong and persistent beta power suppression has been associated with sustained attention and maintenance processes during spatial WM (Proskovec et al., 2018).

Though the sources of beta oscillations are unknown, it is proposed that beta is either generated in the cortex (Jensen et al., 2005) or generated in the basal ganglia and propagated to cortex via the thalamus (Holgado et al., 2010). Beta oscillations have also been associated with top-down controlled processing and are thought to facilitate long range interaction between brain regions at the cortical network level (Engel & Fries, 2010). Though age-related changes to beta activity are not well understood, older adults generally demonstrate lower beta power than younger adults at rest and during task performance (Kellaway, 2003).

1.8.4 Gamma oscillations

The gamma frequency band involves oscillations in the 30-80 Hz range and was first identified when applying odorous substances to the olfactory mucosa of the hedgehog (Adrian, 1942). Further research led to the identification of gamma activity in the frontal and parietal cortices of cats in attentive behavioural states, such as when watching for prey, suggesting a role for gamma activity in attention (Bouyer et al., 1981). Studies in humans have now confirmed that gamma oscillations are modulated by attention (Debener et al., 2003), and are involved in cognitive processes such as WM and object recognition (Herrmann et al., 2004).

Compared with other frequency bands, much less is known about age-related changes in the gamma rhythm. A recent EEG study found that gamma power and frequency decreased with age in a sample of cognitively normal older adults (Murty et al., 2020). AD patients have been shown to demonstrate greater resting gamma power compared with healthy older adult controls (Wang et al., 2017). During WM performance, younger adults demonstrate lower gamma power than older adults, even when no age differences in performance are present (Barrouillet & Camos, 2012).

As a caveat, some researchers question the validity of gamma oscillatory activity detected by EEG due to the overlap between electromyographic (EMG) activity of the scalp muscles and the gamma frequency band (Whitham et al., 2008).

1.9 ALPHA OSCILLATIONS

1.9.1 Origin

The alpha rhythm was the first to be discovered by Berger (1929) and is defined as the 8-12 Hz rhythm occurring during wakefulness. Despite Berger observing alpha as a global cerebral rhythm, the alpha rhythm is spatially distributed over occipital, parietal, and posterior temporal regions. Adrian and Matthews replicated Berger's original findings and expanded upon them by demonstrating that alpha oscillations could be entrained by flickering lights, providing evidence that the rhythm is of cortical origin (Adrian & Matthews, 1934).

The cerebral generators of the alpha rhythm have been highly debated and the physiological basis remains unclear. The alpha rhythm is likely of cortical origin, but the theory of a thalamic pacemaker function was suggested by Berger (1929), who presumed alpha to be of cortical genesis but under thalamic control. As the field developed and gained traction, invasive human EEG studies confirmed the presence of the alpha rhythm not only in cortical, but in subcortical areas such as the thalamus, and specifically, the pulvinar nuclei (Gücer et al., 1978). Further, thalamic lesions have been associated with diminished alpha activity (Ohmoto et al., 1978).

To further investigate the physiological basis of the alpha rhythm, a series of pharmacological experiments were conducted on anaesthetised cats. Andersen and Andersson (1968) used GABAergic agonists to create an animal model that produced spindle-like activity that oscillated at a similar frequency as the resting alpha rhythm. Using this model, they suggested that the origin of the resting alpha rhythm recorded from occipital regions was a result of a thalamic pacemaker which consisted of inhibitory neurons that projected into the cortex (Andersen & Andersson, 1968). However, work conducted in the 1970's convincingly demonstrated that the spindle activity recorded by Anderson and Andersson, and the classical alpha rhythm were of different physiological origin (da Silva et al., 1973), placing doubt for the thalamus as the source of the alpha rhythm. However, it was demonstrated that certain thalamic nuclei have a strong influence on alpha activity recorded from the cortex.

There is a body of evidence suggesting that the alpha rhythm is of cortical origin. For example, it has been shown that cortical pyramidal neurons from deep cortical layers demonstrate rhythmic firing in the 8-12 Hz range in in vitro preparations (i.e., when the neurons are isolated from the thalamus) (Lopes da Silva, 1991). The idea that the cortex independently generates the alpha rhythm is also supported by the fact that stronger alpha coherence is exhibited between cortical areas than between the cortex and thalamus (da Silva et al., 1973). For example, structural and functional connectivity between posterior brain regions and primary visual cortex is correlated with alpha power in posterior regions (Hindriks et al., 2015). Finally, transcranial magnetic stimulation (TMS) to occipital cortical regions has been shown to evoke alpha oscillations, whereas stimulation to parietal regions evoked beta oscillations, suggesting that alpha may represent an intrinsic rhythm of the visual cortex (Rosanova et al., 2009).

Despite the extensive work to understand the neural origin of alpha oscillations, its physiological basis remains elusive. However, the current state of the literature suggests that both cortical and thalamic sources contribute independently and presumably interact with each other to produce the alpha rhythm.

1.9.2 Function

Alpha is reactive and is temporarily reduced when the eyes open and when engaging in mental activities. Berger termed this phenomenon the ‘alpha blocking’ response. The decrease in alpha activity with mental engagement led to accounts that alpha activity reflects ‘cortical idling’ (Pfurtscheller et al., 1996), as alpha activity increases when subjects are awake but not engaging in a task. Though the alpha blocking response suggests that the decreases in alpha power are a result of bottom-up processing (i.e., visual stimulation via light), decreases in alpha activity also occur when the eyes open in a room without visual stimulation, suggesting that changes in alpha activity are triggered by top-down processes (Moosmann et al., 2003). Therefore, there is strong evidence to suggest that alpha oscillations play a functional role in the modulation of cortical excitability.

A leading theory on the functional role of alpha oscillations is that alpha reflects functional inhibition (Jensen & Mazaheri, 2010). Early evidence against the cortical idling hypothesis came from studies employing verbal WM tasks, where increases in alpha power that scaled with task difficulty were observed during the task (Jensen et al., 2002). The interpretation of this finding was that alpha power reflects a suppression of sensory input from the visual stream to prevent disruption from WM processes occurring in frontal brain regions (Jensen & Mazaheri, 2010). The pattern of alpha modulation during WM will be discussed in more depth in section 1.10.3.

Further evidence for the functional inhibition hypothesis arose from studies using covert attention tasks where subjects attend to either the left or right hemifield. In these tasks, alpha power decreases in the contralateral hemisphere, but increases in the ipsilateral hemisphere, suggesting a role for alpha power in attentional control (Rihs et al., 2007; Thut et al., 2006). In these tasks, larger differences in alpha power between the two hemispheres is associated with improved detection of attended to stimuli (Gould et al., 2011). This effect is not limited to visual brain regions, as studies employing somatosensory tasks have demonstrated that relative to the side of the engaged hand, alpha activity decreases in the contralateral, and increases in the ipsilateral primary somatosensory cortical area (Haegens et al., 2010).

Consequently, alpha suppression is proposed to reflect cortical engagement (Jensen & Mazaheri, 2010; Klimesch, 2007). Evidence for alpha suppression as an indicator of cortical engagement comes from studies investigating whether pre-stimulus alpha power suppression predicts perceptual outcomes. It has been shown that stimuli at the just noticeable difference threshold are more easily detected when alpha power is low (Mathewson et al., 2009). Likewise, in a study employing combined TMS and EEG, it was shown that pre-stimulus alpha power suppression led to a greater chance of detecting TMS induced phosphenes, suggesting that posterior alpha power appears to be linked to visual cortex excitability (Romei et al., 2008).

The ability for alpha activity to modulate the excitability of the cortex has led to alpha being implicated in top-down modulation. In section 1.10, the concept of top-down modulation of alpha oscillations and how this process supports WM performance will be described.

1.9.3 Alpha peak frequency

Far less research has focused on the functional relevance of alpha peak frequency. The alpha rhythm is detectable around the age of 4 months at a frequency of 4 Hz, and progressively increases in frequency to around 6 Hz at 12 months, 8 Hz at 3 years, and 10 Hz at 10 years—the mean frequency throughout adulthood (Eeg-Olofsson et al., 1971). The peak alpha frequency then declines throughout older adulthood with an average of 8.5-9.7 Hz in adults over 60 (Babiloni et al., 2006; Lindsley, 1939), and the slowing of alpha frequency has been observed in people with dementia (Babiloni et al., 2020; Montez et al., 2009).

Alpha frequency has been associated with the speed of cognitive and memory performance (Klimesch, 1999). Early findings demonstrated that alpha frequency was associated with RT, which was interpreted to reflect speed of information processing (Surwillo, 1961). Other studies have demonstrated that participants with higher alpha frequency show faster RTs (Klimesch et al., 1996), and those with better memory performance have an alpha frequency of approximately 1 Hz higher than that of age-matched samples of poor performers (Klimesch, 1999).

Though resting state peak alpha frequency has been shown to be a stable neurophysiological trait in both younger and older adults (Grandy et al., 2013), recent evidence suggests that alpha peak frequency undergoes state dependent shifts, such as during and after cognitive tasks. For example, a study employing a WM task (*n*-back) demonstrated a load dependent increase in alpha peak frequency in healthy younger adults (Haegens et al., 2014), while another study using a verbal WM task (modified Sternberg) demonstrated a load-dependent decrease in alpha frequency during encoding, and a decrease during retention, in healthy younger adults (Babu Henry Samuel et al., 2018). Far less research has been directed towards state-dependent shifts in alpha peak frequency in older adults, despite alpha frequency slowing with age. In Chapter 2 of this thesis, age-related changes in alpha peak frequency during WM performance will be explored.

1.9.4 Age-related changes to alpha oscillations

Changes to the alpha rhythm are one of the most prominent hallmarks of brain ageing. These changes include a decrease in peak alpha frequency (i.e., a slowing of the alpha rhythm) (Başar, 2012; Gaál et al., 2010), a decrease in alpha power (Babiloni et al., 2006; Başar, 2012; Lindsley, 1939), and a shift of alpha activity from posterior to anterior sources (Babiloni et al., 2006; Rossini et al., 2007). However, though the decrease in alpha frequency has been reliably reported, decreases in alpha power are less reliable.

One account suggests that decreases in alpha power and frequency with age are a result of age-related changes to the functioning of the cholinergic basal forebrain system (Sarter and Bruno, 1998). It is suggested that an increase in excitatory activity of the cholinergic brainstem pathway may lead to greater cortical excitability (i.e., decreased alpha power) due to excitation of the thalamocortical pathway (Babiloni et al., 2006). Previous studies have also demonstrated that resting alpha power reduces with experimentally induced impairment of the cholinergic pathways stemming from the basal forebrain in rats (Holschneider et al., 1998). Further evidence for this account comes from the fact that patients with MCI and mild AD are thought to experience impairment of cholinergic basal forebrain function, and also show lower alpha power (Babiloni et al., 2004). Further, acetylcholinesterase inhibitors have been shown to increase alpha activity in Alzheimer's disease patients (Babiloni et al., 2013), potentially implicating early changes to the cholinergic system in the decrease of alpha activity in normal ageing.

The relationship between alpha activity and white matter lesions and integrity has also been investigated. Alpha peak frequency has been associated with both increases and decreases (region dependent) in the microstructure of thalamocortical and corticothalamic fibres, as assessed by diffusion tensor imaging (Valdes-Sosa et al., 2011). In contrast, it was recently shown that a higher occurrence of white matter lesions in the corona radiata and thalamic radiation were related to higher relative alpha power (Kumral et al., 2022). Though counter intuitive, this result was interpreted to reflect the fact that if white matter disturbances disrupt thalamocortical circuitry, cortical patches of enhanced and suppressed alpha oscillations can become demarcated, leading to a larger spread of alpha activity across the cortex that is less spatially specific, and therefore ineffective in preserving cognitive performance.

There are a range of more simplistic explanations that explain the decrease of alpha power with age. There are some reports that low alpha power with age is simply due to reduced skin, cortical bone, and brain conductivity with increasing age (Johnson et al., 2010). It has also been argued that reduced alpha power is due to the slowing of the alpha peak frequency. A study investigating the relationship of age-related peak alpha frequency reductions and EEG power and connectivity found that upper alpha power (10-12 Hz) was significantly reduced in older compared with younger adults, but power at alpha peak frequency was preserved, suggesting that age-related alpha power differences are merely a measurement related effect when not accounting for peak alpha slowing with age (Scally et al., 2018) .

Despite many theories attempting to explain age-related changes to the alpha rhythm, there is no one account that captures the phenomenon of age-related decreases in alpha power and a slowing of the alpha frequency.

1.10 NEURAL OSCILLATIONS DURING WM

The evidence for the role of neural oscillations in supporting WM encoding and retention in younger and older adults will now be outlined, with a discussion about how selective attention also aids in successful WM performance via top-down modulation. The focus will be on the pattern and functional relevance of alpha oscillatory activity as this is the core focus of the experiments contained in this thesis, but the role of theta and beta oscillations in WM performance will also be briefly described.

1.10.1 Anticipation and selective attention for WM performance

Given the storage limits of WM, it is important to selectively attend to task-relevant, while ignoring task-irrelevant information. Top-down modulation has been suggested as a mechanism linking WM and selective attention and can be deployed to improve WM performance when participants are provided with an informative, pre-stimulus cue that predicts a feature of the task that is relevant for performance. For example, providing a cue about where a stimulus to be remembered will appear (Posner, 1980) or when it will appear (Nobre, 2010). The goal-directed modulation of alpha oscillatory activity in sensory cortices is one way that top-down modulation operates within the brain (Gazzaley & Nobre, 2012). Therefore, alpha power has been linked to selective attention in response to preparatory cues of various types, including spatial, temporal, and alerting cues, each of which can be used to improve WM performance.

Spatial cues provide participants with information about where a stimulus will appear (i.e., to the left or right) (Posner, 1980), and are most commonly used in lateralised WM tasks where participants are instructed to attend to a task-relevant and ignore a task-irrelevant hemifield before the onset of the memory set (Vogel and Machizawa, 2004). In these tasks, alpha power tends to decrease in the task-relevant hemifield while increasing in the task-irrelevant hemifield, suggesting a role of alpha suppression in the selective encoding of task-relevant information, and alpha facilitation in the ignoring of distractors (Sauseng et al., 2009). While alpha oscillatory dynamics in lateralised WM tasks have been heavily researched in younger adults, fewer studies have investigated the role of lateralised alpha activity during WM in older adults, and existing literature is conflicting. In a study using a delayed match-to-sample task with attentional cues, older adults showed the expected pattern of lateralised alpha power relative to the attended to hemifield at medium loads, but not at higher loads, yet younger adults showed lateralisation at all loads (Sander et al., 2012). However, it has also been shown that attentional control during WM, as indexed by alpha power, is preserved in ageing (Mok et al., 2016).

Attention can also be allocated to specific points in time to optimise WM performance by forming an expectation about when a memory set will appear. Decreases in alpha power in response to anticipatory cues are thought to represent increases in visual cortex excitability (Romei et al., 2008). For example, when younger adults are provided with a temporal cue that indicates when a stimulus (such as a memory set) will appear, anticipatory alpha power suppression is seen before the onset of the expected stimulus, and the magnitude of alpha power suppression predicts task performance (Romei et al., 2010). Compared with younger adults, older adults are less able to use temporal cues to form an expectation about when a stimulus will appear, as indexed by performance deficits and less alpha power suppression in expectation of the stimulus (Zanto et al., 2011).

To summarise, modulation of alpha power in response to informative cues seems to support WM performance in younger adults. However, an inability to modulate alpha power in response to cues likely reflects deficits in top-down modulatory processes and explains why older adults are less able to use predictive cues to support WM performance (as discussed in section 1.6.2).

1.10.2 Encoding

Given that alpha activity decreases during visual stimulation, it is unsurprising that alpha is modulated during the encoding period of WM tasks. Early evidence for the role of alpha oscillations during memory encoding was reported by Klimesch, who found that decreases in parietal alpha power during semantic encoding was related to later retrieval of those items (Klimesch, 1997). When encoding verbal stimuli, decreases in alpha/beta power are most evident in frontal regions (Hanslmayr et al., 2011), which is thought to reflect semantic processing. Decreases in alpha and beta power are also seen when encoding visual stimuli (such as pictures of objects, coloured squares), with the effect most prominently seen in parieto-occipital regions (Noh et al., 2014). Regardless of stimulus type, the decrease in alpha power during encoding has been interpreted to reflect an increase in cortical excitability to enhance stimulus processing (Klimesch, 2012).

Oscillatory signatures of WM encoding in younger and older adults have recently been captured in verbal WM tasks. A study in which young adults completed a modified Sternberg task with memory sets consisting of 6 letters found that presentation of the memory set resulted in a strong decrease in alpha power in occipital cortices that was sustained for the entirety of the 2 s encoding period and the first 1 s of the retention period, before rebounding and increasing in the late retention period before retrieval (Heinrichs-Graham & Wilson, 2015). Using the same task in both younger and older adults, a similar decrease in alpha and beta activity was reported in bilateral occipital regions during early encoding, that spread to left temporal and frontal cortices as the encoding period elapsed (Proskovec et al., 2016).

Encoding processes during WM have also been associated with increased theta activity. During intracranial EEG, Raghavachari and colleagues (2001) observed a strong increase in theta activity during the encoding stage of a Sternberg-like verbal memory task, which was sustained over the duration of the retention phase until retrieval. The authors suggested that theta activity reflects a gating mechanism, in which focus is directed towards task-relevant information, and task-irrelevant information processing is suppressed (Raghavachari et al., 2001).

1.10.3 Retention

Most of the research into oscillatory signatures of WM in younger and older adults has focused on the retention period. There are two things to note before discussing the EEG correlates of the WM retention period. First, the pattern of alpha power modulation during the retention period of WM tasks depends on both stimulus modality (i.e., verbal vs. visual) and method of stimulus presentation (i.e., sequential vs. simultaneous), leading to many conflicting findings in the field. Second, the change in oscillatory activity when distractors are present during the retention period will also be discussed, as this forms a key component in the interpretation of the functional relevance of alpha power modulation during WM. For the sake of clarity, this section will be split into several subsections to discuss the wide range of literature that attempts to describe and explain the oscillatory mechanisms supporting WM retention in younger and older adults.

1.10.3.1 Alpha oscillations during verbal WM retention

In verbal WM studies where stimuli are presented simultaneously (e.g., modified Sternberg tasks), alpha power tends to increase from baseline during the retention period, with this effect scaling with load (Jensen et al., 2002; Meltzer et al., 2008; Proskovec et al., 2019). The increase in alpha power in these tasks has been interpreted to reflect a suppression of sensory input from the visual stream to prevent disruption to WM retention and rehearsal (Jensen et al., 2002; Jensen & Mazaheri, 2010). Accordingly, increases in alpha power are most prominent in sensory regions that are irrelevant to the stimulus type being retained in WM (e.g., in visual brain regions during verbal WM; as in Jensen et al. 2002). Less work has focused on the modulation of alpha power during verbal WM retention in older adults. A study employing a high load (6-letter) modified Sternberg task found that increases in alpha power during the retention period were greater in older, compared with younger adults, despite older adults performing worse on the task (Proskovec et al., 2016). The greater increase in alpha power in older adults was interpreted to reflect CRUNCH, in which older adults recruited greater neural resources, as indexed by alpha power, to cope with task difficulty. However, this study did not manipulate WM load, so it is currently unclear whether alpha power is modulated with load during verbal WM retention in older adults. Likewise, to investigate whether CRUNCH applies to alpha power modulation during WM retention, load must be manipulated to determine whether older adults recruit greater neural resources than younger adults at lower WM loads. This gap in the literature will be addressed in Chapter 2 of this thesis, where age differences in load-dependent modulation of alpha oscillations during verbal WM are explored.

Strong evidence for the role of alpha oscillations in the 'sensory gating' of distracting information comes from studies that have directly manipulated the presence of distracting stimuli during verbal WM retention. Bonnefond and Jensen (2012) employed a Sternberg task in which participants indicated whether a probe letter was part of a sequentially presented memory set. In each trial, a weak (non-letter symbol) or strong (a letter) distractor was presented during the retention period. Distractor types were placed in blocks, allowing participants to anticipate the type of distractor that would be present. Anticipation of strong distractors was associated with greater alpha power in visual brain regions, and this effect correlated with better task performance in the presence of strong distractors (Bonnefond & Jensen, 2012). Employing a similar task but with simultaneously presented memory sets consisting of 5 letters, we have previously shown that alpha power in visual brain regions increased in anticipation of both strong (3 letters) and weak (3 hash symbols) distractors, but the magnitude of effect was not associated with task performance (Sghirripa et al., 2020). However, these studies only involved young participants, and it is currently unclear whether older adults modulate alpha power in anticipation of distractors during verbal WM retention. Failure to modulate alpha power in anticipation of distractors may be indicative of deficits in top-down modulatory processes in older adults.

However, different patterns of alpha power modulation are observed in tasks involving the sequential (classic Sternberg task) or continuous presentation of stimuli (*n*-back task). In *n*-back tasks using verbal stimuli, alpha power tends to decrease with load, which is thought to reflect cortical engagement and active maintenance of stimulus information (Gevins et al., 1997; Pesonen et al., 2007; Stipacek et al., 2003). To investigate the differences in alpha power modulation between task types, Okuhata et al. (2013) compared alpha power modulation differences between sequentially and simultaneously presented memory sets. Alpha power decreased from baseline in the simultaneous presentation condition but increased in the sequential presentation condition, despite each condition being matched for WM load (Okuhata et al., 2013). Therefore, there are a range of task factors that can influence the pattern of alpha power modulation during verbal WM, leading to no clear consensus on the expected patterns of alpha activity during verbal WM, nor the functional relevance of the effect.

1.10.3.2 Alpha oscillations during visual WM retention

In contrast, the simultaneous presentation of visual stimuli such as coloured squares has been shown to result in decreases in alpha power during retention (Adam et al., 2017; Fukuda et al., 2015). One interpretation of this effect is that alpha power suppression reflects storage processes, as alpha power has been shown to decrease with visual WM load and correlates with WM capacity (Fukuda et al., 2015). Another possibility is that decreases in alpha power during visual WM retention support target enhancement or attentional processes (Foster & Awh, 2019). A study involving a visual WM task that manipulated the number of distractors and spatial distribution of targets found that alpha suppression was related to both distractor load and target distribution, suggesting that alpha suppression during visual WM retention reflects perceptual attentional deployment (Wang et al., 2020).

Less work has investigated alpha oscillatory activity during visual WM in older adults, with the existing studies in the literature focusing on lateralised visual WM tasks. In a study employing a hemifield change detection task with spatial cueing, reduced alpha lateralisation during the retention period was seen in older adults at high WM loads, suggesting that inhibitory processes indexed by alpha power modulation break down at higher task difficulties (Sander et al., 2012). A study using a similar paradigm also observed that older adults demonstrated less alpha power lateralisation during the retention period compared with younger adults (Tran et al., 2016). Lastly, in a study where WM performance was matched across age groups, bilateral reductions in alpha power during a lateralised visual WM task led to older adults demonstrating less alpha lateralisation than younger adults during the retention period (Leenders et al., 2018). Age differences in alpha power during visual WM using a whole-field change detection task will be investigated in Chapter 3 of this thesis.

There are a limited number of studies that have investigated the influence of distracting information on alpha power modulation during the visual WM retention period. A study using a lateralised approach where oriented bars were presented as the memory set and strong (more oriented bars) or weak (squares) distractors that persisted throughout the entire retention period found that alpha power decreased in the presence of strong distractors (Schroeder et al., 2018). Though older adults behaviourally perform worse in the presence of distracting information during the visual WM retention period compared to when no distractors are present (McNab et al., 2015), few studies have investigated whether older adults modulate alpha power in anticipation of distractors during visual WM retention. One study found that despite both younger and older adults demonstrating behavioural evidence of suppressing irrelevant information, only younger adults showed alpha power modulation in the condition requiring participants to ignore the irrelevant stimuli (Vaden et al., 2012). However, it remains unclear whether older adults modulate alpha in anticipation of distractors in visual or verbal WM tasks, and whether they modulate alpha power based on the strength of distraction. This gap in the field will be addressed in Chapter 5, where a study investigating age differences in alpha power for distractor inhibition during visual WM will be presented.

1.10.3.3 Theta oscillations during retention

Many verbal WM studies have reported an increase in theta power during retention, particularly with increasing load. Increases in theta power with increasing load have been reported in tasks using simultaneously presented memory sets (Jensen & Tesche, 2002; Meltzer et al., 2008) as well as in *n*-back style paradigms (Gevins et al., 1997). However, a recent study employing a lateralised approach to displaying verbal stimuli demonstrated an increase in theta power during retention that did not scale with load (Kustermann et al., 2018), and another found no change in theta power across the encoding or retention periods (Heinrichs-Graham & Wilson, 2015). Like alpha power modulation, it is possible that memory set presentation methods lead to differing results across studies. Studies involving sequential presentation of information tend to report increases in theta power (Gevins et al., 1997; Jensen & Tesche, 2002), while those finding no difference between loads or from baseline have used simultaneously presented memory sets (Heinrichs-Graham & Wilson, 2015; Kustermann et al., 2018).

Theta power has also been shown to be modulated during visual WM retention, with far greater variation in results than the verbal WM literature. In a spatial WM study, increases in theta power were observed early during the retention period, before decreasing below baseline level until the presentation of the probe (Proskovec et al., 2018). However, two studies using the same paradigm as Proskovec et al. (2018) reported increases in theta power throughout the retention period (Berger et al., 2019; Eschmann et al., 2018).

Less is known about theta power modulation during WM retention in older adults. In a study employing a verbal WM task with varying loads, older adults demonstrated lower theta power during the retention period than younger adults (Cummins & Finnigan, 2007). In a visual WM task, older adults also exhibited reduced theta modulation during retention which was associated with poorer visual WM performance (Kardos et al., 2014).

One interpretation of the increase in theta activity with memory demands is that it reflects attentional processes (Gevins et al., 1997). Further, frontal theta activity increasing with memory load may be a consequence of sustained neuronal activity that relates to active maintenance of memory representations (Jensen & Tesche, 2002). Theta-based fronto-parietal phase synchronisation has also been suggested to reflect the phonological loop related to the verbal stimuli presented (Kustermann et al., 2018), which would explain why increases in theta power are commonly reported in verbal, rather than visual WM tasks.

1.10.3.4 Beta oscillations during retention

Far less research has investigated the role of beta oscillatory activity in WM retention, with even less focus on beta activity in older adults. Beta power in the ~13-20 Hz frequency range has been shown to increase during retention during verbal WM tasks, with this effect increasing with load (Deiber et al., 2010; Onton et al., 2005). In a study employing a verbal WM task involving both a retention (remembering letters) and manipulation condition (remembering letters in alphabetical order), beta oscillations in the 13-20 Hz range decreased with load during the retention condition, but increased with load in the manipulation condition (Pavlov & Kotchoubey, 2017). In this study, participants who performed better on the manipulation task demonstrated stronger decreases during retention, suggesting a role for beta power in the continuous updating of information and WM contents.

A study employing a spatial WM task demonstrated strong beta suppression during early retention in parietal, temporal, and occipital regions, which was suggested to represent sustained attention and maintenance of information (Proskovec et al., 2018). However, much of the evidence for beta modulation during WM retention seems tightly linked to the pattern of alpha power modulation, suggesting that beta oscillatory activity may be a harmonic of alpha activity, particularly if it is observed in posterior electrodes (Pavlov & Kotchoubey, 2022). This account is also supported by studies employing both verbal and visual WM tasks that report strong alpha/beta suppression following the onset of memory sets, given the role of alpha power suppression in response to visual input (Erickson et al., 2019; Pavlov & Kotchoubey, 2017).

Little research has investigated beta oscillatory activity during WM in older adults. Consistent with the account that beta activity is a harmonic of alpha activity, in the verbal WM study conducted in older adults by Proskovec et al. (2016), alpha/beta suppression persisted from encoding into early retention, before evolving into a narrower alpha band. However, it is unclear whether beta oscillatory activity has clear functional relevance for WM performance in both young and older adults.

1.11 SUMMARY

WM is one of the cognitive functions most vulnerable to age-related decline, with healthy older adults reporting WM deficits that can impact quality of life even in the absence of pathology such as Alzheimer’s disease. While there is an enormous amount of literature exploring the oscillatory signatures of WM performance in younger adults, far less attention has been directed towards understanding the neural oscillatory mechanisms underlying age-related decline in WM performance. The experiments described in this thesis will explore the EEG correlates of both verbal and visual WM performance in younger and older adults across a range of WM tasks to investigate the neurophysiological underpinnings of WM decline with age.

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Chapter 2: Load-dependent modulation of alpha oscillations during working memory encoding and retention in young and older adults

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Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
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By signing the Statement of Authorship, each author certifies that:

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ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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2.1 ABSTRACT

Working memory (WM) is vulnerable to age-related decline, particularly under high loads. Visual alpha oscillations contribute to WM performance in younger adults, and although alpha decreases in power and frequency with age, it is unclear if alpha activity supports WM in older adults. We recorded electroencephalography (EEG) while 24 younger (aged 18–35 years) and 30 older (aged 50–86) adults performed a modified Sternberg task with varying load conditions. Older adults demonstrated slower reaction times at all loads, but there were no significant age differences in WM capacity. Regardless of age, alpha power decreased, and alpha frequency increased with load during encoding, and the magnitude of alpha suppression during retention was larger at higher loads. While alpha power during retention was lower than fixation in older, but not younger adults, the relative change from fixation was not significantly different between age groups. Individual differences in alpha power did not predict performance for either age groups or at any WM loads. We demonstrate that alpha power and frequency are modulated in a similar task- and load-dependent manner during WM in both older and younger adults when WM performance is comparable across age groups.

2.2 INTRODUCTION

Verbal working memory (WM), the ability to actively maintain and/or manipulate verbal information to guide immediate cognitive processing (Baddeley, 1992), is vulnerable to age-related decline. Compared to younger adults, healthy older adults are able to store fewer items in WM, are less able to manipulate those items (Fisk & Warr, 1996), and are more susceptible to interference from distracting information (Gazzaley & D'esposito, 2007). This age difference is particularly salient under high WM demands, with older adults demonstrating poorer performance with higher loads relative to younger adults (McEvoy et al., 2001; Wild-Wall et al., 2011). Despite this, the neural mechanisms underlying such age differences at varying WM loads are not well understood.

Advancing age is associated with progressive changes in the frequency and power of neural oscillations (Klass & Brenner, 1995; Klimesch, 1999). Alpha (~8-12Hz) is perhaps the most affected frequency band in ageing, with alpha oscillations significantly lower in magnitude and slower in frequency in healthy older adults compared with younger adults at rest (Babiloni et al., 2006; Klimesch, 1997; Lindsley, 1939). As alpha oscillations in posterior brain regions are thought to support WM performance (Klimesch, 2012), age-related changes to alpha activity may underlie WM performance deficits in healthy older adults.

WM is typically divided into three stages: encoding, retention and retrieval (Baddeley, 1992). Most of the research in this area has focused on the retention period, with a large body of evidence suggesting that alpha is modulated during this stage, though the location, direction and magnitude of this change depends on the type of task. Using modified Sternberg tasks, it has been reliably shown that alpha power increases in visual brain areas during retention, particularly under higher WM loads (Jensen et al., 2002; Meltzer et al., 2008; Proskovec et al., 2019). The predominant interpretation of this finding is that alpha activity reflects a suppression of sensory input from the visual stream to prevent disruption to WM maintenance occurring in frontal brain regions (Jensen and Mazaheri, 2010). In lateralised WM tasks where subjects attend to and memorise the information in one hemifield, and ignore the other, parieto-occipital alpha power decreases in the task-relevant, and increases in the task-irrelevant hemisphere (Sauseng et al., 2009). Finally, alpha suppression with increasing WM load in parieto-occipital sites has been reported in n-back style paradigms (Gevins et al., 1997; Krause et al., 2000; Pesonen et al., 2007; Stipacek et al., 2003) and delayed match-to-sample tasks (Fukuda et al., 2015). Less is known about the alpha oscillatory dynamics underlying the WM encoding period, although posterior alpha power has been shown to decrease in this stage, likely reflecting attentional processes (Heinrichs-Graham & Wilson, 2015). Likewise, alpha frequency has been linked to WM performance as a trait variable at rest (Klimesch, 1999) and during task performance in younger adults (Haegens et al., 2014).

Much of the research investigating age and load-related changes in alpha activity during WM have involved lateralised, visual WM tasks. In a study involving a hemifield change detection task with spatial cueing, it was found that while younger adults demonstrated higher alpha power ipsilateral to the attended hemifield during the retention period at medium and high loads, older adults only showed lateralisation at medium loads. This suggests that inhibitory processes indexed by alpha power modulation are not present in older adults when task difficulty increases (Sander et al., 2012). Likewise, a study employing a hemifield change detection task with an alerting cue showed that older adults had reduced alpha amplitude lateralisation during the retention period compared with younger adults, though between-load differences in alpha lateralisation did not predict performance at high WM loads in each age group (Tran et al., 2016). Lastly, using a lateralised delay match-to-sample paradigm with spatial cueing, it was found that at matched WM difficulty, alpha lateralisation during retention was minimal in older adults due to bilateral reductions in alpha power, while younger adults demonstrated lower alpha power contralateral to the attended hemifield (Leenders et al., 2018).

However, as the aforementioned studies involved visual WM tasks and a lateralised approach, and the majority of prior work investigating alpha activity during WM using Sternberg tasks have only included younger adults, it is unclear whether alpha activity contributes to verbal WM performance in older adults. A recent study employing magnetoencephalography during a high load (6-letter) modified Sternberg task reported that increases in visual alpha power during the WM maintenance period were present in both older and younger adults (Proskovec et al., 2016). However, relative to younger subjects, the increase in alpha activity was more rapid, widespread and persistent for longer in older adults, which was interpreted to reflect a compensatory mechanism to aid WM performance in older age (Proskovec et al., 2016). However, as WM load was not manipulated in this study, it is unclear whether older adults modulate visual alpha activity in order to facilitate verbal WM performance under varying WM loads. Likewise, while previous studies have found evidence for task- and load-related alpha frequency modulation during WM, these studies have only involved younger adults (Babu Henry Samuel et al., 2018; Haegens et al., 2014).

In the present study we investigated the age-related differences in visual alpha activity during verbal WM in response to increasing memory load. We applied a modified Sternberg task with 1-letter, 3-letter and 5-letter load conditions where WM processes were temporally delineated, in order to identify the alpha oscillatory dynamics underlying the WM encoding and retention stages. We ensured that any observed changes in the power of alpha oscillations were not due to age-related changes in peak alpha frequency by matching power measurements to individual alpha peaks. We sought to test the following hypotheses. First, older adults will show greater performance deficits at higher WM loads than younger adults. Second, older adults will show increased load-dependent modulation of visual alpha power during WM encoding and retention compared to younger adults. Third, age-related differences in visual alpha power during WM will correlate with task performance. Finally, cognitive reserve refers to the ability to maintain cognitive function in the presence of age-related changes to the brain, and can be acquired through socially and cognitively enriching activities throughout the lifetime (Barulli & Stern, 2013). As a secondary aim, we investigated whether cognitive reserve in older adults was associated with WM performance and alpha activity during the task.

2.3 METHODS

2.3.1 Participants, demographics, and cognitive reserve

24 younger adults (mean age: 23.2 years, *SD*: 4.60, range: 18-35 years, 8 male) and 30 older adults (mean age: 62.7 years, *SD*: 9.09, range: 50-86 years, 17 male) participated in the

study. The samples in each group were not significantly different for years of education (older adults: *M* = 15.87 years, *SD* = 4.45 years; younger adults: *M* = 15.71 years, *SD* = 1.97 years, $t_{43.51}$ = 0.182, *p* =.857). All older adults were without cognitive impairment (Addenbrooke's Cognitive Examination score (ACE-III) > 82) (Mioshi et al., 2006). Exclusion criteria were a history of neurological or psychiatric disease, use of central nervous system altering medications, history of alcohol/substance abuse, uncorrected hearing/visual impairment and an ACE-III score of less than 82. All participants gave informed written consent before the commencement of the study, and the experiment was approved by the University of Adelaide Human Research Ethics Committee.

Cognitive reserve (CR) was calculated for each older adult participant by z-transforming their total years of education and scores on the National Adult Reading test (NART), which is used to estimate verbal IQ (Blair & Spreen, 1989). The z-scores were then averaged to form a cognitive reserve score, and participants were divided into high and low cognitive reserve groups using a median split.

2.3.2 Working memory task

The modified Sternberg WM task used stimuli presented by PsychoPy software (Peirce, 2007) (figure 1). At the beginning of each trial, the participant fixated on a cross in the centre of the screen for 2 s. A memory set consisting of either 1, 3 or 5 consonants was then shown for 1 s, followed by a 4 s retention period. For load-1 and load-3 trials, the consonants were presented centrally, with filler symbols (#'s) added to maintain equal sensory input for each condition. A probe letter was then shown, and the subject was instructed to press the right arrow key on a standard keyboard if the letter was in the memory set, or the left arrow key if it was not. The probe remained on the screen until the subject responded. Probe letters were present in the memory set at 50% probability. Participants received a practice block of 20 trials to familiarise themselves with the task, before performing 20 blocks of 15 trials, yielding 300 trials overall (i.e. 100 trials per load). Each block contained an equal number of trials for each load, presented pseudorandomly and a short break was allowed between blocks.

To quantify WM performance, reaction time (RT) for correct trials and WM capacity were calculated for each load condition. The participants' WM capacity was quantified using Cowan's *K* (Cowan, 2001), defined by *K* = set size x (hit rate – false alarm rate).

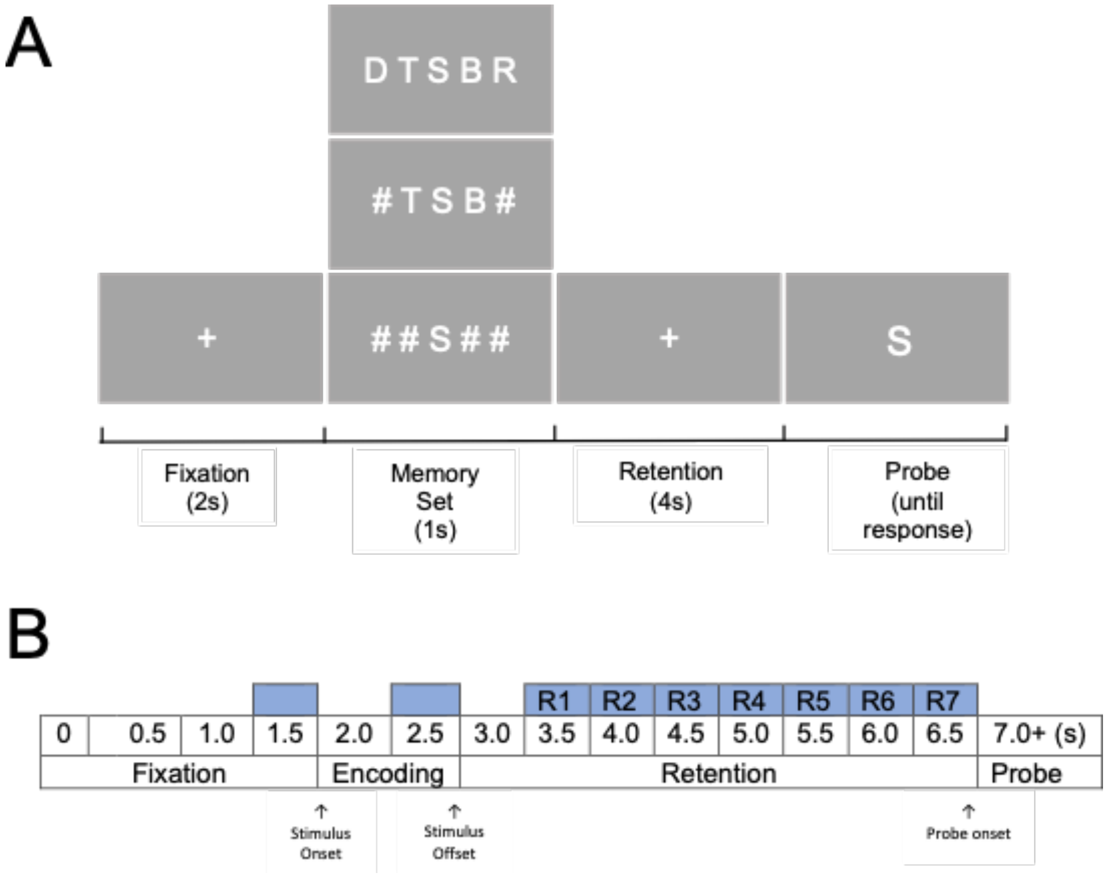

Figure 2.1: Task diagram. *(A) Modified Sternberg WM task. Each trial contained four stages, including fixation lasting for 2 s; encoding, where a 1, 3 or 5 load memory set was displayed for 1 s; a 4 s retention stage and a retrieval stage where the subject responded to whether the probe was part of the memory set. (B) Schematic for EEG analysis periods (shown in blue) for fixation, encoding and retention.*

2.3.3 EEG data acquisition

EEG data were recorded from a 64-channel cap containing Ag/AgCl scalp electrodes arranged in a 10-10 layout (Waveguard, ANT Neuro, Enschede, The Netherlands) using a Polybench TMSi EEG system (Twente Medical Systems International B.V, Oldenzaal, The Netherlands). Due to technical issues, data from the mastoids was not able to be recorded, and as such, data were recorded from 62 channels. Conductive gel was inserted into each electrode using a blunt-needle syringe in order to reduce impedance to < 5 kΩ. The ground electrode was located at AFz. Signals were amplified 20x, online filtered (DC-553 Hz) and sampled at 2048 Hz. Due to the lack of data from the mastoids, data were referenced to the average of all electrodes. EEG was recorded during each block of 15 trials of the WM task.

2.3.4 Data pre-processing

Task EEG data were pre-processed using EEGLAB (Delorme & Makeig, 2004) and custom scripts using MATLAB (R2018b, The Mathworks, USA). Each block of EEG data was merged and incorrect trials, as well as trials with outlier RT (defined as >3xSD) were flagged for removal at the epoch stage.

Noisy and unused channels were then removed based on visual inspection, with an average of 2 channels removed from each age group (range old: 1-5, range young: 1-7). The data were then band-pass (1-100 Hz) and band-stop (48-52 Hz) filtered using zero-phase fourth-order Butterworth filters, down-sampled to 256 Hz and epoched -6s to 1s relative to the beginning of the probe. Only correct trials were included in further analysis. Independent component analysis (ICA) was then conducted using the FastICA algorithm (Hyvärinen & Oja, 2000), with the 'symmetric approach' and 'tanh' contrast function to remove artefacts resulting from eye-blinks and persistent scalp muscle activity. Data were then checked for remaining artefact via visual inspection and trials were removed if necessary (e.g. remaining blinks, non-stereotypic artefacts). Remaining trials were then split according to memory load condition.

After removing trials due to incorrect answers, outlier RTs or excessive artefact, on average, 254 trials were accepted in the final analysis for younger adults (range 171-294). 85 trials were retained in load-1 and load-3 and 84 in load-5. An average of 271 trials were accepted for final analysis for older adults (range 198-297). 91 trials were retained in load-1 and load-3, and 89 in load-5. A mixed effects linear model revealed a significant difference in the number of remaining trials across age groups $F_{1,52} = 9.0, p = .04$, but not across WM loads $F_{2,104} = 2.8, p = .07$, nor an age by load interaction, $F_{2,104} = 0.7, p = .50$.

2.3.5 Spectral analysis

FieldTrip toolbox (Oostenveld et al., 2011) was used to analyse task EEG data. Time frequency representations of power to a 0.5 Hz frequency resolution were performed using a multi-taper time-frequency transformation based on multiplication in the frequency domain, a time window 3 cycles long and a Hanning taper. Power was calculated for individual trials before averaging for each load condition. The first 0.5 s of the encoding and retention periods were excluded to avoid spectral contributions from stimulus evoked responses to the memory set (figure 1B) (Babu Henry Samuel et al., 2018; X. Wang & Ding, 2011).

To account for age-related slowing of alpha (Klimesch, 1999), the alpha band frequency range was defined for each participant based on their peak alpha frequency at each stage of the task (fixation, encoding, retention) and for each load. Alpha frequency range was defined as 2

Hz above and below the peak frequency between 6 to 13 Hz (Klimesch, 1999). Alpha power was then averaged over this frequency range and across parieto-occipital and occipital electrodes (PO7, PO5, PO3, POz, PO4, PO6, PO8, O1, Oz and O2) at each WM stage (fixation, encoding and retention; figure 1B), as well as during each 0.5 s segment of the retention period.

2.3.6 Statistical analyses

Statistical analyses were performed using R version 3.4.2. Mixed effects linear models were used to analyse the behavioural and neurophysiological data. For behavioural data, performance (RT or Kc) was the outcome variable, WM load and age were fixed effects and subjects as the random effect. To investigate whether cognitive reserve influenced behavioural performance in the older adult group, a mixed effects model was conducted with fixed effects of load and cognitive reserve group, RT or Kc as the outcome variable and subject as the random effect. For neurophysiological data, alpha power and alpha frequency were the outcome variable, age, WM load, WM stage and cognitive reserve (older adults only) were fixed effects and subjects as the random effect. Alpha power was log-transformed to normalise the data. Post-hoc pairwise t-tests were performed in case of significant main effects or interactions, with Bonferroni correction for multiple comparisons. Data were checked for normality using Shapiro-Wilk tests, and the residuals for the mixed effects models were examined via histograms and QQ plots. Associations between alpha power (calculated as a change from fixation) and task performance were performed using Spearman's correlation, as normality was violated in this case. In all tests, a p-value of less than 0.05 was considered statistically significant. Data were presented as mean ± SD in text and mean ± SEM in figures.

Cluster-based permutation tests were used to assess topographical differences in alpha power between age groups at each WM stage and load, between WM stages, and interactions between WM stage and age group at each load. Cluster-based permutations control for the type 1 error rate when comparing across multiple channels (Maris & Oostenveld, 2007). Clusters were defined as two or more neighbouring electrodes for which the difference in alpha power between age groups (independent samples t-test) or between WM stages (dependent samples t-test) exceeded $p < .05$. Identified clusters were tested for significance using a permutation distribution, which was generated by combining alpha power values from both age groups/WM stages into a single set, randomly partitioning into two subsets, and taking the largest cluster-level statistic (i.e. the sum of t-values within a cluster) from this random partition (Monte Carlo method; 2000 random permutations). If the cluster-level statistic observed from the original data was larger in absolute value than >95% of random partitions, then it was deemed significant (p < .05, two-tailed).

2.4 RESULTS

2.4.1 Behavioural results

While all participants performed the task successfully, task performance differed between memory load and age groups. A mixed effects linear model revealed significant main effects of age ($F_{1,52} = 47.5, p < .001$) and load ($F_{2,104} = 241.3, p < .001$) on RT, with a significant age by load interaction ($F_{2,104} = 17.8$, $p < .001$). Bonferroni corrected post-hoc tests revealed that younger adults responded significantly faster than older adults on load-1, load-3 and load-5 trials ($p < .001$ for all). Likewise, RT for load-5 trials was significantly slower than load-3 and load-1 trials, and load-3 was significantly slower than load-1 in both age groups ($p < .001$ for all) (figure 2A).

To examine the interaction between age and load on RT, we examined the change in RT relative to load-1 between age-groups. A mixed effects linear model revealed significant main effects of age ($F_{1,52} = 18.97, p < .001$) and load ($F_{2,52} = 94.96, p < .001$) on RT, with a significant age by load interaction ($F_{2,52} = 15.88$, $p < .001$). Bonferroni corrected post-hoc tests revealed that the increase in RT from load-1 to load-5 was larger in older adults compared to younger adults ($p < .001$). The increase in RT from load-1 to load-3 did not differ between age groups ($p = .16$) (figure 2B). Likewise, a model investigating the effect of age and load on WM capacity revealed a main effect of load ($F_{2,104} = 1959, p < .001$). There was no significant main effect of age ($F_{1,52} = 1.03, p = .32$), nor a significant interaction between age and load ($F_{2,104} = 0.78, p = .46$) (figure 2C).

A composite score of education years and NART results was used to calculate cognitive reserve in the older adults. The average score on the NART was 38.7 ± 5.25, which corresponds to an average pre-morbid verbal IQ of 106.6 ± 6.8. There was no significant difference in the age of the low and high cognitive reserve groups ($t_{28} = 0.27, p = .79$).

For RT, the model revealed a significant main effect of load ($F_{2,56} = 123.4$, $p < .01$), but no main effect of cognitive reserve ($F_{1,28} = 0.92$, $p = .34$), nor a load by cognitive reserve interaction ($F_{2,56} = 0.62, p = .54$) (figure 2D).

For WM capacity, the model revealed a significant main effect of load ($F_{2,56} = 1604, p < .001$), a significant main effect of cognitive reserve ($F_{1,28} = 6.83, p = .014$) and a significant load by cognitive reserve interaction ($F_{2,56} = 4.58$, $p = .014$). Bonferroni corrected post-hoc tests revealed that on average, older adults with higher cognitive reserve had higher WM capacity than those with lower cognitive reserve (*p* = .014). Likewise, older adults with higher cognitive reserve had higher WM capacity in load-5 trials (*p* < .001). No significant differences in WM capacity were found between the high and low cognitive reserve group in load-3 (*p* = .99) or load-1 (*p* = .99) trials (figure 2E).

Given that prior studies have demonstrated sex differences in verbal WM performance at high loads (Reed et al., 2017), we examined whether sex differences in RT and accuracy were present in our sample. A mixed effects linear model revealed no main effect of sex on RT ($F_{1, 50} = 0.49$, $p = .48$), nor interactions between sex and age ($F_{1, 50} = 0.11$ $p = .74$), sex and load ($F_{2, 100} = 0.35$, $p = .70$) or age, sex and load ($F_{2, 100} = 3.1$, $p = .51$). Likewise, there was no main effect of sex on accuracy ($F_{1, 50} = 1.2$, $p = .28$), nor interactions between sex and age ($F_{1, 50} = 0.14$, $p = .71$), sex and load ($F_{2, 100} = 1.6$, $p = .21$), or age, sex and load ($F_{2, 100} = 0.08$, $p = .92$).

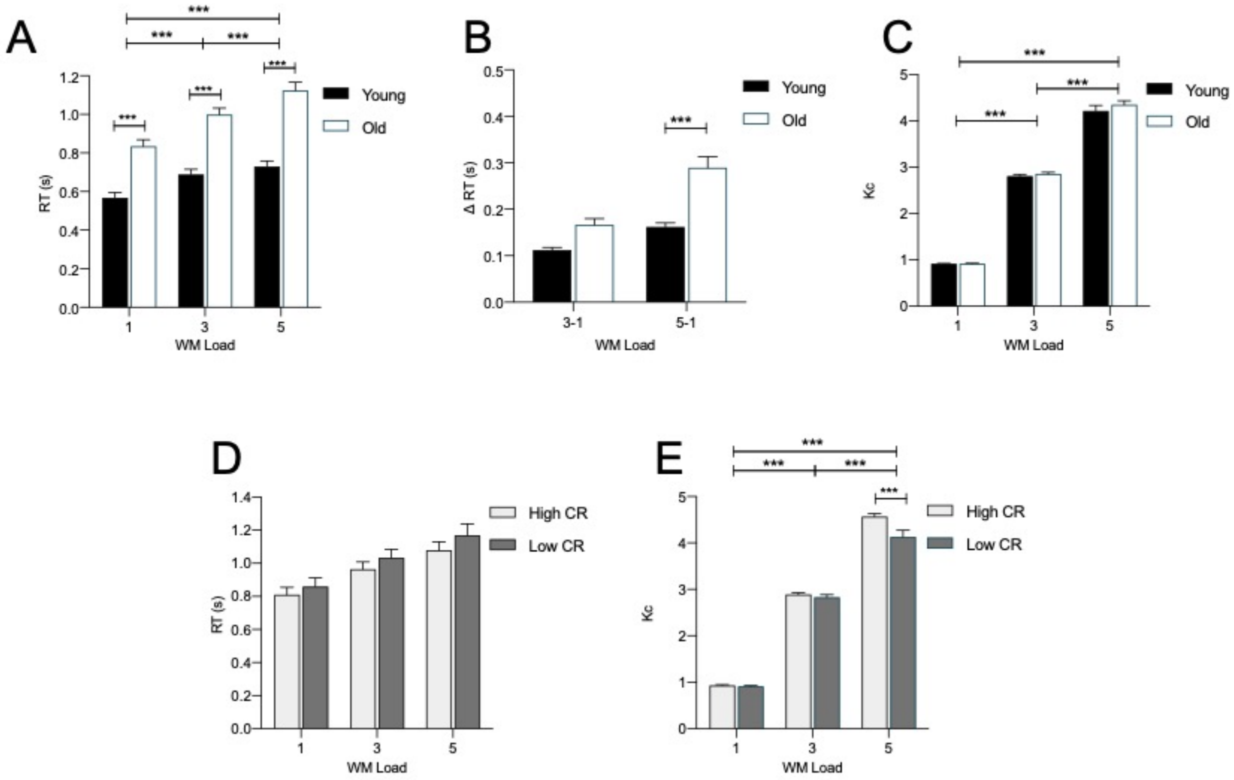

***Figure 2.2: Behavioural data**. (A) RT for correct responses, (B) change in RT from load-1, and (C) Cowan's K for each WM load in younger and older adults. (D) RT for correct responses and (E) Cowan's K for older adults with high and low cognitive reserve. * p <0.05 ***p<0.001.*

2.4.2 Alpha frequency and power modulation

Time frequency representation of power for young and older adults at each load are shown in figure 3.

Participants in which an alpha peak was not detected at any WM stage or load were excluded from analysis of alpha peak frequency (4 older adults). A linear mixed effects model revealed significant main effects of age ($F_{1,48} = 4.7, p = .04$), WM stage ($F_{2,347} = 8.0, p < .001$) and load ($F_{2,347} = 5.8, p = .009$). There were no significant interactions. Bonferroni corrected post-hoc tests revealed that on average, older adults had lower alpha frequency than younger adults ($p = .04$) (figure 3B). Alpha frequency was significantly higher in load-5 compared with load-1 trials ($p = .008$), but was not different between load-3 and load-5 trials or load-1 and load-3 trials (Figure 3C). Alpha frequency was significantly higher during encoding compared with fixation ($p = .006$) and retention ($p = .003$), but did not differ between retention and fixation (Figure 3D).

Alpha power was calculated using individual peak frequency at each WM stage (fixation, encoding, and retention) for each load. If a peak was not found in the retention period, the value for fixation was used to determine the frequency band for power calculations. If no peaks were found in any WM stage, the participant was excluded from further analysis (4 older adults). A mixed model revealed main effects of age ($F_{1,48} = 13.5, p < .001$), WM stage ($F_{2,384} = 240.4, p < .001$) and load ($F_{2,384} = 16.6, p < .001$), as well as an age x WM stage ($F_{2,384} = 3.6, p = .03$) and WM stage x load ($F_{4,384} = 7.1, p < .001$) interaction. Bonferroni corrected post-hoc tests revealed that overall, alpha power was significantly lower in older adults compared with younger adults ($p < .001$) (figure 3B). Alpha power was significantly higher in load-1 trials compared with load-5 trials ($p < .001$), in load-3 trials compared with load-5 trials ($p < .001$), but not different between load-1 and load-3 trials (figure 3C). Alpha power was significantly lower during encoding compared with both fixation ($p < .001$) and retention ($p < .001$), and alpha power during retention was significantly lower than in fixation ($p = .03$) (figure 3D).

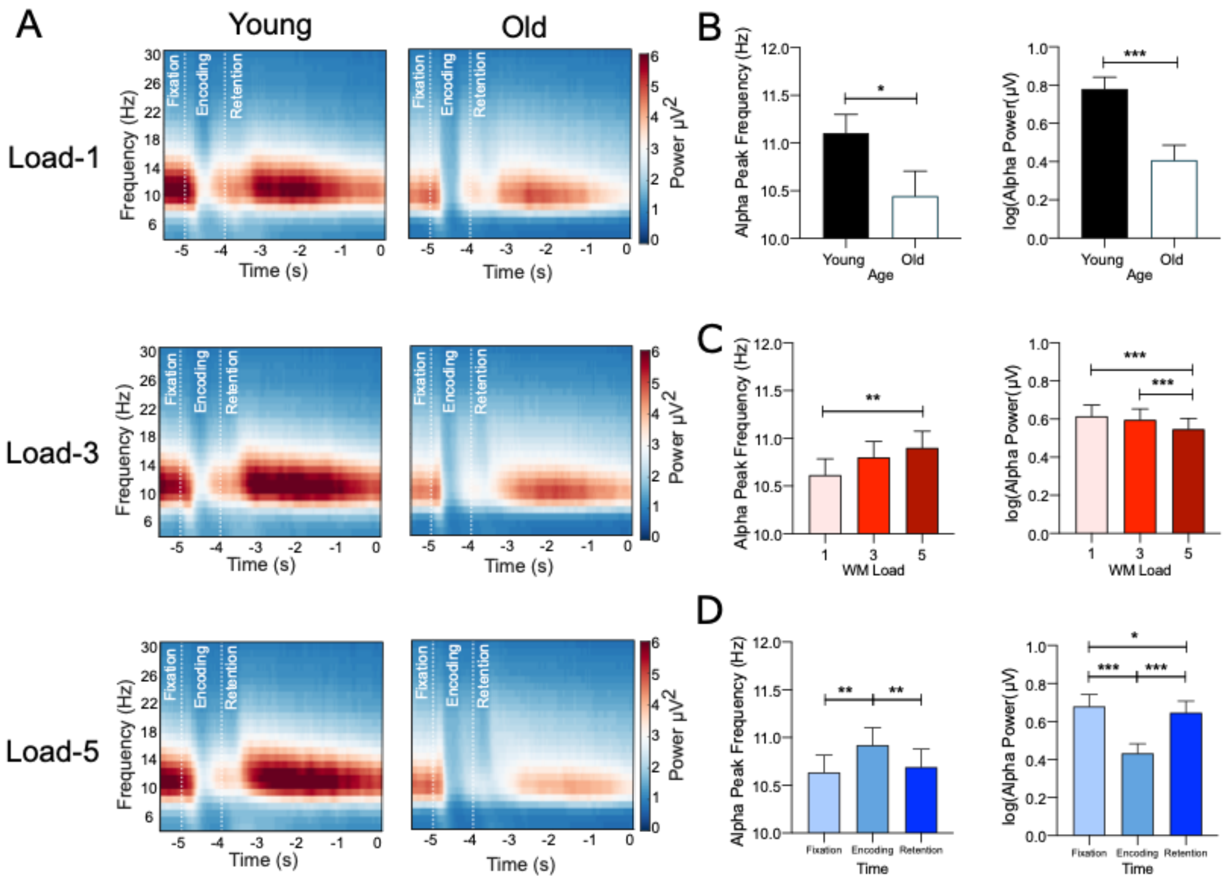

Figure 2.3: Alpha power and frequency during the WM task. *(A) Raw time frequency representations of power for each WM load and age group (B-D). Peak alpha frequency (left) and alpha power (right) between (B) age groups, (C) WM load and (D) stages of the WM task. * p <0.05, ** p <0.01, *** p<0.001*

To examine the interaction between age and WM stage, mixed models were conducted separately in each age group with alpha power as the outcome variable, WM stage as the fixed effect and subject as the random effect. In older adults the model was significant ($F_{2,206} = 105.3$, $p < .001$), with Bonferroni corrected post-hoc tests revealing that for older adults, alpha power was significantly lower during encoding compared with fixation ($p < .001$) and retention ($p < .001$), and that alpha power during retention was significantly lower than during fixation ($p = .003$). The model was also significant in younger adults ($F_{2,190} = 108.8$, $p < .001$), with Bonferroni corrected post-hoc tests revealing that for younger adults, alpha power during encoding was lower compared with both fixation ($p < .001$) and retention ($p < .001$), but there was no difference between fixation and retention (figure 4A). However, an independent samples t-test revealed that the change in alpha power from fixation to retention was not significantly different between age groups ($t_{42} = -1.4$, $p = .17$).

To investigate the interaction between WM stage and load, a mixed model was conducted for each WM stage, with load as the fixed effect and subjects as the random effect. For alpha power during the fixation period, the model was significant ($F_{2,98} = 3.4$, $p = .004$), though Bonferroni corrected post-hoc tests revealed no differences in alpha power between loads. For alpha power during encoding, the model was significant ($F_{2,98} = 66.3$, $p < .001$). Bonferroni corrected post-hoc tests revealed that during encoding, alpha power decreased with increasing memory load (all comparisons $p < .001$). For alpha power during retention, the model was significant ($F_{2,98} = 11.7$, $p < .001$). Bonferroni corrected post-hoc tests revealed that during retention, alpha power was significantly lower in load-5 trials compared with both load-1 ($p = .002$) and load-3 trials ($p < .001$), but did not differ between load-1 and load-3 trials (figure 4B).

When examining the effect of cognitive reserve group on alpha activity in older adults, the model for alpha frequency revealed no significant main of WM stage ($F_{2,\,157} = 1.71$, $p = .18$), cognitive reserve group ($F_{1,\,24} = 2.07$, $p = .16$) or load ($F_{2,\,15} = 2.36$, $p = .097$), and no significant interactions. For alpha power, the model revealed main effects of WM stage ($F_{2,\,192} = 118.6$, $p < .001$), load ($F_{2,\,192} = 10.7$, $p < .001$) and a WM stage by load interaction ($F_{4,\,192} = 3.75$, $p = .006$), but no main effects or interactions involving cognitive reserve ($p \geq .41$ for all).

2.4.3 Retention period time course

For closer inspection of the temporal changes during the retention period, we calculated alpha power and peak frequency for each 0.5 s segment of the retention period. Only participants who had an alpha peak at each time point during the retention period were included in this analysis (19 older adults, 23 younger adults).

A mixed model with peak alpha frequency as the outcome, age, load and time as fixed effects, and subjects as the random effect revealed main effects of time ($F_{7,982} = 20.2$, $p < .001$) and load ($F_{2,982} = 23.0$, $p < .001$). There were no other significant main effects or interactions. Bonferroni corrected post-hoc tests revealed that in R1 (i.e. 0.5-1 s from the start of the retention period), alpha frequency was higher than in all subsequent time increments (all $p < .001$). Likewise, alpha frequency was higher in load-5 during retention when compared with load-1 ($p < .001$) and load-3 ($p < .001$) (figure 4C).

A mixed model with alpha power as the outcome, age, load and time as fixed effects, and subjects as the random effect, revealed main effects of age ($F_{1,440} = 109.4$, $p = .025$), time ($F_{3,440} = 16.7$, $p < .001$) and load ($F_{2,440} = 15.5$, $p < .001$). There were no significant interactions. Bonferroni corrected post-hoc tests revealed that older adults had lower alpha power during fixation and retention than younger adults (*p* = .007) (figure 4D and 4E). Alpha power was significantly greater in the fixation period compared with each time point except R1. Further, alpha power was lower in load-5 trials compared with load-1 (*p* < .001) and load-3 (*p* < .001), but there were no differences between load-1 and load-3 (figure 4D and 4E).

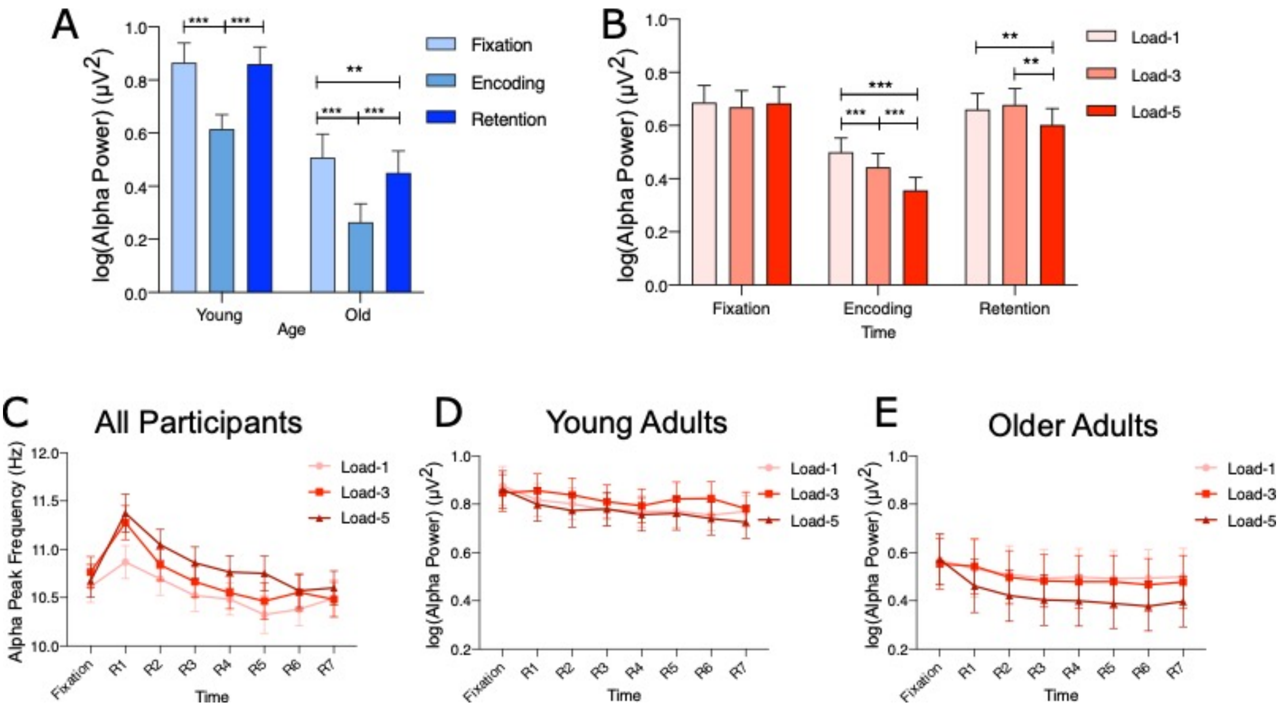

Figure 2.4: Interactions between age group, load, and task stage. *Alpha power modulation during the stages of the WM task between age groups (A) and WM loads (B). (C) Alpha peak frequency modulation across time and load during fixation and retention for all participants. (D-E) Alpha power modulation across time and load during fixation and retention for (D) young and (E) older adults. * p <0.05, ** p <0.01, *** p<0.001*

2.4.4 Relationship between alpha power and frequency on task performance

Spearman correlation analyses revealed no significant association between alpha power during the encoding or retention period (relative to fixation) and RT or WM capacity for all WM loads in both age groups (table 1). Likewise, there was no significant relationship between alpha frequency and RT at each load for younger (*p* > .23 for all) and older (*p* > 0.22 for all) adults.

Table 1. Associations between WM performance and alpha power. *Coefficients for correlations between RT and WM capacity (Kc), and alpha power during encoding and retention, relative to fixation, at each WM load for younger and older adults.*

		Encoding				**Retention**			
		Young		**Old**		**Young**		**Old**	
		RT	Kc	RT	Kc	RT	Kc	RT	Kc
Load-1	*rho*	-0.17	0.15	0.10	-0.09	-0.16	0.01	0.02	-0.17
	p	0.43	0.48	0.62	0.45	0.45	0.98	0.94	0.42
Load-3	*rho*	-0.21	0.24	-0.09	-0.20	-0.20	-0.12	0.01	-0.09
	p	0.33	0.26	0.68	0.34	0.34	0.59	0.97	0.67
Load-5	*rho*	-0.28	0.13	-0.06	-0.22	-0.22	-0.23	-0.02	0.02
	p	0.18	0.54	0.75	0.31	0.29	0.29	0.92	0.93

To further examine whether alpha frequency and power influenced WM performance, we sorted trials within each subject to a high or low RT group according to a median. Alpha frequency and power were then averaged over each RT group for each load during the encoding and retention periods. A mixed model with alpha frequency as the outcome, age, load, WM stage and RT group as fixed effects and subject as the random effect revealed a main effect of age ($F_{1,50} = 12.37$, $p < .001$), but no main effects or interactions involving RT group ($p \geq .09$ for all). Likewise, a mixed model with alpha power as the outcome revealed main effects of WM stage ($F_{1,572} = 646.2$, $p < .001$), age ($F_{1,52} = 13.77$, $p < .005$) and load ($F_{2,572} = 26.26$, $p < .001$), but no main effects or interactions involving RT group ($p \geq .08$ for all).

2.4.5 Scalp distribution of alpha power

In order to rule out the effect of topographical shifts in our data and determine whether electrodes other than those in the parieto-occipital/occipital region showed similar patterns of alpha activity during the task, we investigated whether the spatial distribution of alpha power (averaged over individualised alpha bands) differed between age groups at each WM stage and load. Likewise, given that our task involved verbal, rather than visual WM, to determine whether the pattern of alpha power changes we observed during the task were similar in nonposterior electrodes, we compared 500 ms of the encoding and retention periods (R4 time point) with fixation, within each age group.

After averaging the alpha frequency band (+/- 2 Hz peak alpha frequency), cluster-based permutation tests revealed no significant differences in the spatial distribution of alpha power between age groups at any WM stage or load (no significant clusters) (figure 5). Therefore, we did not find evidence to suggest that the raw alpha power scalp distributions differ across age groups.

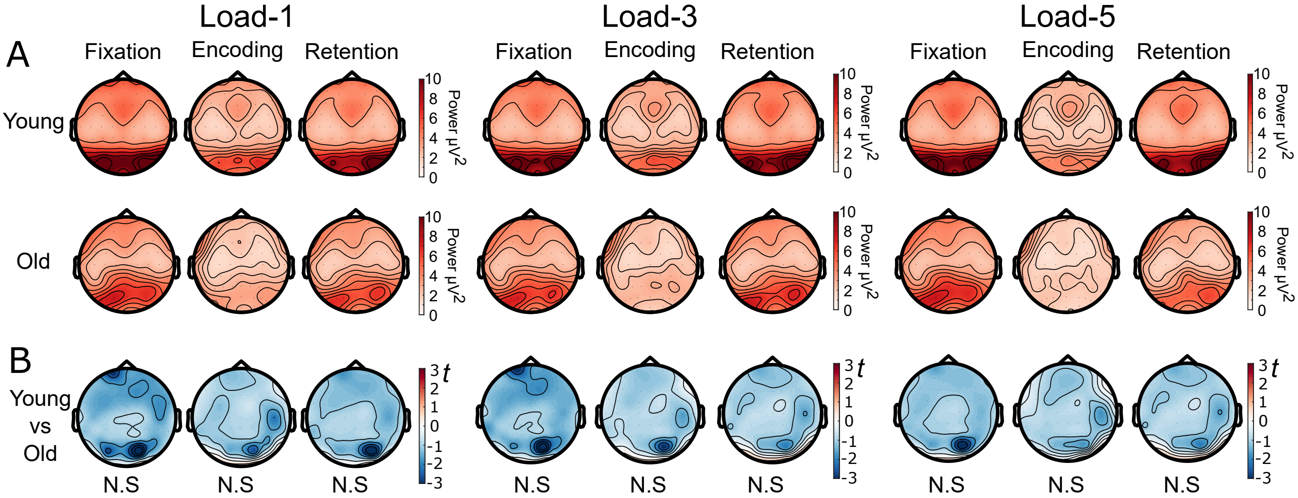

Figure 2.5. Raw alpha power. *(A)Topographical representation of raw power for young and older adults at each WM load and stage. (B) t-statistics for cluster-based permutation tests for age comparisons at each WM stage and load.*

In both age groups, cluster-based permutation tests revealed a significant decrease in alpha power in encoding from fixation in load-1, load-3 and load-5 trials (all comparisons $p < .001$). Conversely, significant increases in alpha power in retention from fixation were seen in load-3 for both younger ($p = .03$) and older ($p = .04$) adults, which were most pronounced over the right parietal, parieto-occipital and occipital electrodes. No significant differences between fixation and retention were seen in load-1 in younger ($p = .08$) or older ($p = .10$) adults. While no significant differences between fixation and retention were seen in load-5 for young adults, there was a significant decrease in alpha power from fixation in older adults ($p = .03$), most pronounced in the left centro-parietal, central and fronto-central electrodes. However, changes in alpha power between WM stages did not differ between age groups at any load (no significant clusters) (figure 6).

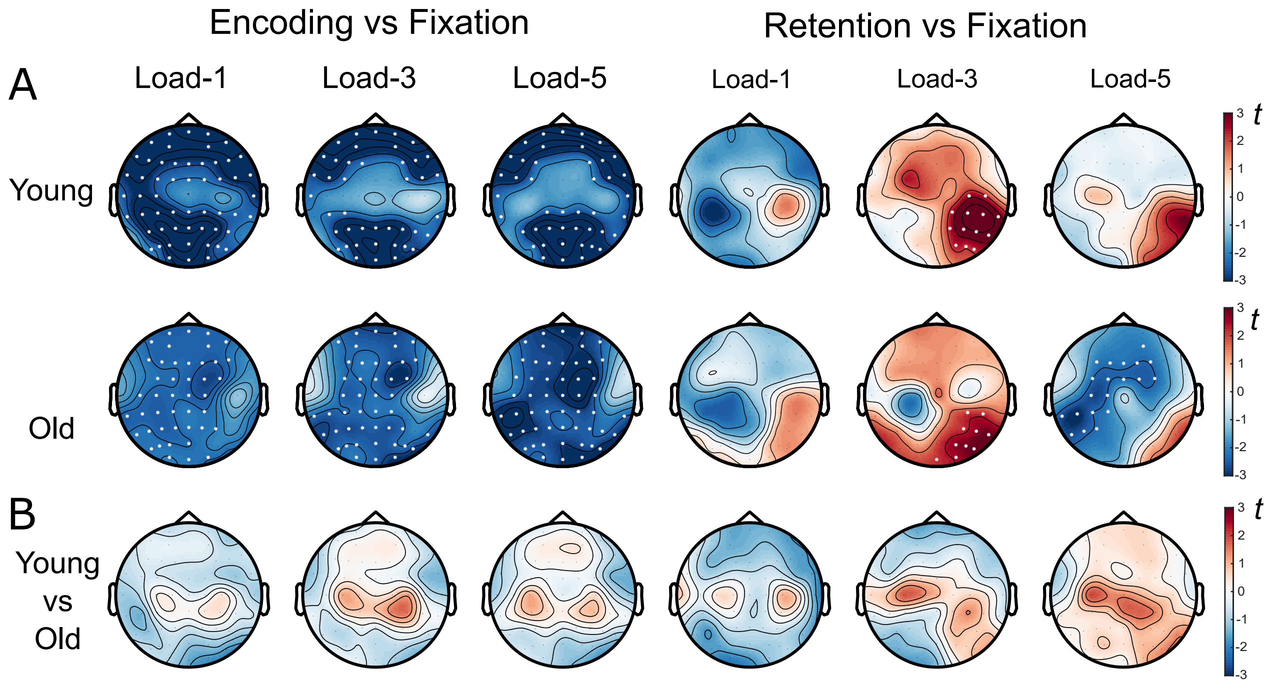

Figure 2.6. ***Results of cluster-based permutation tests.*** *(A) t-statistics for cluster-based permutation tests for encoding and retention compared with fixation at each WM load and each age group. (B) t-statistics for cluster-based permutation tests for an interaction effect between age groups and the difference between encoding and retention from fixation, at each WM load.*

2.5 DISCUSSION

In this study, we investigated age-related differences in visual alpha power and frequency during the encoding and retention stages of WM in response to varying loads. Behaviourally, older adults were slower to respond at all WM loads compared to younger adults, but there were no age differences in WM capacity. However, older adults with higher cognitive reserve performed better on load-5 trials compared with those with lower cognitive reserve. Overall, both alpha frequency and power were lower in older adults than in younger adults in each WM stage. During encoding, alpha power decreased with increasing WM load and alpha frequency increased. Regardless of age, alpha power was lower in load-5 than in load-1 and load-3 trials, but alpha frequency increased with load during retention. While alpha power during retention was lower than fixation in older, but not younger adults, the relative change from fixation was not significantly different between age groups. Further, individual differences in visual alpha power did not predict individual task performance within age groups, at any WM loads.

2.5.1 At all WM loads, older adults are slower to respond to the probe than younger adults, but WM capacity does not differ across age groups

As expected, older adults were slower to respond to the probe at all WM loads compared with younger adults. However, we found no age differences in WM capacity, with many participants from both age groups performing at near ceiling level. Therefore, the difference in RT in the older group likely does not reflect WM deficits, but rather age-related changes in processing speed (Salthouse, 1996). It has been shown that verbal WM might be more resistant to age effects than visual WM (Hale et al., 2011), and it is possible that our task was not difficult enough to capture age-differences. Taken together, we did not find strong evidence for working memory impairment with ageing in our sample, although this may be specific to the type of task performed.

2.5.2 Alpha power is modulated by load during the encoding and retention period for both younger and older adults

Alpha suppression occurred during the encoding period in both age groups, with a strengthening of this response with increasing WM load. Alpha suppression has long been thought to reflect attentional processes (Klimesch, 1997), as when attention is directed to external visual events, alpha power in visual cortex decreases with increasing attention demands (Rajagovindan & Ding, 2010; Sauseng et al., 2005). Therefore, a decrease in alpha power during encoding likely reflects an increase in cortical excitability to enhance stimulus processing (Heinrichs-Graham & Wilson, 2015; Klimesch, 1997; Murphy et al., 2019; Romei et al., 2010; Thut et al., 2011). Although alpha power was lower in older relative to younger adults, our results suggest that alpha suppression during encoding follows a similar pattern across age groups. This is consistent with previous studies that have shown that suppression processes during the encoding period, as indicated by alpha activity, remain relatively intact in older adults (Gazzaley et al., 2008). However, even though both age groups demonstrated poorer performance with increasing WM load, individual differences in alpha suppression during encoding did not support WM performance under varying loads in our task.

In both age groups, we found that alpha power decreased under higher WM loads during the retention period. This contrasts with the previously reported increase in visual alpha power during retention in younger adults completing modified Sternberg tasks (Jensen et al., 2002; Proskovec et al., 2019; Tuladhar et al., 2007; Wang et al., 2016). Though an increase in alpha power during retention has been interpreted to reflect inhibition of task irrelevant information, in lateralised tasks, alpha power decreases in task-relevant brain regions, but increases in task-irrelevant regions, and the magnitude of this reduction correlates with WM load (Sauseng et al., 2009). Likewise, in a study employing a delayed match-to-sample task, stronger alpha suppression during the retention period was seen under higher visual WM loads, which was interpreted to reflect increased activation of visual cortex to maintain the neural representation of remembered items (Fukuda et al., 2015). It is possible that the decrease in alpha power during retention for load-5 trials in the current study reflects specific features of the task and the strategies used by participants. Whereas encoding stimuli are presented sequentially in the classical Sternberg paradigm (Sternberg, 1966), our encoding stimuli were presented simultaneously, similar to the approach taken in visual WM delay match-to-sample tasks. Therefore, it is possible participants were using a visual strategy to retain the information in higher loads, leading to decreases in alpha power

In terms of age-related findings, our results contrast with a recent study employing a 6-letter modified Sternberg task, where it was observed that older adults exhibited a greater increase in visual alpha power during the retention period compared to younger adults (Proskovec et al., 2016). This was interpreted in that study to align with the Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH) (Reuter-Lorenz & Cappell, 2008), which suggests that generally, people recruit more brain regions when task-difficulty increases. Older adults are thought to recruit more cortical regions at lower loads than younger adults to compensate for cognitive decline. In our study, however, while younger adults demonstrated no difference in alpha power during the retention period compared with fixation, older adults demonstrated a decrease in power from fixation, regardless of load. While this difference in alpha power relative to fixation was not significantly different between age groups, if alpha suppression is indicative of the active maintenance of WM representations, the decrease in alpha power seen at load-5 in older adults may be another form of compensatory neural strategy.

Along with the characteristic decrease in alpha power and frequency, previous research has also shown a posterior to anterior shift in the topographic distribution of alpha with age (McEvoy et al., 2001).While we did not find evidence for age differences in the spatial distribution of alpha power during the task, we found that in the retention period of load-5 trials, older adults demonstrated a decrease in alpha power in left centro-parietal, central and fronto-central electrodes. It is possible that this decrease in alpha power may reflect engagement of brain regions involved in verbal processing (Rottschy et al., 2012), or potentially another form of compensatory strategy for older adults at higher WM loads.

However, there was no interaction between age group and the difference in alpha power between fixation and retention in load-5. As such, clarifying the role of alpha suppression during verbal WM and cognitive ageing is a topic for future research.

Further, studies investigating the alpha rhythm in both younger and older adults tend to define alpha as a narrow band (usually 8-12Hz) and average over spectral activity in that range for all subjects. Given that peak alpha frequency decreases with age, alpha power may fall outside of the fixed alpha frequency band, or activity in theta/beta frequencies may be included in the alpha window. Our results show that when alpha power is calculated based upon individual peak alpha frequency, the pattern of alpha activity across WM stages in older adults appears similar to that of younger adults but lower in magnitude, even when WM performance is matched to that of younger adults.

2.5.3 Age, task and load modulation of alpha frequency

Age has long been known as one of the most important factors influencing the frequency of the alpha rhythm (Klimesch, 1997). Resting state alpha peak frequency has been shown to be a stable neurophysiological trait in healthy younger and older adults (Grandy et al., 2013), however, it is becoming increasingly clear that alpha peak frequency shifts during cognitive tasks. In particular, a study employing an n-back task demonstrated a load-dependent increase in alpha frequency in healthy young adults (Haegens et al., 2014), while in a modified Sternberg task, a load-dependent decrease in alpha frequency during encoding and an increase during retention were apparent (Babu Henry Samuel et al., 2018).

One hypothesis that may explain the changes in peak alpha frequency during WM postulates that alpha frequency is a manifestation of an ‘internal clock’ which controls the brain’s speed of information processing (Klimesch et al., 1996). According to this theory, the higher the alpha frequency, the faster the cognitive processing, for example, during WM performance. In line with this, alpha frequency should increase with load during encoding to meet the sensory demands of encoding more information, and decrease with load during retention to reduce the rate of sensory processing, as slower alpha frequency may allow for longer windows of suppression (Jensen & Mazaheri, 2010; Sadaghiani & Kleinschmidt, 2016), and therefore facilitate protection against interference during WM. Our results partially support this idea. We found an increase in alpha frequency during encoding, but while there was a decrease in alpha frequency in retention from encoding, we did not find evidence for a decrease from fixation. Likewise, while we did observe an overall decrease in alpha frequency as the retention period progressed, it was highest in load-5 trials. According to the internal clock theory, higher alpha frequency during retention should be counterproductive to performance, as presumably this reflects less inhibition to protect the WM store. The proposed deleterious role of high alpha frequencies was shown in a recent study which demonstrated that higher peak frequency during retention led to slower RT (Babu Henry Samuel et al., 2018). The link between alpha frequency and processing speed, however, depends on alpha power representing an inhibitory mechanism during retention- an idea which is inconsistent with the findings of this study. Therefore, determining the task-relevance of alpha peak frequency during WM is a topic for future research.

2.5.4 Cognitive reserve

Within the older adult group, we found that participants with higher composite cognitive reserve had a higher WM capacity at load-5, but not at load-3 and load-1, than those with low cognitive reserve. A previous study employing a verbal WM Sternberg task that increased in load from 1 to 7 reported similar results, with subjects with higher cognitive reserve performing more accurately in the task at higher loads than those with lower cognitive reserve (Speer & Soldan, 2015). However, within the older adult group, we did not see differences in alpha power or frequency during the task between cognitive reserve groups. Theoretically, it is proposed that cognitive reserve does not directly alter age-related neural changes, but rather modifies the behavioural outcome of these anatomical or physiological changes (Barulli & Stern, 2013). Our findings align with this interpretation, given that alpha frequency and power decreased with age at all loads, but the high cognitive reserve group were able to perform better at higher loads compared with the low cognitive reserve group. However, cognitive reserve may influence other oscillatory dynamics at rest and during task performance that were not investigated in this study, presenting an avenue for further investigation.

2.5.5 Limitations

There are several limitations of this study. First, the age range of the older adult sample is much larger (36 years) than the younger adult sample (17 years). Given that trajectories of change in cognitive performance are largely heterogeneous across older adults (Hayden et al., 2011), future work should take into account individual differences in age-related WM decline. Second, though the modified Sternberg task used in this study allowed the temporal delineation of the encoding and retention stages of WM, this task does not assess the manipulation of items in WM (Baddeley, 1992). Further research is required to expand upon whether alpha activity is altered with age during the manipulation component of WM processing. Third, when WM accuracy is high, values of *K* may underestimate WM capacity (Rouder et al., 2011). As participants in both age groups performed at a ceiling level, our task may not have been difficult enough to capture true WM capacity. Fourth, due to technical reasons, we were not able to collect clean data from the mastoids and opted to use average reference instead. We recognise that this may be a limitation when comparing our results to others in the literature. Finally, lower alpha power seen with age might be due to structural brain differences such as atrophy in cortical tissue seen with age, brain size or skull thickness which are not able to be accounted for or assessed with EEG (Frodl et al., 2001). Future work may investigate how structural brain changes influence oscillatory activity recorded during WM task performance.

2.5.6 Conclusion

Our results suggest that alpha power and frequency were reduced with advanced age; however, both frequency and power were modulated in a similar task- and load-dependent manner during WM in both younger and older adults. Additionally, these age-related changes in alpha do not differ based on an individual's composite cognitive reserve, even when WM performance differs across cognitive reserve groups. Future research should elaborate the functional significance of alpha power and frequency changes that accompany WM performance in cognitive ageing.

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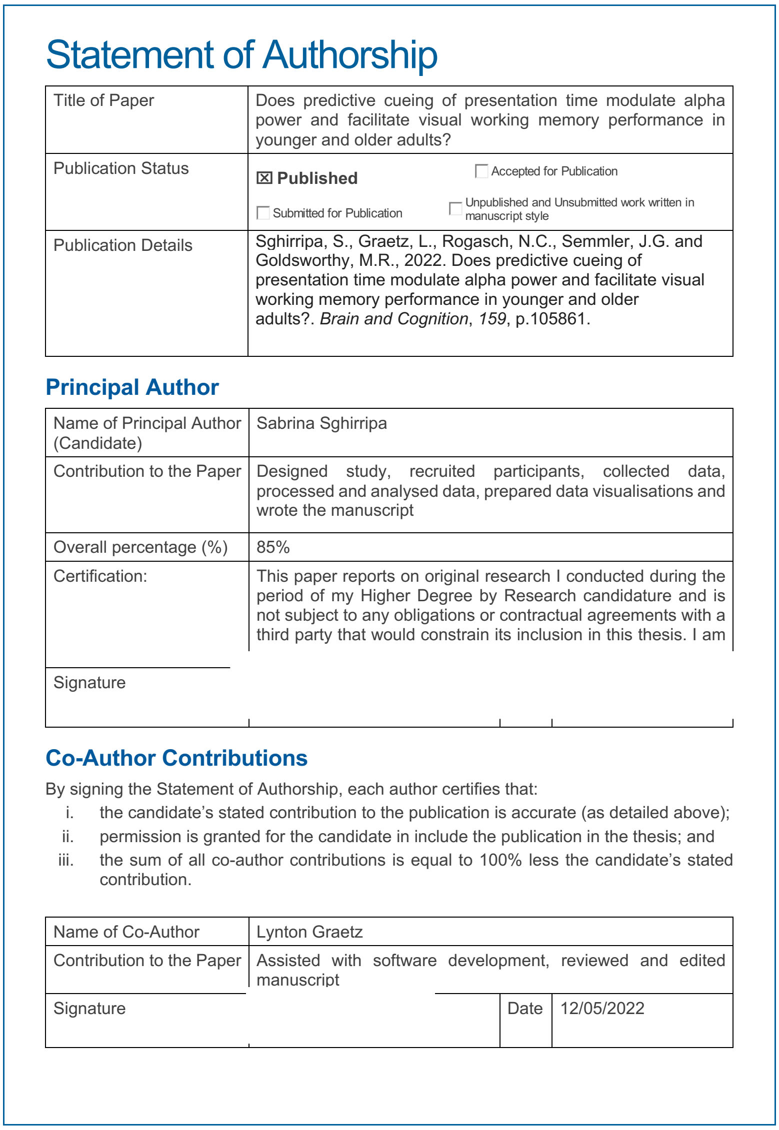
Chapter 3: Does predictive cueing of presentation time modulate alpha power and facilitate visual working memory performance in older and younger adults?



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Overall percentage (%)	85%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am
Signature	

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
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3.1 ABSTRACT

Selective attention and working memory (WM) are vulnerable to age-related decline. Older adults perform worse on, and are less able to modulate alpha power (8-12Hz) than younger adults in tasks involving cues about 'where' or 'when' a memory set will appear. However, no study has investigated whether alpha power is modulated by cues predicting the presentation time of a memory set. Here, we recorded electroencephalography while 24 younger (18-33 years) and 23 older (60-77 years) adults completed a modified delay match-to-sample task where participants were cued to the duration of a memory set (0.1s or 0.5s). We found: (1) predictive cues increased WM storage; (2) no differences in preparatory alpha power between predictive and neutral cue types, but preparatory alpha suppression was weaker in older adults; (3) retention period oscillatory power differed between presentation times, but these differences were no longer present when comparing trial types from the onset of the memory set; and (4) oscillatory power in the preparatory and retention periods were unrelated to performance. Our results suggest that preparatory alpha power is not modulated by predictive cues towards presentation time, however, reductions in alpha/beta power during visual WM retention may be linked to encoding, rather than retention.

3.2 INTRODUCTION

Visual working memory (WM) refers to the ability to temporarily maintain and/or manipulate visual information in the mind for use in goal-directed behaviour (Baddeley, 1992). Given that visual WM resources are limited (Cowan, 2001; Luck & Vogel, 1997), it is important to selectively attend towards task-relevant, and away from task-irrelevant information to ensure successful WM performance (Gazzaley & Nobre, 2012). Both WM and selective attention are vulnerable to age-related decline, with older adults less able to use selective attention processes to guide the encoding of relevant stimuli during WM (Gazzaley et al., 2005). However, the neural mechanisms underlying such age differences are not well understood.

One concept thought to link WM and selective attention is top-down control, which underlies the ability to enhance neural activity in task-relevant, while suppressing activity in task-irrelevant brain areas (Gazzaley & Nobre, 2012). Top-down control can be encouraged during WM by providing a pre-stimulus, informative cue that predicts features of the task relevant for performance, such as where a stimulus will appear (e.g. to the left or right) (Posner, 1980; Sauseng et al., 2009), when it will appear (A. Nobre et al., 2007; K. Nobre, 2010) or what stimulus type (e.g. faces, scenes, coloured squares etc.) will be present in a trial (Bollinger et al., 2010). While some evidence suggests older adults are able to use spatial cues to guide WM performance (Mok et al., 2016), older adults are less able to use anticipatory processes to facilitate performance (Bollinger et al., 2010) and less able to use temporal cues in anticipation of an incoming stimulus during attention (Zanto et al., 2011) and WM tasks (Zanto et al., 2010), potentially implicating deficits in anticipatory top-down control in age-related WM performance decline.

For each of these cue types, oscillatory power in the alpha frequency range (8-12 Hz) has been linked to selective attention in response to the cue (Samaha et al., 2015; Thut et al., 2006; van Diepen et al., 2015; Zanto et al., 2011). In lateralised WM tasks where subjects attend to and memorise the information in a cued hemifield and ignore the information in the un-cued hemifield, visual alpha power tends to increase in the task-irrelevant hemisphere and decrease in the task-relevant hemisphere in both the cueing period (Sauseng et al., 2009) and the retention period (Leenders et al., 2018), suggesting a role of alpha power in both the suppression of task-irrelevant information and facilitation of visual WM processes. In tasks involving anticipation of stimuli, a decrease in alpha power is thought to represent increased visual cortex excitability for an impending stimulus (Romei et al., 2008, 2010; Zanto et al., 2020). For example, decreases in alpha power are seen before the onset of an expected stimulus in temporal attention tasks, and the magnitude of this response predicts behavioural performance (Hanslmayr et al., 2007; Praamstra et al., 2006; Rohenkohl & Nobre, 2011). Likewise, pre-stimulus alpha suppression has been shown to reflect pre-stimulus top-down processing in preparation for subsequent task performance (Min & Herrmann, 2007).

Given that advancing age is associated with progressive changes in the frequency and power of alpha oscillations (Klimesch, 1997; Rossini et al., 2007), an inability to modulate alpha oscillations in response to a cue may explain why older adults are less able to use predictive cues to facilitate WM performance (Gazzaley et al., 2005). Specifically, it has been shown that older adults show less alpha desynchronisation in expectation of when a stimulus will occur (Zanto et al., 2010, 2011).

One task feature that has not yet been manipulated in a cueing paradigm is the presentation time of memory sets in visual WM. Studies in younger adults have suggested that visual WM capacity for simple objects such as coloured squares does not depend on presentation time (Bays et al., 2011; Luck & Vogel, 1997). However, in a behavioural study manipulating presentation time to investigate the contribution of top-down control processes to WM performance, it was found that short presentation times were associated with disproportionately poorer WM performance in older, compared with younger adults (Sander et al., 2011). The performance deficit with shorter presentation times was suggested to reflect an inability for older adults to deploy time-consuming top-down control processes over visual input during encoding, leading to the use of automatic, low-level binding processes instead (Sander et al., 2011; Shing et al., 2010). However, as EEG was not collected in this study, the neural mechanisms underlying the ability to deploy top-down processing under varying presentation times are unclear.

Given that top-down control processes can be elicited prior to stimulus onset using predictive cues (Gazzaley & Nobre, 2012), and that alpha suppression is associated with pre-stimulus top-down processing (Min & Herrmann, 2007) and anticipation (Zanto et al., 2011), we hypothesise that a cue indicating the presentation time of the upcoming memory set may allow for earlier engagement of top-down control processes, indicated by pre-stimulus alpha suppression, to facilitate visual WM performance under short presentation times.

Therefore, the first aim of this study was to determine whether manipulating the presentation time during a visual WM task led to differences in WM performance in both younger and older adults, and whether predictive cues denoting the length of presentation time led to improved WM performance and modulation of alpha power in preparation of the memory set. Based on the results of Sander et al. (2011), we expected that WM performance would be better for trials with long presentation times in both age groups. However, as older adults are less able to use predictive cues to guide processing of an upcoming stimulus (Zanto et al., 2010, 2011), we expected younger adults to behaviourally benefit more from predictive cues than older adults. As alpha suppression is associated with pre-stimulus top-down control (Min & Herrmann, 2007) and older adults experience deficits in using top-down control to guide processing (Gazzaley et al., 2005), we expected that alpha power suppression in preparation of the memory set would be greater following predictive, compared with neutral cues, particularly when cued towards short presentation times, and that preparatory alpha power suppression would be greater in younger than older adults. Finally, we expected that alpha power suppression during the preparatory period would correlate with WM performance, with stronger alpha power suppression present in trials with correct relative to incorrect responses.

As a secondary aim, we were interested in exploring how alpha power during the retention period changes with presentation time. In verbal WM tasks such as Sternberg tasks, alpha power during the retention period increases with WM load (Jensen et al., 2002; Proskovec et al., 2019; Sghirripa et al., 2020). In visual WM tasks, however, alpha power tends to decrease with increased WM load during the retention period, and the level of suppression is linked to WM capacity (Fukuda et al., 2015; Sauseng et al., 2009). If longer presentation times allow more time for items to be ‘loaded’ into WM (Sander et al., 2011; Shing et al., 2010), then we hypothesise that alpha suppression during retention will be stronger in trials with longer presentation times.

3.3 METHOD

3.3.1 Participants

24 younger adults (mean age: 25.3 years, SD: 4.26 years, range: 18-33 years, 14 male) and 23 older adults (mean age: 66.7 years, SD: 4.48 years, range: 60-77 years, 8 male) participated in the study. The groups were similar in number of years of education (older adults: M= 16.1 years, SD = 4.04 years; younger adults: M = 15.8 years, SD = 1.54 years, $t_{45} = 0.29$, $p = 0.78$). Exclusion criteria were a history of neurological or psychiatric disease, use of central nervous system altering medications, history of alcohol/substance abuse, uncorrected hearing/visual impairment and for older adults, an Addenbrooke’s Cognitive Examination (ACE-III) score of less than 82 (Mioshi et al., 2006). All participants gave informed written consent before the commencement of the study, and the experiment was approved by the University of Adelaide Human Research Ethics Committee.

3.3.2 Working memory task

The modified delay match-to-sample task stimuli were presented using PsychoPy software (Peirce, 2007) (figure 1A). At the beginning of each trial, participants were provided with a cue that signalled whether the memory set would appear for a short (S; 0.1 s) or long period (L; 0.5 s) or received a neutral cue (N) which was not predictive of whether the presentation time would be short or long. We chose 0.1 s and 0.5 s for memory set presentation as these are popular choices in visual WM tasks involving coloured squares (Luck & Vogel, 1997), and is where performance plateaued in Sander et al. (2011). A fixation cross was then displayed for 1 s as a preparatory period. To favour voluntary orienting and expectation, we kept the period between the cue and memory set relatively long (Weinbach & Henik, 2012), and the memory set always proceeded the cue by 1 s. The memory set, consisting of 4 coloured squares, was displayed for either 0.1 or 0.5 s. To avoid the contribution of ignoring distractors on alpha power during the task (Fukuda et al., 2015), participants remembered items across both visual fields (i.e. a whole-field task with no accompanying distractors). The colour of each square was randomly selected from a set of 9 colours: black, white, red, blue, yellow, green, orange, cyan and magenta. Following a retention period of 1 s, a single probe square appeared in the location of a randomly selected square from the memory set. Participants were instructed to respond with the right arrow key if the probe square was the same colour in the memory set and respond with the left arrow key if the square was a different colour. In each block, 50% of the trials required a right arrow key response (same colour), and 50% required a left arrow key response (different colour). The probe remained on the screen until the participant responded. Participants received a practice block to familiarise themselves with the task, before performing 10 blocks of 40 trials, yielding 100 trials per condition (i.e., predictive short, neutral short, predictive long, neutral long). Each block contained an equal number of trials for each condition, presented pseudorandomly. A short break was allowed between blocks.

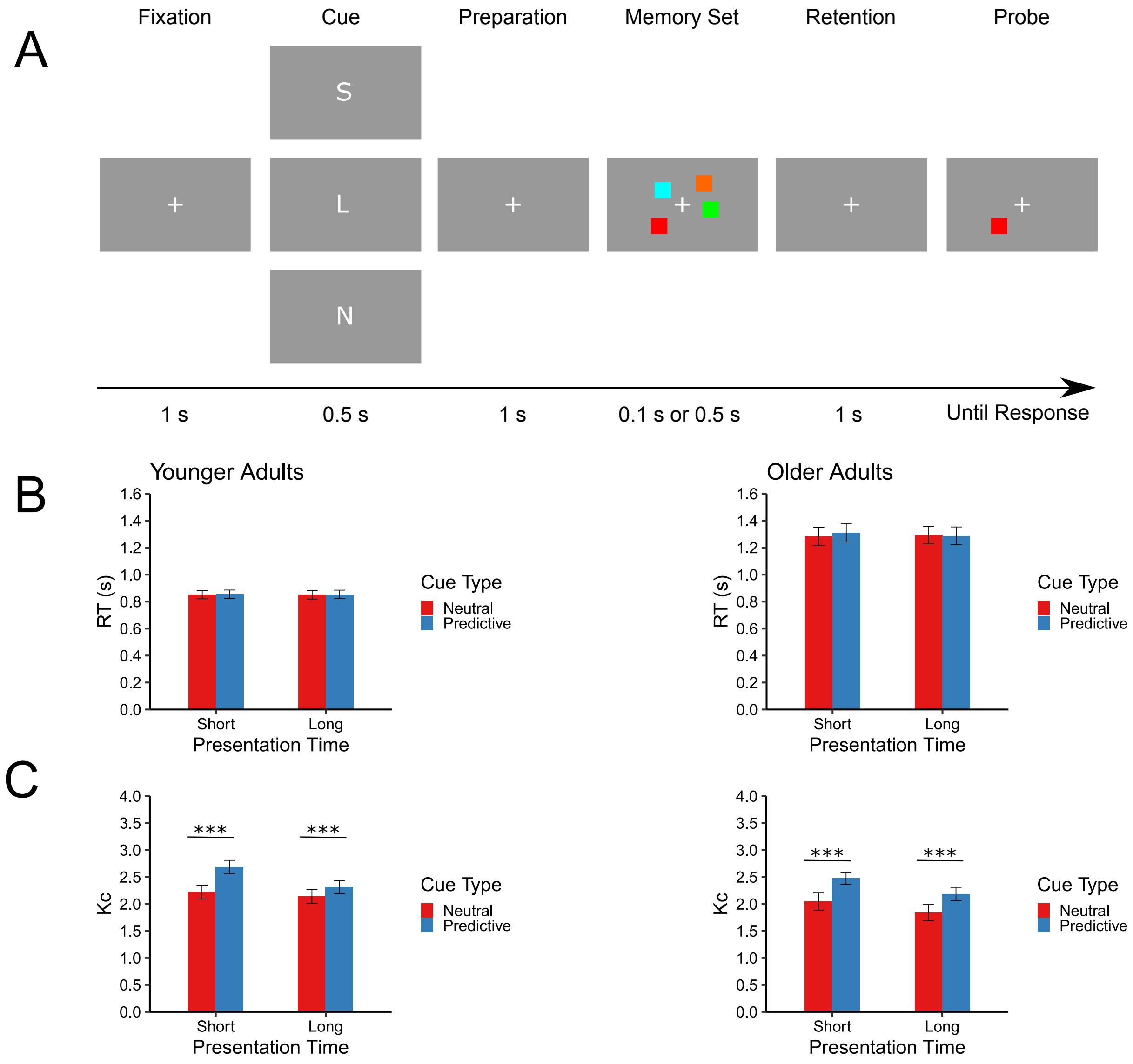

Figure 3.1. Task diagram and behavioural data. *A) Modified delay match-to-sample task. Participants were provided with a cue which indicated whether the encoding period would be short (0.1 s), long (0.5 s) or neutral (0.1 s or 0.5 s). After a 1 s retention period, participants indicated whether the probe square was the same colour seen in the encoding set. B)*

Response time (RT) (s) for each cue type and presentation time for younger (left) and older (right) adults. C) WM capacity (Cowan's Kc for) each cue type and presentation time for younger (left) and older (right) adults.

3.3.3 EEG data acquisition

EEG data were recorded with a 64-channel cap arranged in a 10-10 layout (Waveguard, ANT Neuro, Enschede, The Netherlands) using a Polybench TMSi EEG system (Twente Medical Systems International B.V, Oldenzaal, The Netherlands). Conductive gel was inserted into each electrode using a blunt-needle syringe to reduce impedance to <5 kΩ. The ground electrode was located at AFz. Signals were amplified 20x, online filtered (DC-553 Hz), sampled at 2048 Hz and referenced to the average of all electrodes. EEG was recorded during each block of the WM task.

3.3.4 Data pre-processing

EEG data were pre-processed using EEGLAB (v14.1.2) (Delorme & Makeig, 2004), TMS-EEG signal analyser (TESA v1.1.1) (Rogasch et al., 2017) and custom scripts using MATLAB (R2019b, The Mathworks, USA).

Each block of EEG data was merged into a single file and correct, and incorrect responses were identified for separation at the epoch stage. Data were then down sampled to 256 Hz and unused channels such as the mastoids were removed. Data were band-pass (0.2-100 Hz), and band-stop (48-52 Hz) filtered using the EEGLAB 'eegfiltnew' function, and epoched -2.5 s to 2.5 s relative to the beginning of the memory set. Channels and trials were then visually inspected and removed if contaminated with residual artefacts (e.g. muscle activity and non-stereotypical artefacts). An average of 1 channel was removed from each age-group (range young: 0-4, range old: 0-3). Independent component analysis (ICA) was then completed using the FastICA algorithm (Hyvärinen & Oja, 2000), with the 'symmetric approach' and 'tahn' contrast functions selected. Components corresponding to eye blinks and persistent muscle activity were detected using the TESA 'compselect' function and manually checked before being removed from the data. Missing channels were then interpolated, and data were again re-referenced to the common average. Epochs were then split into each condition type, and correct and incorrect trials were separated. For younger adults, an average of 80 correct trials were accepted for final analysis in the predictive short, 72 for neutral short, 73 for predictive long and 76 for neutral long conditions. For older adults, an average of 78 correct trials were accepted for final analysis in the predictive short condition, 72 for the neutral short, 71 for the predictive long and 70 for the neutral long conditions.

3.3.5 Time frequency analysis

FieldTrip (v20200820) (Oostenveld et al., 2011) was used for time-frequency analysis of EEG data. Data were converted to the time-frequency domain using a multi-taper transformation based on multiplication in the frequency domain (cfg.method = 'mtmconvol'). A time window of 3 cycles was used for each frequency (0.5 Hz steps between 3 and 45 Hz) and time point (50 ms steps). Spectral power was calculated for individual trials before being averaged over trials for each cue and presentation time condition. Data were baseline corrected to the fixation period (-2.5 to -2 before the onset of the memory set) using the dB method.

3.3.6 Statistical analysis of behavioural data

To quantify WM performance, both response time (RT) (s) for correct trials and Cowan's K as a measure of WM capacity were calculated for each condition. Cowan's K was defined as Kc = set size x (hit rate – false alarm rate) (Cowan, 2001).

Statistical analyses on behavioural data were performed using R version 3.4.2. In all tests, a p-value of < 0.05 was considered statistically significant. Data are presented as mean ± SD in text and mean ± SEM in figures.

Mixed effects linear models were used to analyse behavioural data. For these analyses, performance (RT or Kc) was the outcome variable; presentation time, cue type and age group were fixed effects; and subject was the random effect. Bonferroni corrected post-hoc pairwise t-tests were performed in the case of significant main effects or interactions. Data were checked for normality using Shapiro-Wilk tests, and the residuals for the mixed effects models were checked via histograms and QQ plots.

3.3.7 Statistical analysis of EEG data

Statistical analyses on EEG data were performed using Fieldtrip toolbox (Oostenveld et al., 2011). We used cluster-based permutation tests in order to control for the type 1 error rate when comparing across multiple channels, times and frequencies (Maris & Oostenveld, 2007). Clusters were defined as two or more neighbouring electrodes, time points or frequency bins for which the difference in spectral power between age groups (independent samples t-test) or between presentation times and cue types (dependent samples t-test) exceeded $p < .05$. Identified clusters were tested for significance using a permutation distribution, which was generated by combining spectral power values from both conditions into a single set, randomly partitioning into two subsets, and taking the largest cluster-level statistic (i.e., the sum of t-values within a cluster) from this random partition (Monte Carlo method; 2000 random permutations). If the cluster-level statistic observed from the original data was larger in absolute value than > 95% of random partitions, then, it was deemed significant (p < .05, two-tailed). Effect sizes (Cohen's *d*) were calculated for the average of all significant channels, frequencies and times for each task stage (cfg.method = 'analytic', cfg.statistic = 'cohensd').

We did not have an a-priori hypothesis regarding the time windows where alpha suppression may have occurred during preparation or retention, nor the electrodes where this effect may occur given that both parieto-occipital alpha and frontal alpha have respectively been linked to WM performance (Klimesch, 1999) and alertness (Sadaghiani et al., 2010). We also chose to include all electrodes in the analyses to account for any age-related shifts in the scalp distribution of alpha power (McEvoy et al., 2001). Likewise, as peak alpha frequency is known to change with age (Babiloni et al., 2006; Klimesch, 1997) and during task performance (Sghirripa et al., 2021), and both alpha and beta power have been implicated in attention and WM processes (Erickson et al., 2019; Griffiths et al., 2019), we used an extended 3-30 Hz frequency range and all electrodes in each test. Baseline corrected data were used in all analyses.

To test whether alpha power suppression in the preparatory and retention stages were greater for predictive compared to neutral cues in correct trials, we used cluster-based permutation tests to examine all electrodes across the 3-30 Hz frequency range over the 1 s preparatory and retention stage for each age group and presentation time separately. Using the same parameters, we tested whether age-differences existed in the preparatory and retention stages for both predictive and neutral cues across each presentation time by comparing the 3-30 Hz frequency range and all electrodes in younger and older adults.

To test for interactions between cue type and age-group for each presentation time and task stage for correct trials, we employed a 2x2 factorial design. A difference power spectrum was calculated, consisting of the difference between cue types for each age group (i.e., Young difference = Young/Predictive – Young/Neutral, Old difference = Old/Predictive – Old/Neutral), and then an independent samples t-test was performed on the difference power spectrums (Young Difference vs. Old Difference) for both short and long presentation times.

To determine whether oscillatory power during the preparation and retention periods influenced behavioural performance, we compared correct with incorrect trials from each participant across conditions. Cluster based permutation tests were used to compare correct and incorrect trials across the 3-30 Hz frequency range and all electrodes for each age group, cue type and presentation time.

3.4 RESULTS

3.4.1 Behavioural data

3.4.1.1 RT

For RT, there was a significant main effect of age ($F_{1,47} = 39.8$, $p < 0.001$), but no main effect of cue type ($F_{1,135} = 1.04$, $p = 0.31$), presentation time ($F_{1,135} = 0.25$, $p=0.62$) or any significant interactions (all $p>0.24$). Post-hoc tests revealed that RT was slower for older than younger adults ($p<0.001$) (figure 1B).

3.4.1.2 WM Capacity

For WM capacity, there was a significant main effect of presentation time ($F_{1,135} = 21.14$, $p < 0.001$) and a significant main effect of cue type ($F_{1,135} = 46.6$, $p < 0.001$). Bonferroni corrected post-hoc tests revealed that WM capacity was higher for predictive cues than neutral cues in each age group ($p<0.001$); however, contrary to expectations, WM capacity was higher, not lower, for trials with short presentations than long ($p<0.001$) (figure 1C). There was no significant main effect of age ($F_{1,45} = 1.54$, $p = 0.22$) or significant interactions involving age (all $p>0.13$), nor was there a presentation time by cue type interaction ($F_{1,135} = 3.30$, $p = 0.07$).

3.4.2 Fixation period

To ensure age-group analyses using baseline corrected data were not biased by age-related changes in oscillatory power, we first sought to determine whether age-differences in oscillatory power were present in the fixation period used for baseline correction. Cluster-based permutation tests revealed no evidence for a significant age-difference in oscillatory power in the fixation period of predictive short ($p = 0.09$, $d = 0.14$), predictive long ($p = 0.10$, $d = 0.12$), neutral short ($p = 0.30$, $d = 0.17$) or neutral long presentation trials ($p = 0.09$, $d = 0.13$).

3.4.3 Preparation period

We sought to determine whether oscillatory power differed across cueing conditions during the 1 s preparatory stage. Upon visual inspection of the time-frequency representations of power, we observed that across all conditions and in both age groups, oscillatory power for alpha and beta frequencies decreased during the preparatory period compared to baseline.

Cluster-based permutation tests revealed no evidence for a significant difference in alpha/beta power suppression during the preparatory period following predictive and neutral cues for either short (*p* = 0.78, *d* = 0.10) or long presentation trials (*p* = 0.96, *d* = 0.12) for younger adults (figure 2A). Likewise, we could not find evidence for a difference between predictive and neutral cue types for short (*p*=0.99, *d* = 0.05) or long presentation trials (*p*=0.99, *d* = 0.11) in older adults.

When investigating whether preparatory power differed between age groups, we found that in all conditions, older adults demonstrated less alpha/beta power suppression during the preparatory stage than younger adults. Specifically, older adults had less alpha/beta power suppression following both cue types for both short (predictive: p<0.001, *d* = 1.2, -1 to -0.4 s relative to the start of encoding, 8 to 25 Hz; neutral: p<0.001, *d* = 1.1, -1 to -0.6 s relative to the start of encoding, 8 to 30 Hz) (figure 2A) and long presentation times (predictive: p<0.001, *d* = 1.3, -1 to -0.6 s relative to the start of encoding, 8 to 30 Hz; neutral: p<0.001, *d* = 1.2, -1 to -0.6 s relative to the start of encoding, 8 to 30 Hz) (figure 2B), with the effect prominent across most electrodes in all conditions. However, there were no cue type by age group interactions for either short (*p* = 0.99, *d* = 0.03) or long presentation trials (*p* = 0.99, *d* = 0.21). Thus, while we could not find evidence for a difference in alpha/beta power between cue types, older adults demonstrated lower alpha/beta power than younger adults during the preparatory period in all conditions.

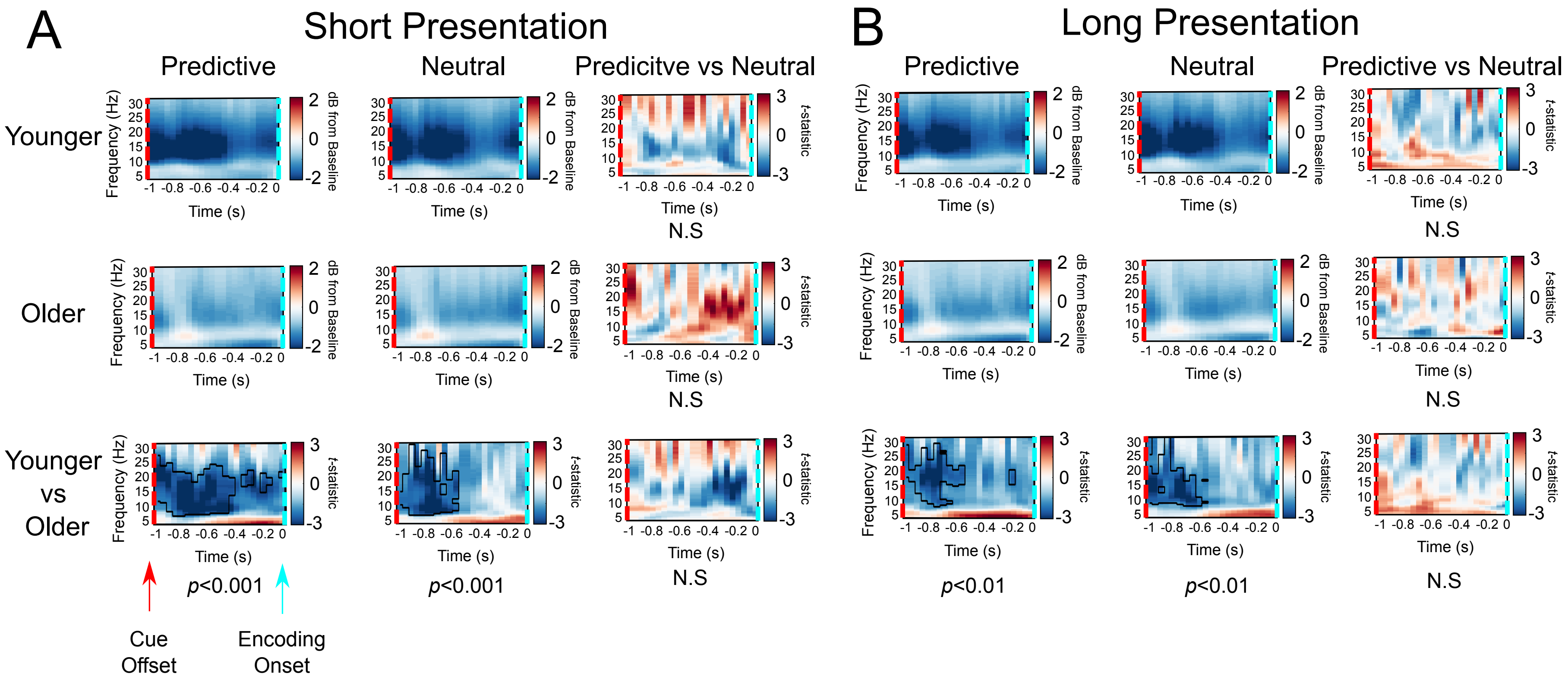

Figure 3.2. Preparation period. *Baseline corrected time-frequency representations of power during the preparation period for younger (top) and older adults (middle) in predictive and neutral trials, and t-statistics for younger vs. older adults (bottom), and predictive vs. neutral cues (right) for short (A) and long (B) presentation time trials. Significant clusters are plotted from PO4, and non-significant clusters are plotted from the average of all channels. Red dotted lines denote the offset of the presentation time cue, and light blue dotted lines denote the onset of the memory set.*

3.4.4 Retention period

3.4.4.1 Effect of Predictive Cueing on Retention Period Alpha/Beta Power in Young and Older Adults

We assessed whether oscillatory power differed across cueing conditions during the 1 s retention period. Upon visual inspection of the time-frequency representations of power, we observed that oscillatory power for alpha and beta frequencies decreased during the retention period compared to baseline across all conditions and in both age groups.

When comparing predictive and neutral cue conditions for short presentation trials in younger adults, we found less alpha/beta power suppression in predictive compared to neutral trials during the retention period (p=0.03, d = 0.64, 0.5 to 0.8 s relative to the start of encoding, 10 to 22 Hz). Similarly, there was less alpha/beta suppression during retention in trials predictive of a long presentation compared with trials with a neutral cue across all electrodes (p=0.01, d = 0.81, 1.3 to 1.5 s, 10 to 30 Hz). However, no differences in the retention period were seen between predictive and neutral cues for both short (p=0.45, d = 0.23) and long (p=0.95, d = 0.1) presentation trials for older adults.

When comparing age groups, we found that younger adults demonstrated stronger alpha/beta suppression during retention in short presentation trials with both predictive (p=0.04, d = 0.73, 0.1 to 0.7 s, 10 to 30 Hz) and neutral cues (p=0.02, d = 0.82, 0.1 to 0.7 s, 10 to 30 Hz) compared to older adults. Conversely, no significant age differences were seen during retention for long presentation trials with either a predictive (p=0 .08, d = 0.53) or neutral (p=0.053, d = 0.54) cue. There were no interactions between cue type and age for either short (p=0.79, d = 0.40) or long presentation trials (p=0.53, d = 0.31).

Therefore, while we found evidence for an effect of cue type on alpha and beta power during the retention period of both short and long presentation trials in younger adults, no such effect was seen in older adults. In short presentation trials however, younger adults demonstrated stronger alpha/beta power suppression during retention than older adults, regardless of cue type.

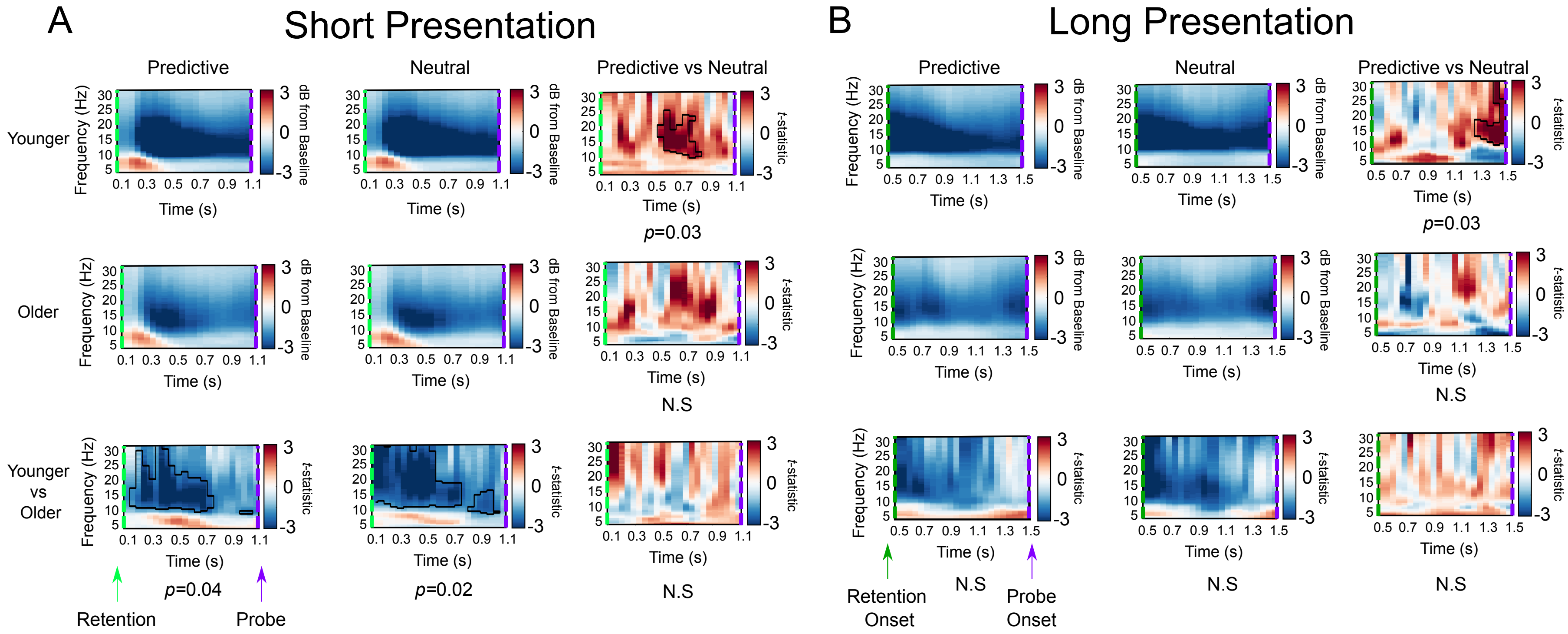

Figure 3.3. Retention period. *Baseline corrected time-frequency representations of power during the retention period for younger (top) and older adults (middle) in predictive and neutral trials, and t-statistics for younger vs. older adults (bottom), and predictive vs. neutral cues (right) for short (A) and long (B) presentation trials. Significant clusters are plotted from PO4. Light green dotted lines represent the onset of the retention period in short presentation time trials. Dark green dotted lines represent the onset of the retention period in long presentation time trials. Purple dotted lines reflect the onset of the probe.*

3.4.4.2 Effect of Presentation Time on Retention Period Alpha/Beta Power in Young and Older Adults

We next assessed whether presentation time influenced oscillatory power during the retention period for both age groups. We limited this analysis to short and long encoding presentation times with a neutral cue due to the influence of the cue on oscillatory power during the retention period.

When comparing the retention period of short and long presentation trials, we found significant differences across the broad frequency range in the early stages of the retention period, with increased theta power and less alpha/beta power suppression in the short, relative to long presentation trials for both younger ($p<0.001$, $d = 0.90$, 0 to 0.2 s, 3 to 30 Hz) and older adults ($p<0.001$, $d = 0.73$, 0 to 0.3 s, 3 to 30 Hz). This was followed by stronger alpha/beta power suppression from ~0.3 s until the end of retention for short, compared to long presentation trials for both age groups (younger: $p<0.001$, $d = 0.5$, 0.3 to 1 s, 10 to 30 Hz; older: $p=0.01$, $d = 0.7$, 0.3 to 0.8 s, 6 to 30 Hz) (figure 4A).

However, as an incidental finding, visual inspection of the time-frequency representations of power revealed little difference between presentation time conditions when viewing each condition from the beginning of encoding. When comparisons using cluster-based permutation tests were made relative to the start of encoding instead of the start of retention, we did not find evidence for a difference between short and long presentation trials in any frequency band or time period ($p=0.054$, $d = 0.02$ for young, $p=0.15$, d¬ = 0.03 for older) (figure 4B). This suggests that the differences in retention period oscillatory power between short and long presentation trials were caused by the time shift from having different memory set durations and may also indicate that the changes in oscillatory power observed during visual WM retention may reflect encoding of the stimulus, rather than a process specific to WM retention.

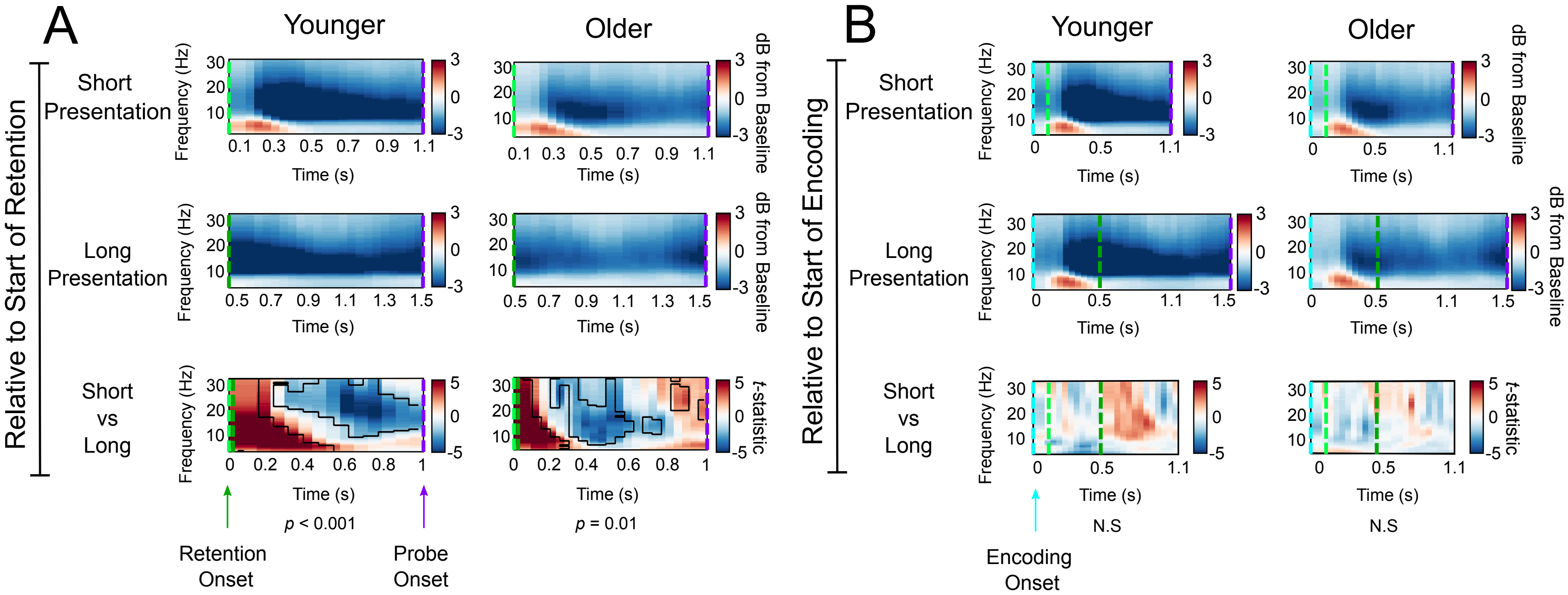

Figure 3.4. Comparison of oscillatory power from encoding and retention. *A) Time frequency representations of baseline corrected power relative to the onset of the retention period for neutral short (top) and long (middle) presentation time trials for young (left) and older (right) adults. The bottom row contains t-statistics for the comparison between short and long presentation time trials. B) Time-frequency representations of baseline corrected power relative to the start of the encoding period. Light green dotted lines represent the onset of the retention period in short presentation time trials. Dark green dotted lines represent the onset of the retention period in long presentation time trials. Purple dotted lines reflect the onset of the probe.*

3.4.5 Oscillatory power and task performance

To determine whether oscillatory power during the preparation and retention periods influenced behavioural performance, we compared correct with incorrect trials from each participant across conditions. Cluster-based permutation tests revealed no significant difference between correct and incorrect trials in any condition, for both age groups (all $p>0.32$, all $d<0.2$).

3.5 DISCUSSION

In this study, we investigated age-related differences in oscillatory power in response to predictive cues about the presentation time of an upcoming memory set, and how oscillatory power during the visual WM retention period varied with presentation time. Behaviourally, we found that for both age groups, predictive cues increased WM storage and, contrary to expectations, task performance was better in trials with short presentation times. While we found no evidence for differences in preparatory alpha power between trials with predictive and neutral cues for either short or long presentation times, younger adults demonstrated stronger suppression of alpha and beta power during the preparatory period in all conditions compared to older adults. During the retention period, alpha/beta power suppression was stronger in neutral, relative to predictive cue trials for both short and long presentation times in younger, but not older adults. Younger adults also demonstrated stronger alpha/beta power suppression than older adults during the retention period of short presentation trials. However, oscillatory power in the preparatory and retention periods did not differ between correct/incorrect trials. Finally, while retention period oscillatory power differed between short and long presentation trials, these differences were no longer present when comparing the trial types from the onset of the memory set.

3.5.1 Predictive cues improve WM storage at both short and long presentation times

Regardless of age, participants demonstrated higher WM capacity when cued to the presentation time of the memory set, relative to receiving a neutral cue. Unlike prior studies investigating attentional cues (Bollinger et al., 2010; Zanto et al., 2010, 2011), we found that both younger and older adults benefit from the presence of a predictive cue that denotes the presentation time of the memory set. As short presentation times presumably lead to the use of automatic, low-level binding instead of top-down control processes during encoding (Sander et al., 2011; Shing et al., 2010), the increased WM performance in the predictive cue condition may be due to the early activation of top-down control processes, leading to the creation of a more durable WM store (Sander et al., 2011).

Interestingly, we found that irrespective of age and cue type, participants performed better on trials with short compared to long presentation times. Initial studies found that visual WM has a fixed capacity of approximately 3-4 items, regardless of the length of time available for encoding (Luck & Vogel, 1997), while others have shown improvements in WM performance with longer presentation times for both young and older adults (Sander et al., 2011). One explanation for our result is that assuming information is encoded at the beginning of stimulus presentation, participants may have held information in mind for longer period in long presentation trials, increasing the chance of forgetting. However, this is unlikely given the research suggesting visual WM for colours can be held for at least 4 seconds without loss in quantity or quality of the WM store (Zhang & Luck, 2009). Alternatively, participants may have employed a verbal strategy in long presentation trials, which may require more effortful processing. The fact we did not control for verbal input by including a rehearsal task is a limitation of this study.

Though we found that older adults were slower to respond to the probe in all conditions, we did not find a difference in WM capacity between age groups. An absence of age differences is inconsistent with extensive literature documenting age-related decline in WM performance (Cabeza et al., 2018; Craik & Salthouse, 2011; Grady, 2012). Convenience sampling of healthy older adults often leads to self-selection bias whereby participants are more educated (Dixon et al., 2004; Geldmacher et al., 2012) and perform better cognitively (Brodaty et al., 2014) than older adults in the population, which may explain comparable WM performance between age groups in this study.

3.5.2 Predictive cues do not modulate alpha power during the preparatory period for young or older adults

Alpha oscillations (~8-12Hz) have long been associated with selective attention processes (Klimesch, 2012) in both space (Gould et al., 2011) and time (Zanto et al., 2010), and have shown to be under top-down control (Bonnefond & Jensen, 2012; Haegens et al., 2011; Wang et al., 2016). The predominant interpretation of this phenomenon is that alpha oscillations reflect functional inhibition and are inversely related to the excitability of sensory cortices (Jensen & Mazaheri, 2010). In support of the functional inhibition hypothesis, anticipatory attention reduces alpha power during the period before the onset of a stimulus, presumably reflecting reduced inhibition/increased excitability of sensory cortices (Rohenkohl & Nobre, 2011; Zanto et al., 2011, 2020).

Here, we explored whether expectation of a memory set of different presentation times modulated pre-stimulus alpha power. Unlike previous studies, we measured changes in oscillatory power that were not limited to the canonical alpha frequency band. We found that while alpha and beta power decreased during the preparation period until the onset of the memory set, this was not further modulated by the type of cue provided in either younger or older adults. Therefore, we could not find evidence to suggest that decreases in alpha power reflected top-down control mechanisms that were deployed in response to the content of the cue.

Older adults demonstrating less alpha suppression across conditions aligns with prior work suggesting that older adults are less able to modulate alpha power in response to a cue (Hong et al., 2015; Zanto et al., 2010, 2011). Given that the offset of the cue predictably signalled the onset of the memory set, alpha/beta suppression in response to the cue likely reflects a state of general alertness or anticipation of an impending stimulus rather than selective attention or top-down control processes linked to the content of the cue (Nenert et al., 2012; Romei et al., 2008; Sadaghiani et al., 2010). Our results suggest that older adults are less able to modulate alpha/beta power in anticipation of stimulus onset, however, this does not seem to influence WM performance. Though it remains unclear whether changes in alpha/beta power seen here reflect selective attention or general alertness (Nenert et al., 2012), it was recently reported that age-related differences in arousal could be indexed by alpha/beta suppression (Dahl et al., 2020).

Our findings suggest that despite the presence of preparatory alpha/beta suppression in the task, alpha/beta suppression is not differentially modulated by the content of the cue in both young and older adults. This is further supported by the finding that alpha power during the preparatory period did not differ between correct and incorrect trials within participants, despite the better behavioural performance on trials with a predictive cue.

3.5.3 Predictive cues modulate alpha power during the retention period for younger adults

Additionally, we also identified changes in the retention period between predictive and neutral cue conditions in younger, but not older adults. In both short and long presentation trials, alpha/beta suppression was stronger in trials with a neutral, relative to a predictive cue. Given the behavioural benefit of a predictive cue, and the role of alpha suppression with increasing WM load (Fukuda et al., 2015; Sauseng et al., 2009), it is possible that trials with a predictive cue were perceived to be of lower cognitive load and therefore, less alpha power suppression was required to support WM performance. The fact that this pattern of activity during the retention period occurred in only younger adults aligns with a prior study investigating age-related differences in alpha lateralisation during spatial attention and visual WM performance (Leenders et al., 2018). Though we did not find evidence for an interaction between age-group and cue type on alpha power, nor age differences in task performance, it is possible that younger adults are better able to modulate oscillatory power during the retention period after being presented with a predictive cue to guide task performance.

3.5.4 The effect of presentation time on alpha power during the retention period

When comparing the retention periods of short and long presentation trials in each age group, we found widespread differences in theta, alpha and beta oscillatory power across conditions. However, these differences were no longer present when comparing the time course of activity from the beginning of the memory set, suggesting that the pattern of retention period oscillatory power was time locked to the presentation of the memory set rather than WM retention. Therefore, the relationship between oscillatory changes and stimulus encoding observed in our data raises questions about the role of alpha power suppression during visual WM, particularly in change detection tasks with retention periods of 1 s in duration.

One possibility is that alpha suppression during the early retention interval is indicative of encoding or attention related processes, aligning with the idea that decreases in alpha power support sensory gating or target enhancement (Foster & Awh, 2019; Jensen & Mazaheri, 2010). A recent study involving the manipulation of the number of distractors and spatial distribution of targets in a visual WM task found that alpha suppression was related to both distractor load and target distribution, suggesting that alpha suppression during visual WM reflects perceptual attentional deployment, and is distinct from mechanisms that store target representations in WM (S. Wang et al., 2020). Similarly, studies investigating episodic memory suggest a role for alpha/beta suppression in the successful encoding of information (Fellner et al., 2019). In our study, we observed age differences during the retention period that were only present in short presentation time trials, with younger adults showing stronger alpha/beta suppression than older adults in the presence of both predictive and neutral cues. Therefore, age differences present here could possibly be related to the orientation of attention towards the memory set, rather than reflecting processes specific to WM retention.

Conversely, alpha power suppression during visual WM has also been shown to reflect storage of information, rather than attention or encoding related processes. Evidence for this account includes that alpha power reduces with WM load, plateaus at WM loads above an individual's capacity, and correlates with WM capacity (Fukuda et al., 2015). In support of these findings, a recent study employing a series of change detection paradigms found that alpha/beta suppression correlated with WM capacity, and was greater in tasks involving active WM processes, relative to the task variants that only involved perceptual gating or engagement of attention (Erickson et al., 2019).

Regardless, the specific role of alpha suppression during change detection tasks of this type remains unclear. If alpha/beta suppression is a result of processes specific to WM retention, then presumably, activity in these frequency bands should be time-locked to the retention period rather than the memory set. One interpretation supported by the time-locking of alpha suppression to the memory set is that alpha/beta suppression reflects WM consolidation, a process in which sensory input is transformed into a memory representation (Jolicœur & Dell'Acqua, 1998). A role for alpha/beta suppression in WM consolidation was also suggested by Erickson and colleagues (2019), given that differences in alpha/beta suppression between active WM and passive tasks were prominent early in the retention period following the memory set. As such, determining the role of alpha suppression during consolidation processes in visual WM presents an avenue for further research.

Additionally, increases in theta power have been linked to successful encoding of items into the WM store (Klimesch et al., 1996), the manipulation of items in WM (Itthipuripat et al., 2013) and are modulated with WM load during the retention period (Jensen & Tesche, 2002). Our results demonstrate an increase in theta power that appears temporally linked to the encoding rather than retention period in both age groups, possibly suggesting a role for theta in the loading or consolidation of items into WM.

There are several caveats to our results discussed in this section. First, we cannot rule out from our study alone whether alpha suppression during the encoding and retention periods are merely due to viewing the memory set due to the absence of a passive viewing condition. Second, it is unclear whether this pattern of alpha/beta suppression would been seen in tasks with a memory set 0.5 s or greater in duration, or a retention period of greater than 1 s. Finally, we also cannot rule out that this pattern of alpha suppression would occur in a verbal WM task. In modified Sternberg tasks, alpha power tends to increase during retention (Jensen et al., 2002; Proskovec et al., 2019; Sghirripa et al., 2020), which is thought to reflect a suppression of sensory input from the visual stream to prevent disruption to the WM store (Jensen & Mazaheri, 2010). Future work should investigate the interplay between presentation time and WM load and modality.

3.5.5 Conclusion

The results of the present study suggest that cues denoting memory set presentation time do not differentially evoke preparatory changes in alpha power in both younger and older adults. However, we have demonstrated that the pattern of oscillatory power seen during the retention period of visual WM is seemingly linked to the memory set rather than WM retention processes. Future work should now further investigate the precise role that alpha/beta suppression plays during visual WM performance.

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Chapter 4: Age-related changes in visual working memory consolidation

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Contribution to the Paper	Conceived and designed study, recruited participants, collected data, processed, and analysed data, prepared data visualisations and wrote the manuscript
Overall percentage (%)	95%
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.

Signature		Date	10/05/2022

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);
ii. permission is granted for the candidate in include the publication in the thesis; and
iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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4.1 ABSTRACT

Visual working memory (WM) is vulnerable to age-related decline, but the causes of such performance deficits are unclear. Here, we investigated whether the ability to consolidate items into the visual WM store differs between young and older adults. 18 older (aged 60-77) and 17 younger adults (aged 18-35) completed a change detection paradigm that measured visual WM consolidation rate. A memory set of either 2, 4 or 6 coloured squares was presented, followed by a pattern mask to disrupt WM consolidation. The consolidation time between memory set and mask varied between 17 and 484 ms. We found that older adults demonstrated poorer performance (measured by *d'*) across all loads and were particularly affected by shorter consolidation times at load-2 compared with younger adults. However, both young and older adults were equally affected by the masks at load-4 and load-6. We demonstrate evidence for altered WM consolidation in older adults, which may explain poorer visual WM performance with age.

4.2 INTRODUCTION

Visual working memory (WM) is the ability to maintain and/or manipulate visual information to guide cognitive processing (Baddeley, 1992). Visual WM is severely limited in capacity, with resources limited to approximately 3-4 discrete items (Cowan, 2001; Luck and Vogel, 1997). Visual WM capacity limits are affected by age, as older adults demonstrate smaller WM capacities (Fisk and Warr, 1996; Foos, 1989; Schneider-Garces et al., 2009) and poorer WM performance under high loads (Cappell et al., 2010) compared with younger adults. However, the causes of such declines are not well understood.

One theory that attempts to explain age differences in WM ability is the 'processing speed hypothesis', which suggests that older adults experience a general slowing in the execution of processing operations, leading to cognitive impairment (Salthouse, 1994). In relation to WM performance, slower processing speed can limit performance through rapid losses of information (i.e. deficits in the retention of information over time), or by limiting the rate at which items can be encoded into the WM store (Salthouse, 1991). Studies involving continuous paired-associates tasks have shown that older adults require significantly longer stimulus presentation times to achieve a similar level of accuracy as younger adults (Salthouse, 1992). This finding provides evidence that age-related decreases in processing speed impair WM performance by reducing the rate of encoding, or the rate to establish an adequate internal representation of stimuli. Further evidence for slower encoding of information into the visual

WM store has been seen in studies manipulating encoding duration, where older adults display disproportionately poorer visual WM performance under short memory set presentation times than younger adults (Sander et al., 2011).

However, it is possible that age-related reductions in processing speed not only limit the encoding of items into WM, but the consolidation of those items. WM consolidation refers to the transformation of sensory input into a stable memory representation which can be recalled after a delay (Jolicœur and Dell'Acqua, 1998). To empirically test the time course of visual WM, the amount of time allowed for consolidation can be manipulated by presenting a pattern mask at varying stimulus onset asynchronies (SOAs) following a memory set (Vogel et al., 2006). The onset of the mask is thought to interrupt visual sensory memory representation that has not yet been encoded into visual WM, such that WM representations which have been consolidated can survive the pattern masks and remain in the visual WM store. As the SOA between the memory set and mask increases, the number of items encoded into visual WM should increase until a plateau is reached (Vogel et al., 2006).

Evidence for slowed consolidation times in older adults can be found from studies using rapid serial visual presentation tasks, where sequentially presented visual stimuli are rapidly presented in the same location and participants are asked to identify either one or two perceptually distinguishable target items (Shapiro et al., 1997). Although participants are able to identify one target, the second target is often missed when it appears in close proximity to the first—a phenomenon termed the 'attentional blink', in which the encoding of the first target inhibits the encoding of subsequent targets (Giesbrecht and Di Lollo, 1998; Lawrence, 1971; Shapiro et al., 1997). The attentional blink effect has been shown to increase in older adults (Georgiou-Karistianis et al., 2007; Lahar et al., 2001), potentially suggesting age-related deficits in consolidation of stimuli being rapidly presented. However, as attentional blink tasks require the use of cognitive processes such as attention and updating of stimulus information, it is unclear whether age-related differences in WM consolidation are present and limit visual WM performance in older adults.

The aim of this study was to use a masking paradigm to compare the rate at which perceptual representations are consolidated into durable WM representations in younger and older adults under increasing WM loads. We hypothesised that older adults would display poorer WM performance at shorter SOAs and higher WM loads than younger adults.

4.3 METHODS

4.3.1 Participants

18 older adults (mean age: 67.5 years, SD: 5.34, range: 60-77 years, 11 female) and 17 younger adults (mean age: 23.9 years, SD: 5.05, range: 18-35 years, 14 female) participated in the study. The samples in each age group were not significantly different for years of education (older adults: M = 14.92 years, SD = 3.26 years; younger adults: M = 16.68 years, SD = 2.6 years, $t_{32.1} = 1.77$, $p = .087$). Exclusion criteria were a history of neurological or psychiatric disease, use of central nervous system altering medications, history of alcohol/substance abuse, colour blindness, uncorrected hearing/visual impairment and for older adults, an ACE-III score of < 82 (Mioshi et al., 2006). All participants gave informed written consent before the commencement of the study, and the experiment was approved by the University of Adelaide Human Research Ethics Committee

4.3.2 Task and stimuli

Participants performed a change-detection task using stimuli presented by PsychoPy software (figure 1) (Peirce, 2007). On each trial, participants were presented with either 2, 4 or 6 coloured squares. Each square subtended 0.65° x 0.65° of visual angle and the colour was randomly selected without replacement from a set of 10 colours (white, black, red, blue, yellow, green, orange, purple, brown and magenta).

Each mask was composed of 4 randomly selected coloured squares arranged in a checkerboard pattern (1.3° x 1.3°). The mask appeared in the same location as every item presented in the memory array.

Each trial consisted of a 100 ms memory array, a variable pre-mask delay, a mask array, a blank retention delay and then a test array. The blank delay between the memory set and the mask was 17, 134, 250, 367 or 484 ms, which varied across trials. Therefore, the memory/mask SOAs were 117, 234, 350, 467 or 584 ms. The SOA between the memory array and the test array was always 1100ms. As such, the interval between the mask and test arrays depended on the delay between the memory and mask array. On 50% of the trials, the memory and test arrays were identical, while 50% of the trials involved a single colour change. The new colour was chosen at random from the other possible colours. Participants were instructed to respond using the right arrow key on the keyboard if the test array matched the memory array, and to respond with the left arrow key if the arrays were different. As in Vogel et al. (2006), we presented a random two-digit number at the beginning of each trial and instructed participants to say these two digits aloud during each trial to reduce verbal contribution to WM performance. There were 40 trials of each memory/mask SOA and WM load combination, yielding 600 trials in total.

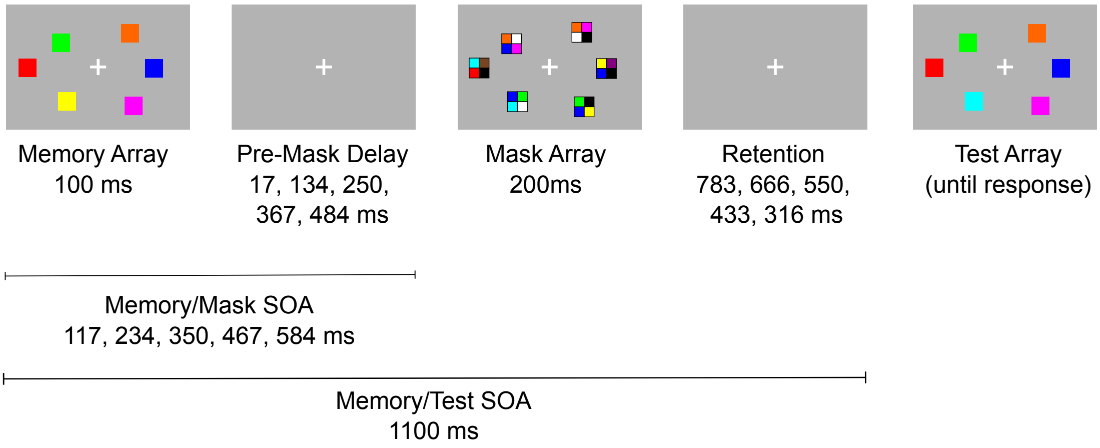

Figure 4.1. Task diagram. *Modified delay match-to-sample task based on the paradigm described by Vogel et al. (2006). Participants were shown either 2, 4 or 6 coloured squares in a memory array, followed by a mask array of 200ms after a variable pre-mask delay. A test array was then shown, and participants indicated whether the array was the same or differed in colour by one item. There were 40 trials at each WM load and SOA.*

4.3.3 Statistics

Statistical analyses were performed using R version 4.1.0. Linear mixed effects models were used to analyse behavioural performance. WM performance was measured using *d’*, which was calculated by subtracting the z-score corresponding to the false alarm rate from the z-score corresponding to the hit rate (Stanislaw and Todorov, 1999). For the mixed models, the outcome variable was *d’*. Age group (younger and older), WM load (load-2, load-4 and load-6) and memory/mask SOA (117, 234, 350, 467 and 584 ms) were fixed effects, and participant was the random effect. Post-hoc pairwise t-tests were performed in case of significant main effects or interactions, with the Holm correction applied for multiple comparisons. Data were checked for normality using Shapiro–Wilk tests, and the residuals for the mixed effects models were examined via histograms and QQ plots. In all tests, a p-value of less than 0.05 was considered statistically significant. Data are presented as mean ± SEM in figures.

4.4 RESULTS

A linear mixed effects model revealed significant main effects of age group ($F_{1,31} = 21.32$, $p < 0.001$), memory/mask SOA ($F_{4,434} = 41.97$, $p < 0.001$) and WM load ($F_{2,434} = 390$, p

<0.001) on *d'*. Holm corrected post-hoc tests revealed that younger adults performed more accurately on the task than older adults ($p<0.001$). Likewise, *d'* was lowest at the shortest memory/mask SOA ($p<0.001$), until a plateau was reached at 350 ms. Finally, *d'* was higher in load 2 than in load 4 ($p<0.001$) and load 6 ($p<0.001$), while performance in load 4 was higher than load 6 ($p<0.001$).

The model also revealed interactions between age and WM load ($F_{2,434} = 5.40$, $p = 0.01$), memory/mask SOA and WM load ($F_{8,434} = 2.17$, $p = 0.03$), and age, memory/mask SOA and WM load ($F_{8,434} = 2.0$, $p = 0.04$). Holm corrected post hoc tests revealed that younger adults performed better at all loads compared with older adults (load 2: $p<0.001$, load 4: $p<0.001$, load 6: $p = 0.02$). Likewise, performance at all memory/mask SOAs was poorest in load-6 relative to load 4 (p<0.001) and load 2 (p<0.001), and in load 4 compared with load 2 (p<0.001).

To explore the interactions between WM load and memory/mask SOA, and age, WM load and memory/mask SOA, separate mixed models were conducted for each WM load condition with *d'* as the outcome variable, age group and memory/mask SOA as fixed effects and participant as the random effect. At load-2, there were significant main effects of age group ($F_{1,31}= 15.61$, $p<0.001$) and memory/mask SOA ($F_{4,124}= 41.57$, $p<0.001$), and a significant age group by memory/mask SOA interaction ($F_{4,124}= 6.42$, $p<0.001$). Holm corrected post-hoc tests revealed that overall, older adults performed worse than younger adults at load-2 ($p<0.001$). Averaged over age group, performance was poorest in the 117 ms condition, compared with all other memory/mask SOAs (all $p<0.001$). A plateau was reached at 350 ms, where performance did not increase beyond this memory/mask SOA (all $p>0.16$). Finally, younger adults performed better than older adults at the 117 ms ($p<0.001$) and 234 ms memory/mask SOA condition ($p=0.035$). No age differences were present at the 350 ms, 467 ms or 584 ms memory/mask SOA conditions (all $p>0.1$).

At load-4, there was a significant main effect of age group ($F_{1,31}= 23.27$, $p<0.001$) and memory/mask SOA ($F_{4,124}= 11.27$, $p<0.001$), but no age group by memory/mask SOA interaction ($F_{4,124}= 0.11$, $p=0.97$). Holm corrected post-hoc tests revealed that overall, older adults performed worse than younger adults at load-4 ($p<0.001$). Averaged over age groups, performance was poorest in the 117ms condition compared with all other memory/mask SOAs (all $p<0.002$), but a performance plateau was reached in the 234 ms condition (all $p>0.39$). Finally, the lack of an age-group by memory/mask SOA interaction suggests that both age groups were affected by the mask similarly, though younger adults performed better at load 4 overall.

At load-6, there was a significant main effect of age group ($F_{1,31}$= 13.93, p<0.001) and memory/mask SOA ($F_{4,124}$= 6.81, p<0.001), but no age group by memory/mask SOA interaction ($F_{4,124}$= 0.54, p=0.71). Holm corrected post-hoc tests revealed that older adults performed worse than younger adults at load-6 (p<0.001). Averaged across age groups, when compared with the 117 ms memory/mask SOA, performance was better in the 350 ms (p = 0.01), 467 ms (p<0.001) and 584 ms (p<0.001) conditions, but no other differences were seen (all p>0.18). As in load-4, both age groups were similarly affected by the mask, as performance continued to increase as the memory/mask SOA increased without reaching a clear plateau.

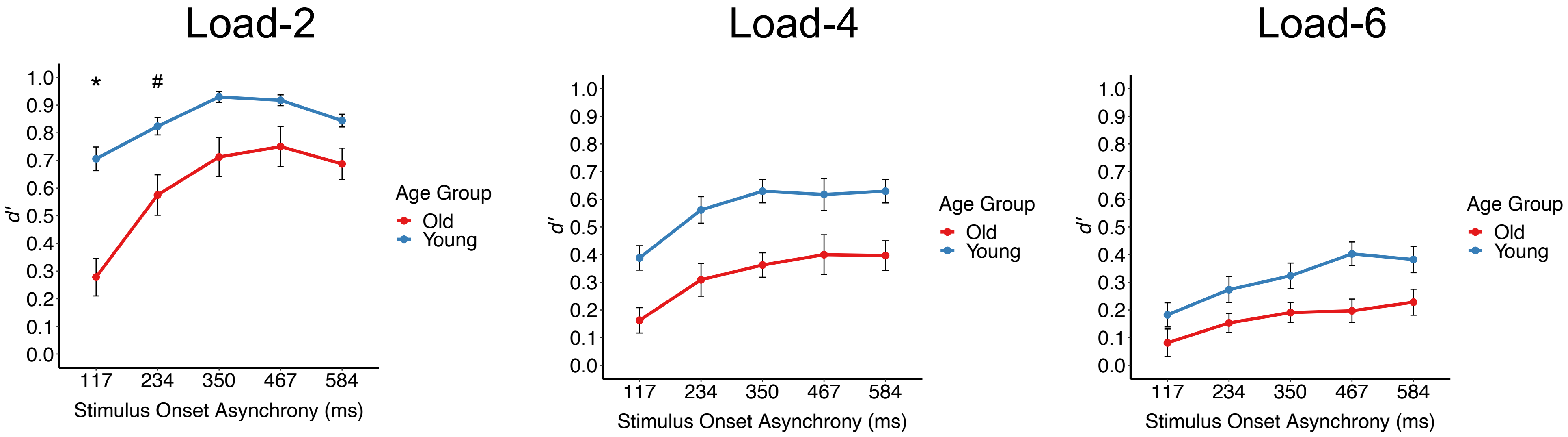

Figure 4.2. Behavioural data. *WM performance as measured by d' at each WM load and memory/mask SOA for older and younger adults, * p<0.001, # p<0.05.*

4.5 DISCUSSION

In this study, we explored whether manipulating the time available for visual WM consolidation influenced visual WM performance in younger and older adults at varying loads. As hypothesised, older adults showed poorer WM performance with increasing WM load compared with younger adults. However, while performance differences between older and younger adults did not vary with memory/mask SOA at load-4 and load-6, older adults demonstrated poorer performance at the shortest memory/mask SOAs (117 ms and 234 ms) at load-2. Overall, we demonstrate evidence for performance deficits under short consolidation times for older adults at lower WM loads, though masking effects are present in both age groups at medium to high WM loads.

The poorer performance of older adults under short memory/mask SOAs in load-2 trials is consistent with the 'processing speed hypothesis', which suggests that processing speed limits WM performance as slowed cognitive operations cannot be completed in the available time (Salthouse, 1992). In this case, older adults may not have had enough time to consolidate the memory array before the mask onset at short memory/mask SOAs, despite there only being two items to process. As the memory/mask SOA increased, age differences in performance were no longer significant, suggesting that the poorer performance is due to slowing of WM consolidation as opposed to WM capacity limits. The poorer performance under short memory/mask SOAs aligns with studies reporting an exaggerated attentional blink in older adults, in which older adults require longer intervals between two rapidly presented target stimuli to perceive the occurrence of the second stimulus, suggestive of prolonged consolidation times of the first stimulus (Georgiou-Karistianis et al., 2007; Lahar et al., 2001; Maciokas and Crognale, 2003).

It is also possible that older adults are more affected by the mask due to their vulnerability to task irrelevant stimuli during WM performance, aligning with the 'inhibitory deficit hypothesis' of ageing (Hasher and Zacks, 1988). Masks likely influence WM performance because the appearance overwrites the perceptual representation of the memory set (Vogel et al., 2006). Therefore, when the mask appears in close temporal proximity to the memory set, it is possible that older adults encode the mask, leading to the trace of the memory set being overwritten. As the mask interval increases to 350 ms and beyond, then older adults can create a stable, consolidated representation of the memory set, which is resistant to distraction from the mask.

As a caveat, it is possible that processing speed limits the speed of encoding rather than consolidation, given that we used a 100 ms presentation time. Prior studies have shown that older adults perform worse under short presentation times (Sander et al., 2011), though we have previously reported that visual WM performance does not vary with presentation time between age groups (Sghirripa et al., 2021). However, encoding deficits are unlikely given that differences between young and older adults were not seen at memory/mask SOAs greater than 350ms, suggesting that older adults were still able to successfully encode items at load-2. Likewise, it is possible that the poor performance of older adults in the 117 ms condition is due to the backward masking effect, in which a visual stimulus (such as a mask) is immediately shown after a target stimulus, resulting in an inability to perceive the first stimulus (Felsten and Wasserman, 1980). However, this is unlikely as older adults were also affected by the mask in the 234 ms condition at load-2, backward masking effects tend to appear at intervals shorter than 117 ms (Felsten and Wasserman, 1980), and that the original study of Vogel et al. (2006) demonstrated that masks in this paradigm at the 117 ms memory/mask SOA do not influence the formation of perceptual representations.

At load-4 and load-6, while older adults performed poorer than younger adults, they were not disproportionately affected by the mask. When WM load increases, the increased visual load requires a longer period to consolidate as more uninterrupted processing time is needed to create a stable WM representation (Vogel et al., 2006). This is evident in load-4, where plateaus were reached after 350ms, but load-6 was likely too difficult for participants in either age group to reach a performance plateau. Given that older adults reach a plateau at a similar memory/mask SOA to younger adults, slowing in consolidation time alone likely does not explain the poorer performance seen in older adults at loads 4 and 6.

A limitation of this study is that we did not include a condition without a mask. However, the fact participants in both age groups reached plateaus before the longest memory/mask SOA suggests that ceiling performance was reached in loads 2 and 4. Likewise, while it has been suggested that to accurately capture WM capacity limits with ageing, higher set sizes should be included in the task (Souza, 2016), load-6 was likely too difficult for the older adults. Testing a wider resolution of WM loads would allow for a more complete understanding of age-related changes to WM consolidation, as it is unclear for example, whether a load-3 task would lead to masking effects in both age groups as seen in load-4, or in older adults only, as seen in load-2. Control groups in studies investigating slowed WM consolidation in schizophrenia demonstrated masking effects at load-3 but not at load-2, while patients demonstrated masking effects at both loads (Fuller et al., 2005). Therefore, future studies should test a higher resolution of WM loads.

In this study, we have demonstrated that older adults display slower WM consolidation at lower WM loads compared with younger adults, but both younger and older adults are affected by a mask at medium and high loads. This provides some evidence for impaired WM consolidation in older adults, but further work should be done to understand the cognitive and neural mechanisms underlying this effect.

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Chapter 5: Age-related differences in alpha power for distractor inhibition during visual working memory

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5.1 ABSTRACT

As visual working memory (WM) is limited in capacity, it is important to direct neural resources towards task-relevant, and away from task-irrelevant information. Neural oscillations in the alpha frequency band (8-12 Hz) have been suggested to play a role in the inhibition of distracting information during WM retention in younger adults, but it is unclear if alpha power modulation also supports distractor inhibition in older adults. Here, we recorded electroencephalography (EEG) while 24 younger (aged 18-35) and 24 older (aged 60-86) adults completed a modified delayed match-to-sample task in which distractors of varying strength appeared during the retention period. We found: (1) strong distractors impaired WM performance compared with weak and no distractors in both age groups, but there were no age-differences in WM performance; (2) while younger adults demonstrated significant increases in alpha power prior to the onset of the distractor in the strong distractor, relative to the weak distractor condition, decreases in alpha power were seen in all distractor conditions in older adults; (3) there was no difference in alpha power between the strong and no distractor conditions; and (4) alpha power in anticipation of the distractor was only associated with task performance in younger adults. Our results suggest that younger adults, but not older adults, modulate alpha power in anticipation of distractors during the visual WM retention period.

5.2 INTRODUCTION

Visual working memory (WM) is severely limited in capacity (Cowan, 2001), highlighting the importance of encoding and retaining task-relevant, and ignoring task-irrelevant or distracting information. An inability to inhibit distracting information is one suggested basis for age-related reductions in WM performance (Hasher and Zacks, 1988), but the neural mechanisms underlying age-related deficits in ignoring distractions during WM are unclear.

Neural oscillations in the alpha (8-12 Hz) frequency range have been implicated in distractor inhibition during WM performance in younger adults (Bonnefond and Jensen, 2012; Sauseng et al., 2009; Sghirripa et al., 2020). While it was initially thought that increases in alpha power reflected ‘cortical idling’ (Pfurtscheller et al., 1996), the modulation of alpha power has now been proposed to dynamically gate sensory input to task-relevant brain regions (Jensen and Mazaheri, 2010). Evidence linking alpha power to distraction inhibition during visual WM was derived from tasks where participants attend to a task-relevant and inhibit a task irrelevant hemifield. These paradigms are associated with decreases in alpha power in the task-relevant, and increases in alpha power in the task-irrelevant hemifield, implicating alpha power in both the facilitation of visual WM performance and inhibition of task-irrelevant information (Sauseng et al., 2009).

During the retention period of verbal WM tasks where participants can anticipate the onset of a distractor, anticipation of strong distractors has been associated with greater alpha power prior to the onset relative to alpha power in anticipation of a weak distractor (Bonnefond and Jensen, 2012). Using a verbal WM paradigm, we have previously reported an increase in alpha power that did not differ based on distractor type (Sghirripa et al., 2020), while others using visual WM tasks have reported lower alpha power in the presence of strong distractors present for the entire retention period (Schroeder et al., 2018).

Alpha oscillations reduce in power and frequency with age (Babiloni et al., 2006), and given that age-related deficits in distractor inhibition may account for age-related deficits in WM performance (Hasher and Zacks, 1988), a link may exist between age-related changes in alpha oscillatory activity and deficits in distractor inhibition during WM. In a study employing a lateralised task to investigate age-differences in alpha power for the suppression of irrelevant information during WM, it was observed that while suppression of visual processing was associated with modulation of alpha power in younger adults, older adults did not modulate alpha power, despite performance indicating that suppression of distractors had occurred (Vaden et al., 2012).

However, older adults demonstrate greater performance declines when distractors match the same category of stimulus as the memory set, suggesting that the strength of the distractor is important in age-related declines in distractor inhibition (Clapp et al., 2009; Clapp and Gazzaley, 2012; Yoon et al., 2006). Despite studies in younger adults reporting differences in alpha power modulation with distractor strength (Bonnefond and Jensen, 2012), no study has investigated whether older adults also modulate alpha power in anticipation of distractors of varying strength, or whether alpha power modulation is absent in older adults, as described by Vaden et al. (2012).

Here, we employed a modified delayed match-to-sample task with strong, weak and no distractor conditions to determine whether young and older adults modulate alpha power in anticipation of distractors of varying strength. We hypothesised that: 1) WM performance would be more impaired by strong and weak distractors in older, compared with younger adults, 2) that younger adults would show stronger alpha power before the onset of strong, compared with weak distractors, while older adults would show no differences in alpha power between conditions, and 3) that stronger alpha power in the lead up to the distractor would correlate with better WM performance.

5.3 METHOD

5.3.1 Participants

24 healthy younger (mean age: 23.36 years, SD: 5.83 years, range:18-35, 22 female) and 24 healthy older adults (mean age: 69.96 years, SD: 6.94 years, range: 60-86, 17 female) participated in the study. The samples in each group were not significantly different for years of education ($t_{47} = 0.50$, $p = 0.62$). All older adults were without cognitive impairment as assessed by Addenbrooke's Cognitive Examination III (ACE-III) (score > 82) (Mioshi et al., 2006).

Exclusion criteria involved a history of neurological/psychiatric disease, use of central nervous system altering medications, history of alcohol/substance abuse and uncorrected hearing/visual impairment (including colour blindness). All participants gave informed written consent before the commencement of the study, and the experiment was approved by the University of Adelaide Human Research Ethics Committee.

5.3.2 Working memory task

Participants first completed a WM load adjustment task consisting of 20 trials at each of load-2, load-3, load-4, load-5, and load-6 with no distractors present. This task trained the participant on the task and allowed us to adjust the WM load for each participant individually before partaking in the distractor visual WM task with EEG. The load for each participant was chosen based on the load where ~80% accuracy was achieved.

The distractor visual WM task used stimuli presented by PsychoPy (Peirce, 2007). Each trial began with the participant fixating on a cross in the centre of the screen for 2 s. A memory set consisting of six squares then appeared for 0.5 s to maintain equal sensory input for each WM load. The position of squares did not change within trials but varied between trials. The number of coloured squares depended on the WM load chosen in the load adjustment task. Each square subtended 0.65° x 0.65° of visual angle. Following a consolidation period of 0.25 s, a pattern mask consisting of coloured static appeared for 0.15 s in the same location as each item presented in the memory set. We chose to include a mask and consolidation period to disrupt residual sensory trace left by the memory set from influencing oscillatory power during the retention period (Woodman and Vogel, 2005). Following the mask, a 4 s retention period began. In the distractor blocks, 2 s into the retention period a strong (4 coloured squares not in the memory set) or weak distractor was shown (4 light grey squares) for 0.5 s, followed by the 1.5 s remainder of the retention period. In the no distractor condition, only the fixation cross was present for 4 s. A single probe coloured square then appeared in the location of a randomly selected square from the memory set. Participants were instructed to respond with the right arrow key if the probe square was the same colour in the memory set and respond with the left arrow key if the square was a different colour. In each block, 50% of the trials required a right arrow key response (same colour), and 50% required a left arrow key response (different colour). The probe remained on the screen until the subject responded.

In the task, there were 5 blocks with strong distractors, 5 blocks with weak distractors and 5 blocks with no distractor. The distractor type blocks were presented randomly throughout the task. Blocks consisted of 20 trials (total = 100 trials per distractor condition), with the blocked design allowing participants to anticipate the strength of the distractor within blocks. However, participants did not know the distractor condition present in each block until the first trial. Distractors were never part of the memory set or probe, and participants were explicitly asked to ignore the distractor. Short breaks were allowed between blocks.

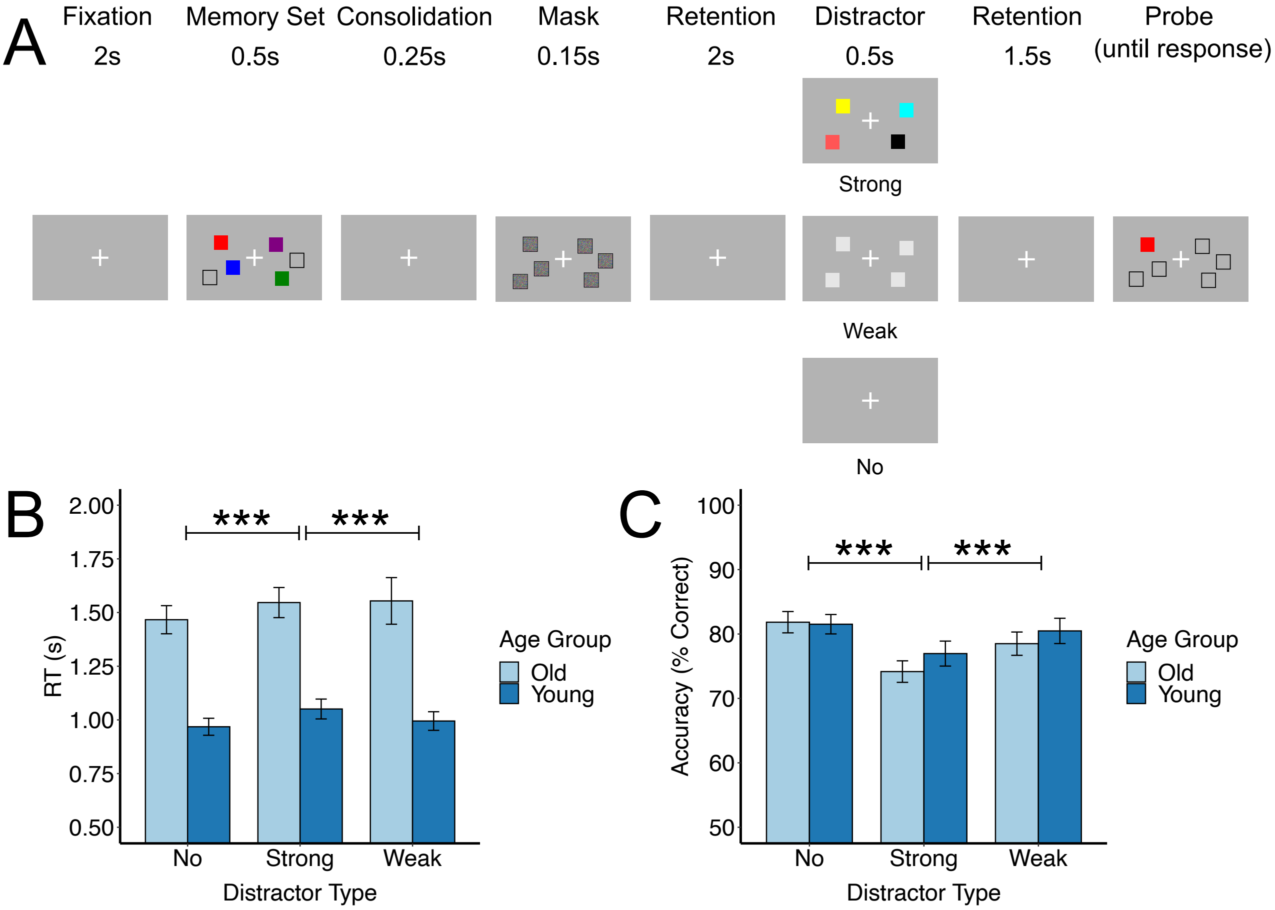

Figure 5.1. Task diagram and behavioural data. *A) Modified delay match-to-sample task. Each trial contained a memory set with a number of squares chosen via performance on the load adjustment task with no distractors present, followed by a pattern mask after a short delay. The retention period was 4 s long, in which a strong (4 coloured squares) or weak (4 grey squares) distractor was shown and persisted for 0.5 s. In the no distractor blocks, only a fixation cross was present for the 4 s retention period. A single probe square was then presented, and participants responded to whether the coloured square was the same colour seen in the memory set. B) Response time (RT) for correct responses to the probe and C) accuracy (% correct) in response to the probe in each distractor condition *** $p < 0.001$*

5.3.3 EEG data acquisition

EEG data were recorded from a 64-channel cap containing Ag/AgCl scalp electrodes arranged in a 10–10 layout (Waveguard, ANT Neuro, Enschede, The Netherlands) using a Polybench TMSi EEG system (Twente Medical Systems International B.V, Oldenzaal, The Netherlands). Conductive gel was inserted into each electrode using a blunt-needle syringe to reduce impedance to < 5 kΩ. The ground electrode was located at AFz. Signals were amplified 20x, online filtered (DC-553 Hz) and sampled at 2048 Hz. Due to the lack of data from the mastoids, data were referenced to the average of all electrodes. EEG was recorded during each block of the distractor visual WM task.

5.3.4 EEG data pre-processing

EEG data were pre-processed using EEGLAB (Delorme and Makeig, 2004), TMS-EEG Signal Analyser (TESA v1.1.1) (Rogasch et al., 2017) and custom scripts using MATLAB (R2020b, The Mathworks, USA). Each block of EEG data was merged, and incorrect trials were flagged for removal at a later stage. Unused channels were removed, data were downsampled to 256 Hz and then band-pass (0.1-100Hz) and band-stop (48-52 Hz) filtered using the EEGLAB 'eegfiltnew' function. Data were epoched -2 to 6 s relative to the onset of the memory set. Channels and trials were then visually inspected and removed if contaminated with residual artifacts (e.g. muscle activity or non-stereotypical artifacts). An average of 1 channel was removed from the younger adult group, and 2 were removed from the older adult group (range young: 0-7, range old: 0-6). Independent component analysis (ICA) was then completed using the FastICA algorithm (Hyvärinen and Oja, 2000), with the 'symmetric approach' and 'tahn' contrast functions selected. Components corresponding to eye-blinks and persistent muscle activity were detected using the TESA (Rogasch et al., 2017) 'compselect' function and were manually inspected before removal from the data. Missing channels were then interpolated, and data were re-referenced to the common average. Epochs were then split into distractor types, and correct and incorrect trials were separated.

For younger adults, an average of 76 trials for the no distractor condition, 76 for the weak distractor condition and 72 for the strong distractor condition were accepted for further analysis. For older adults, an average of 73 trials for the no distractor condition, 72 for the weak distractor condition and 67 for the strong distractor condition were accepted for further analysis.

5.3.5 Spectral analysis

Spectral analysis was performed using FieldTrip toolbox (Oostenveld et al., 2011). Data were converted to the time-frequency domain using a multi-taper transformation based on multiplication in the frequency domain (cfg.method = 'mtmconvol'). A time window of 3 cycles was used for each frequency (0.5 Hz steps between 3 and 45 Hz) and time point (50 ms steps). Spectral power was calculated for individual trials before being averaged over trials for each distractor condition in each age group. Data were baseline corrected -1 to -0.25 s relative to the onset of the memory set.

5.3.6 Statistical analysis of behavioural data

Statistical analyses were performed using R version 4.1.0. Linear mixed effects models with age group and distractor condition as fixed effects, participant as random effect, and accuracy and RT as outcome variables, were used to analyse behavioural data. Bonferroni corrected post-hoc tests were performed in the case of significant main effects or interactions. Correlations between the difference in alpha power between strong and weak distractor conditions and difference in accuracy and RT between conditions were performed using Pearson's correlation. Data were checked for normality using Shapiro-Wilk tests, and the residuals for the linear mixed effects models were checked via QQ plots and histograms. In all tests, a p-value of < 0.05 was considered statistically significant. Data are presented as mean ± SEM in figures.

5.3.7 Statistical analysis of EEG data

Statistical analyses of EEG data were performed using FieldTrip toolbox (Oostenveld et al., 2011). Cluster-based permutation tests were used to assess differences in alpha power between age-groups and distractor types. Cluster-based permutation tests control for the type-1 error rate when comparing across multiple channels, times, and frequencies (Maris and Oostenveld, 2007). Clusters were defined as two or more neighbouring electrodes for which the difference in spectral power between age groups (independent samples t-test) or distractor types (dependent samples t-test), exceeded $p < 0.05$. A permutation distribution was used to test clusters for significance, which was generated by combining alpha power values from both age groups and distractor types into a single set, randomly partitioning into two subsets, and taking the largest cluster-level statistic from this partition (Monte Carlo method; 2000 random permutations). If the cluster-level statistic observed from the original data was larger in absolute value than 95% of random partitions, the cluster was deemed significant ($p < 0.05$, two-tailed test).

To test for interactions between age group and distractor type, we employed a 2x2 factorial design. A difference power spectrum was calculated consisting of the power spectrum differences between distractor types for each combination of no, weak, and strong distractor (e.g., for differences between strong and weak distractors: young difference = Young/Strong - Young/Weak, Old difference = Old/Strong - Old/Weak). Cluster-based permutation tests performed as described above to compare the difference power spectrums between age groups.

5.4 RESULTS

5.4.1 Behavioural data

5.4.1.1 WM load adjustment

In the younger adult group, 9 participants completed the task at load-4 and 15 completed the task at load-5. In the older adult group, 8 participants completed the task at load-3, 13 completed the task at load-4 and 3 completed the task at load-5. The load that was selected for each participant was significantly different between groups ($t_{46} = 4.96, p < 0.001$), with younger adults (M = 4.63, SD = 0.50) being able to perform near 80% accuracy at higher loads than older adults (M = 3.79, SD = 0.66).

5.4.1.2 RT

For RT there were significant main effects of age group ($F_{1,46} = 35.84$, $p < 0.001$) and distractor type ($F_{2,84} = 15.62, p < 0.001$), but no age group by distractor type interaction ($F_{2,84} = 0.08, p = 0.92$). Bonferroni corrected post-hoc tests revealed that older adults were slower to respond in all conditions than younger adults ($p < 0.001$). Response times were slower in the strong distractor condition compared with the no ($p < 0.001$) and weak ($p = 0.005$) distractor conditions, but there was no difference in response times between the weak and no distractor conditions ($p = 0.23$) (Figure 1B).

5.4.1.3 Accuracy

For accuracy there was a significant main effect of distractor type ($F_{2,84} = 23.67$, $p < 0.001$), but no main effect of age ($F_{1,46} = 1.34$, $p = 0.25$), nor an age group by distractor type interaction ($F_{2,84} = 1.72, p = 0.19$). Bonferroni corrected post-hoc tests revealed that accuracy was poorer in the strong distractor condition compared with the no ($p < 0.001$) and weak ($p < 0.001$) distractor conditions, but there was no difference in accuracy between the weak and no distractor conditions ($p = 0.38$) (Figure 1C).

5.4.2 Time frequency analysis

Our a-priori hypothesis was that increases in alpha power would be present prior to the onset of distractors. When we examined the time-frequency representation of raw power averaged across both age groups and all distractor conditions from all participants, and the average of all electrodes, the largest alpha power was observed in the 0.75 s prior to the onset of the distractor in the 9-12 Hz frequency range. In the cluster-based permutation tests, we averaged across the 9-12 Hz frequency range and the 0.75 s prior to distractor onset and tested across all electrodes.

5.4.2.1 Age differences in anticipatory alpha power

We sought to determine whether age differences in alpha oscillatory power existed in the pre-distractor time interval for each distractor type. Upon visual inspection of the time-frequency representations of power, we observed that alpha power increased from baseline in all distractor conditions in younger adults, whereas alpha power decreased from baseline across all conditions in older adults (Figure 2A). In younger adults, the increase in alpha power from baseline was significant for the no distractor (p = 0.01) and strong distractor (p = 0.04) conditions, but not for the weak distractor condition (no significant clusters). The decrease in alpha power from baseline was significant in older adults for the no distractor (p = 0.01), weak distractor (p = 0.002) and strong distractor conditions (p = 0.04).

Cluster based permutation tests revealed that during anticipation of a distractor, younger adults demonstrated larger increases in alpha power in the strong (p = 0.02) and weak (p = 0.02) distractor conditions compared with older adults. However, we also found age differences in alpha power in the no distractor condition (p = 0.01). In all comparisons, the differences in alpha power were prominent across frontal, parietal, and occipital electrodes (Figure 2B).

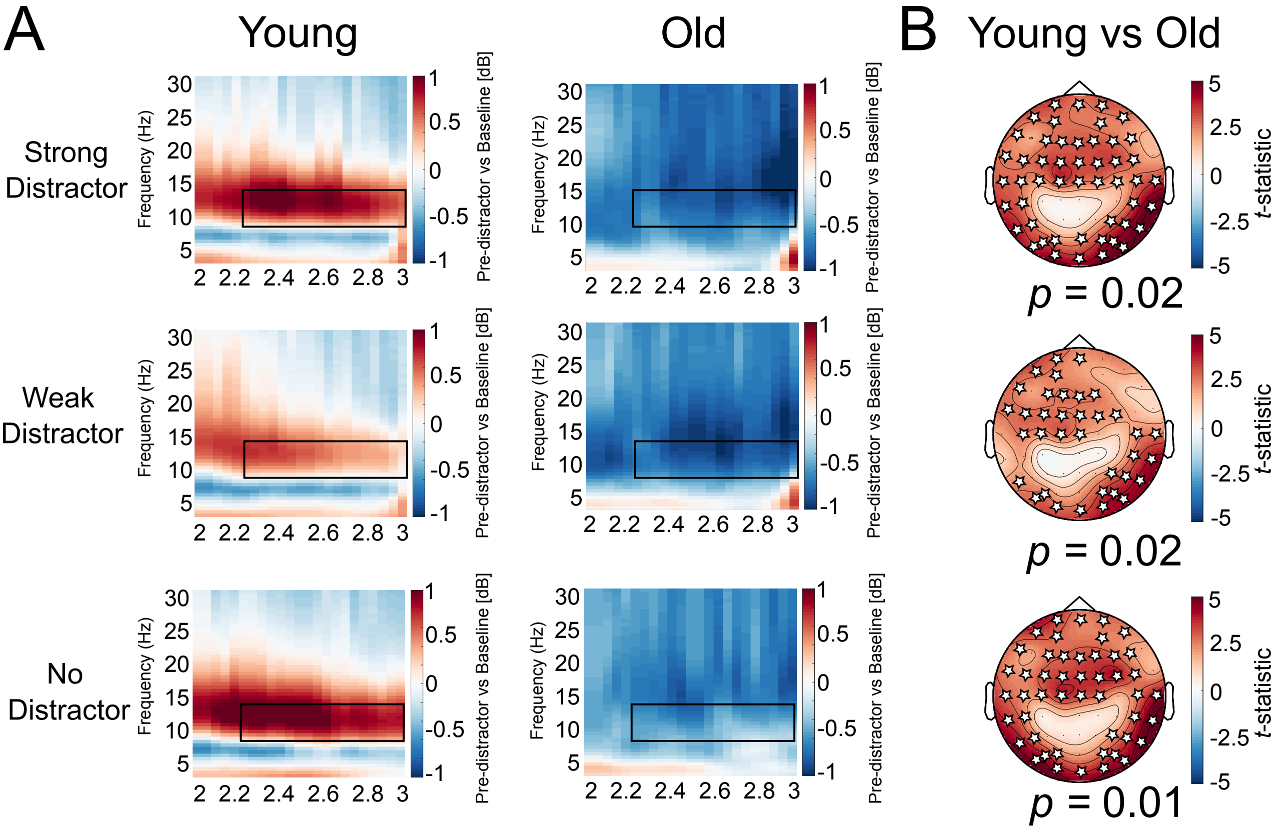

Figure 5.2. Alpha power prior to the distractor. *A) Baseline corrected time-frequency representations of power (average of all electrodes) in the 1 s prior to the onset of the distractor, and B) t-statistics from cluster-based permutation tests demonstrating the difference between age-groups in each distractor condition. Black boxes in time-frequency plots indicate times and frequencies of interest for cluster-based permutation tests, and white stars indicate electrodes in significant clusters.*

5.4.2.2 Differences between distractor types

We then sought out to determine whether alpha power prior to the distractor differed between distractor conditions in both younger and older adults.

In younger adults, cluster-based permutation tests revealed a significant increase in alpha power in the strong, relative to weak distractor condition in the 9-12 Hz range in the 0.75 s preceding the distractor (p = 0.03). These differences were seen in the left frontal and frontocentral, and right parietal, parieto-occipital and occipital electrodes. In contrast, cluster-based permutation tests revealed no significant difference between strong and weak distractor types in older adults (all $p > 0.07$) (Figure 3A). However, we could not find evidence for a distractor type by age group interaction (no significant clusters) (Figure 3B).

We then investigated whether there were differences in alpha power between each distractor condition and the no distractor condition. In both younger and older adults, cluster-based permutation tests revealed no significant differences in alpha power between the no distractor condition and the strong distractor condition (no significant clusters for young, p = 0.08 for old). In both younger and older adults, alpha power was lower in the weak distractor, compared with the no distractor condition (younger adults: $p = 0.01$, older adults: $p = 0.002$).

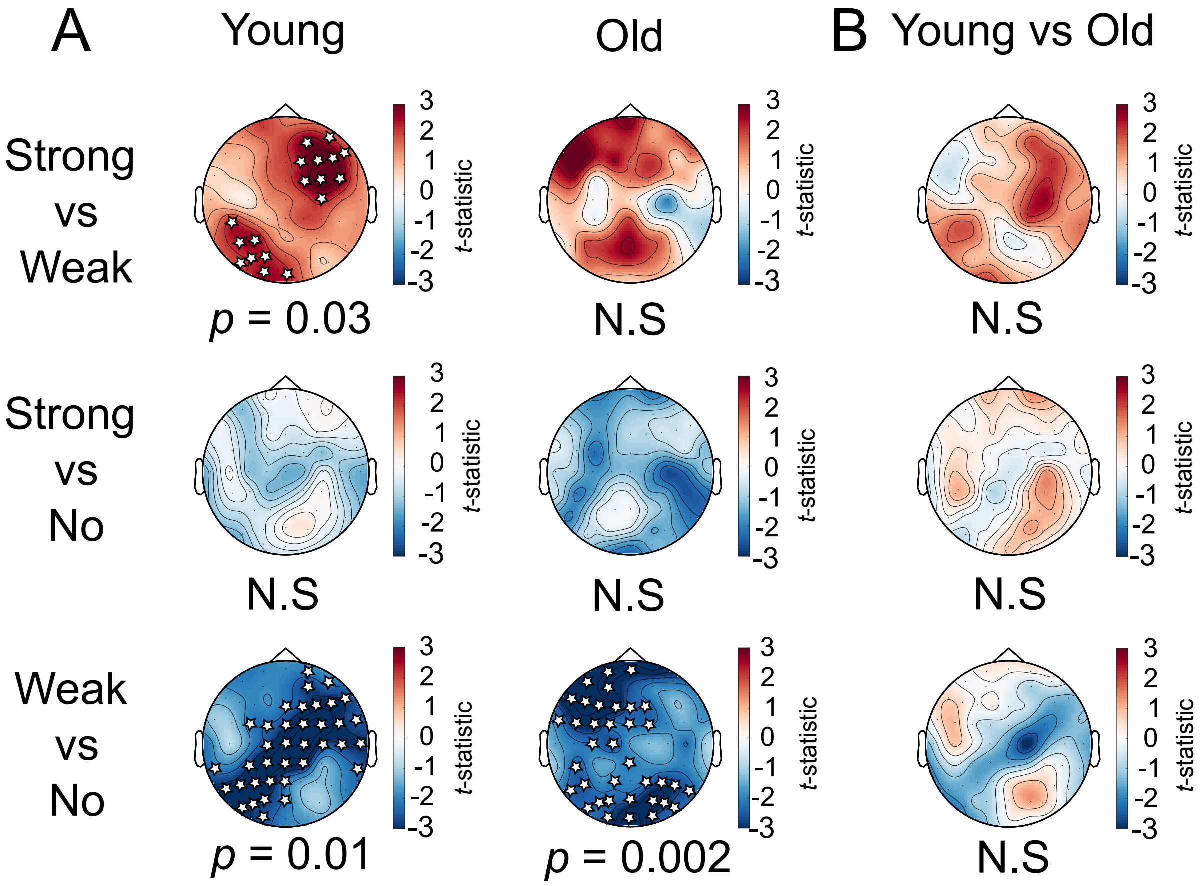

Figure 5.3. Results of cluster-based permutation tests. *A) t-statistics for cluster-based permutation tests comparing the differences in alpha power prior to the distractor for each distractor type. B) t-statistics for cluster-based permutation tests for an interaction effect between age-groups and the difference between distractor types. White stars indicate electrodes in significant clusters.*

5.4.3 Alpha power and task performance

First, we compared correct with incorrect trials from each participant for each distractor condition to determine whether there were differences in alpha power in trials with a correct compared with an incorrect response. Cluster-based permutation tests revealed no significant differences between correct and incorrect trials in any distractor conditions, across each age group (all $p > 0.07$).

To determine whether alpha power prior to the distractor influenced task performance, we conducted a correlation between the difference in alpha power in the 0.75 s before the onset of the distractor (data derived from electrodes in the significant cluster for younger adults, and from all electrodes for older adults) and the difference in accuracy and RT between strong and weak distractor trials. We found a moderate correlation between accuracy and alpha power in younger adults ($r = 0.41$, $p = 0.047$), indicating that participants with stronger difference in alpha power between distractor types demonstrated greater accuracy. However, we did not find a correlation between the difference in alpha power and RT ($r = -0.17$, $p = 0.42$) in younger adults, nor a correlation between the difference in alpha power and difference in accuracy ($r = 0.05$, $p = 0.82$) or difference in RT ($r = -0.03$, p = 0.9) between distractor types in older adults

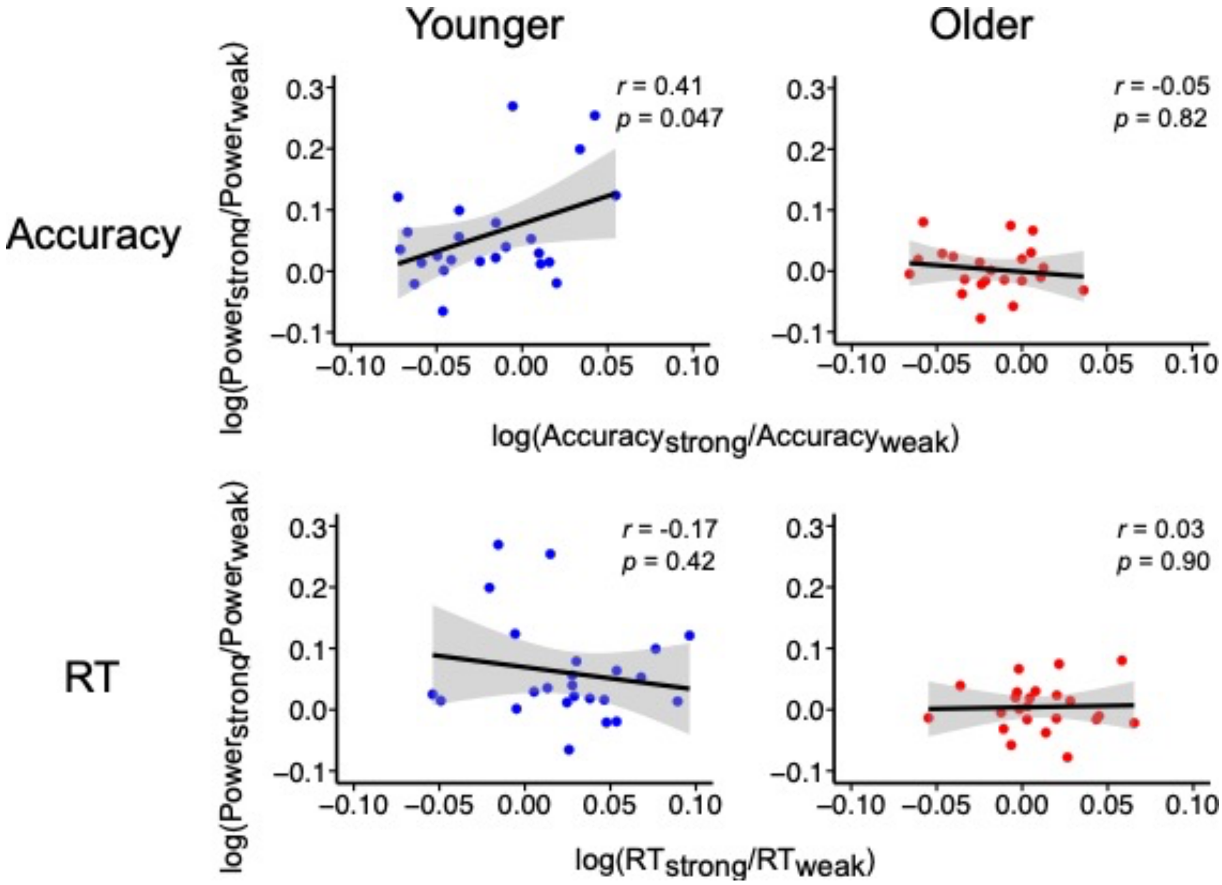

Figure 5.4. Associations between alpha power and WM performance. *Correlations between the difference in alpha power and difference in accuracy (top) and RT (bottom) for younger (left) and older (right) adults.*

5.5 DISCUSSION

In this study, we investigated age differences in alpha oscillatory power in anticipation of distractors of varying strength during the visual WM retention period. Contrary to our hypothesis, we found that when WM load was individualised to each participant, there was no difference in accuracy between age groups in any distractor condition. Despite the lack of behavioural difference, we found that while younger adults demonstrated significant increases in alpha power from baseline prior to the onset of the distractor in the strong and no distractor conditions, decreases in alpha power from baseline were seen in all distractor conditions in older adults. When comparing alpha power between distractor types, younger adults demonstrated greater alpha power before the onset of strong, relative to weak distractors, while older adults demonstrated no difference in alpha power between distractor types. However, there was no difference in alpha power between the strong distractor and no distractor conditions, and surprisingly, alpha power was greater in the no distractor, compared with the weak distractor condition. Finally, alpha power in anticipation of strong distractors was moderately correlated with WM performance in younger adults.

5.5.1 Strong distractors impaired WM performance, but distractor inhibition does not differ between age groups

In this study, we could not find evidence for age-related deficits in distractor inhibition during WM. Regardless of age group, we found that strong distractors impaired WM performance compared with both the weak and no distractor conditions. Although older adults were slower to respond to the probe in each distractor condition and completed the task at a lower WM load on average, we did not find age differences in the cost of distraction.

An absence of age differences is broadly inconsistent with extensive literature detailing the inhibitory deficit hypothesis, which suggests that older adults experience WM deficits due to an inability to inhibit task-irrelevant information (Hasher and Zacks, 1988). Our results are also inconsistent with previous work that has demonstrated that age-related decline in distractor inhibition during visual WM is greater for distractors occurring in the retention period as opposed to those presented in the encoding period (McNab et al., 2015).

However, our results align with the findings of Vaden et al. (2012), who also demonstrated no age-differences in WM performance in the presence of distractors. One explanation for our lack of age difference is that like Vaden et al. (2012), the predictability of the distractor both in temporal onset and strength may have assisted the older adults with ignoring the distractor. Previous work has shown that both distraction (task-irrelevant stimuli) and interruptions (stimuli that must be attended to as a secondary task) negatively impact WM performance, but interrupters disproportionately affect performance in older adults (Clapp and Gazzaley, 2012). The fact that our task only required participants to ignore the distractor rather than respond to it in some way may have been less taxing on executive control systems that are affected by age-related decline (Clapp et al., 2009). Likewise, many studies investigating suppression of task-irrelevant information have used complex stimuli such as faces and scenes (Clapp and Gazzaley, 2012; Gazzaley and D'esposito, 2007), which may be harder to inhibit than simple stimuli like coloured squares.

Finally, we recruited participants for this study via convenience sampling. Convenience sampling of older adults generally results in the recruitment of participants who perform better cognitively than older adults in the wider population (Brodaty et al., 2014), which may explain the lack of age difference seen here.

5.5.2 Younger adults, but not older adults, show increases in alpha power in anticipation of distractors

In the younger adults we found that alpha power in anticipation of distractors was higher in the strong, relative to the weak distractor condition, with some evidence to suggest that higher alpha power before strong distractors is associated with better WM performance. Our results align with those of Bonnefond and Jensen (2012), who found stronger increases in alpha power in occipito-temporal areas in anticipation of strong, compared with weak distractors. However, older adults demonstrated decreases in alpha power in anticipation of distractors, consistent with the findings of Vaden et al. (2012), who also reported that despite successfully ignoring irrelevant information, older adults did not modulate alpha power to suppress distractors.

Alpha oscillations have long been thought to be involved in top-down suppression of task irrelevant information during WM, in tasks both with and without distractors (Bonnefond and Jensen, 2012; Jensen et al., 2002; Jensen and Mazaheri, 2010; Klimesch, 2007). Deficits in top-down suppression have been implicated in age-related declines in WM performance (Gazzaley et al., 2005), and given the suggested role of alpha power in inhibition, it is possible that an inability to modulate alpha power plays a role in impaired suppression of irrelevant information in older adults. Although we found that older adults demonstrated a decrease in alpha power before the distractor as opposed to an increase, suggesting deficits in top-down suppression, we did not find evidence for age-related deficits in distractor inhibition, nor a link between alpha power modulation and behavioural performance in older adults. If the lack of alpha modulation seen in older adults is evidence of altered top-down suppression mechanisms, then it is possible that older adults are using an alternative neural strategy to compensate for their inability to modulate alpha power. At rest, alpha power decreases with advancing age (Babiloni et al., 2006; Lindsley, 1939), which may suggest that alpha power modulation is not a viable neural strategy for older adults to use when ignoring distractions due to their existing low alpha power (Vaden et al., 2012).

Alternatively, the decrease in alpha power prior to the distractor may suggest that older adults are encoding the distractors rather than ignoring them, as decreases in alpha power have been shown to represent increased visual cortex excitability for impending stimuli (Romei et al., 2010, 2008). Older adults may be more susceptible to encoding, rather than inhibiting the distractor, as the 'deletion' facet of the inhibitory deficit hypothesis posits that age related declines in WM performance may be due to older adults allowing task-irrelevant information to enter the WM store, and then being unable to delete the distractions (Hasher and Zacks, 1988). However, the lack of a behavioural difference between younger and older adults suggests that even if older adults are encoding the distractors, their WM performance is not being negatively affected by the distractor, regardless of whether the content of the distractor matches the memory set.

5.5.3 No differences in alpha power between strong and no distractors, despite a difference between strong and weak distractors in younger adults

Visual WM retention is often associated with a decrease in alpha power, which is thought to reflect maintenance of visual information. For example, it has been shown that alpha power decreases with visual WM load and the degree of alpha suppression correlates with individual WM capacity (Fukuda et al., 2015). Given the visual nature of the task, we expected to see decreases in alpha power during the no distractor condition relative to baseline and compared with the strong and weak distractor conditions. Contrary to our hypothesis, we observed no significant difference in alpha power between the strong distractor and no distractor conditions in both young and older adults.

The results of our no distractor condition are at odds with the visual WM literature, and align with the pattern of alpha activity reported in verbal WM tasks, where increases in alpha power are commonly seen during retention (Jensen et al., 2002; Proskovec et al., 2019; Tuladhar et al., 2007; Wang et al., 2016). The increase in alpha power during the verbal WM retention period has been interpreted to reflect inhibition of the visual stream to prevent task-irrelevant information from entering the WM store, even in the absence of visual distractors, which could explain the increase in alpha power in the no distractor condition seen here. While we used a block design to clearly segregate strong and weak distractor trials from no distractor trials, presenting all three conditions in the same session could have led to participants using a similar neural strategy in all conditions, causing a general brain state change even when distractors were not present (van Diepen and Mazaheri, 2017). Therefore, the no distractor condition should be performed in a separate experimental session to confirm whether the demands of distractor conditions induced this change in alpha power, or whether the demands of the visual WM retention period itself, led to increases in alpha power.

Additionally, many visual WM tasks using change detection paradigms that report alpha suppression during the retention period involve tasks with retention periods of approximately 1 s (Adam et al., 2017; Fukuda et al., 2015; Sghirripa et al., 2022). We have previously shown that the alpha suppression seen during retention in tasks with a ~1 s retention period is due to residual alpha suppression from encoding (Sghirripa et al., 2022), which may not be present in longer retention periods. Although Fukuda et al. (2015) performed an experiment with a 4 s retention period and reported alpha suppression for the entirety of retention, participants performed the task at load-1 and load-3, which may not represent a degree of difficulty where participants need to employ neural strategies to prevent task-irrelevant information from entering the WM store. Therefore, more research is required to determine the pattern of alpha power modulation during visual WM, and the functional significance of the effect.

Regardless, it remains unclear why the weak distractor condition resulted in lower alpha power than the no distractor condition, particularly in the younger adult group given the moderate correlation between the difference in alpha power between distractor types and task performance. A potential explanation for this is that some participants may have been encoding the weak distractor while others ignored it, which may have resulted in the aforementioned decreases in alpha power due to visual expectation prior to distractor onset (Romei et al., 2010, 2008); an effect that would not be seen when the participants are aware that no distractor would be present. As the weak distractor did not contain information that would disrupt the memory store of coloured squares, encoding the weak distractor likely did not have deleterious effects on task performance, given the lack of behavioural difference between the weak and no distractor conditions in both age groups.

5.5.4 Conclusion

Supporting the hypothesis that increases in alpha power reflect inhibition of task-irrelevant information, we found that younger adults demonstrate increases in alpha power in anticipation of strong distractors during the visual WM retention period and that this increase supports WM performance. In contrast, older adults demonstrate decreases in alpha power in anticipation of distractors. Despite the differences in alpha power modulation between age groups, we did not find evidence of age-related deficits in distractor inhibition, suggesting that older adults employ different neural strategies to inhibit distractors during visual WM. Further work should now investigate the neural mechanisms underlying distractor inhibition during WM in older adults.

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Chapter 6: General discussion

WM is one of the cognitive functions most vulnerable to age-related decline. Given that WM is crucial for goal-directed behaviours, WM deficits may lead to a lower quality of life for older adults, even in the absence of age-related neurodegenerative conditions such as Alzheimer's disease. One technique that can be used to study the neurophysiological underpinnings of age-related WM decline is EEG, and while much research has investigated the neural oscillatory correlates of WM performance in younger adults, far less has focused on older adults. The experiments presented in this thesis attempted to fill several gaps in the existing EEG literature by exploring: 1) age differences in alpha oscillatory activity during verbal WM at varying loads, 2) age differences in alpha oscillatory activity in response to predictive cues towards memory set presentation time, 3) age differences in the time course of visual WM consolidation, and 4) age differences in the modulation of alpha power in anticipation of distractors during visual WM.

6.1 AGE-DIFFERENCES IN WM PERFORMANCE

In Chapter 1, extensive evidence was outlined for age-related declines in WM performance. On average, older adults demonstrate smaller WM capacities for both verbal and visual information (Park et al., 2002), poorer memory for both features and conjunctions in visual WM (Brockmole et al., 2008), and greater susceptibility to interference from distracting information (Hasher & Zacks, 1988). Unexpectedly, we found little evidence for age differences in WM performance in 3 out of the 4 studies described in this thesis.

The study presented in Chapter 2 involved a modified Sternberg task in which participants were presented with 1, 3 or 5 letters to be retained over a 4 s retention period. Previous research has reported that older adults perform worse than younger adults at higher WM loads (McEvoy et al., 2001; Sander et al., 2012), so it was hypothesised that older adults would perform worse than younger adults at load-3 and 5. While older adults were slower to respond to the probe at all loads, there were no significant age differences in WM capacity. Similar behavioural results were seen in Chapter 3, where a visual WM task consisting of 4 coloured squares presented for either 0.1 or 0.5 s to be retained over a 1 s retention period was employed. Aligning with the processing speed hypothesis (Salthouse, 1992), it was expected that older adults would perform worse than younger adults in the short presentation time condition. Despite older adults showing slower response times to the probe in all conditions, age differences in WM capacity were not found in this study.

The results of the studies in Chapter 2 and 3 are at odds with extensive cognitive ageing literature. An explanation for the lack of age difference in Chapter 2 is that verbal WM is thought to be better preserved with age given that older adults have extensive practice with verbal material over their lifespan (Jenkins et al., 2000; Myerson et al., 1999). However, the study described in Chapter 3 involved a visual WM task, and no age differences were observed there either. An explanation for the lack of age differences in performance across Chapters 2 and 3 is that the WM tasks only assessed rote maintenance, rather than manipulation of items in WM; an ability thought to be spared with age (Craik & Jennings, 1992). For example, studies employing maintenance tasks such as digit span measures do not reliably find age differences in performance (Dobbs & Rule, 1989), while older adults tend to perform worse than younger adults on tasks involving executive functions such as inhibitory control (Gazzaley et al., 2005).

The study presented in Chapter 5 investigated whether distractors of varying strength during the retention period influenced visual WM performance. As distractor inhibition requires high levels of executive and inhibitory control over the contents of WM, it was hypothesised that older adults would show greater performance deficits in the presence of distractors than younger adults. Like Chapters 2 and 3, while older adults were slower to respond to the probe in all distractor conditions, there were no age differences in accuracy at any distractor condition. The behavioural findings in Chapter 5 are inconsistent with the inhibitory deficit hypothesis (Hasher & Zacks, 1988), with studies that have shown greater impacts of distractions in older, compared with younger adults (Clapp & Gazzaley, 2012), and with predictions about the null findings in Chapters 2 and 3 being due to the assessment of rote maintenance rather than executive processes.

However, age-related deficits in WM performance were found in Chapter 4. According to the processing speed hypothesis, processing speed likely limits performance by either slowing the rate at which information can be encoded into WM, or limiting the rate at which a stable WM representation can be formed (Kail & Salthouse, 1994). Given that the study presented in Chapter 3 found no differences between age groups when manipulating time available for encoding, the study in Chapter 4 tested WM consolidation—that is, the rate at which WM contents become stable. In this study, older adults demonstrated poorer WM performance at all loads and were disproportionately affected by short consolidation times at low loads. Together, these results provide evidence for disrupted visual WM consolidation processes in older adults, and evidence for the processing speed hypothesis.

Ultimately, the behavioural results presented throughout this thesis do not align with most of the literature investigating WM in ageing. While some evidence was provided for the processing speed hypothesis in Chapter 4, the findings of Chapter 5 did not provide behavioural evidence for the inhibitory deficit hypothesis, nor were common findings such as poorer WM capacity with age, both in verbal and visual modalities, replicated in Chapters 2 and 3, respectively.

It is possible that the lack of age differences in WM performance seen in this thesis are, in part, due to demographic characteristics of the older adults who participated in this research. Participants in all 4 studies contained in this thesis were recruited via convenience sampling methods such as advertising on the university website, placing flyers in various areas such as on campus, libraries, and gyms (in the CBD and close surrounding suburbs), and using targeted advertisements on social media websites such as Facebook.

Convenience sampling of healthy, cognitively normal older adults has been shown to result in samples consisting of younger and better educated participants with higher socioeconomic status than those recruited via population sampling (Brodaty et al., 2014; Dixon et al., 2004; Ganguli et al., 2015). The act of voluntarily participating in research provides some evidence that the older adults seeking out these experiences live a more active lifestyle than those who do not. Not only did they see the advertisement in a library or gym, suggestive of a physically and cognitively active lifestyle, seeing an advertisement on social media or the university website suggests technological literacy, which in itself, has been shown to be a protective factor against age-related memory decline in healthy older adults (Xavier et al., 2014). Given that the lifestyle factors that are protective against cognitive decline include high educational attainment in early life, physical activity in late life, and cognitive and social engagement in late life (Livingston et al., 2017; Valenzuela & Sachdev, 2007), it is, in hindsight, unsurprising that older adults who participated in the studies described in this thesis demonstrated high cognitive performance.

The aforementioned protective factors are closely linked to the concept of cognitive reserve, which suggests that individuals who are more cognitively active or engaged throughout the lifespan may accrue greater ‘reserve’ which can reduce the impact of, or delay the onset of age-related cognitive decline (Stern, 2009; Stern et al., 2020). In Chapter 2, the influence of cognitive reserve on verbal WM performance was investigated, and it was found that that older adults with high cognitive reserve performed better than those with low cognitive reserve at load-5. Higher cognitive reserve has been shown to be associated with better performance on tasks requiring attention, executive function and working memory (Lavrencic et al., 2018), such as those presented in this thesis. Although cognitive reserve data was not reported in all studies, this information was captured for the participants of each study as a part of standard laboratory procedures. In Chapter 2, years of education and performance on the National Adult Reading Test (Blair & Spreen, 1989) were combined and used as a proxy for cognitive reserve, while Chapters 3, 4 and 5 involved the use of the Cognitive Reserve Index Questionnaire (CRIq) as a cognitive reserve proxy (Nucci et al., 2012). Comparison of the older samples in each study against normative data for the CRIq suggests that majority of the older adults recruited for the studies in Chapters 3,4 and 5 had medium to high cognitive reserve (Appendix I), which may explain the high level of performance in older adults and lack of age-differences in WM performance observed throughout this thesis.

Interestingly, cognitive reserve has been shown to be unrelated to processing speed abilities (Lavrencic et al., 2018). The task used in Chapter 4, where age differences in WM performance were identified, was highly dependent on processing speed to support performance compared to the other WM tasks employed in this thesis. Perhaps when processing speed is heavily taxed, for example, by allowing only short periods for WM consolidation, cognitive reserve can no longer exert protective effects over WM performance– a theory presenting an avenue for further investigation.

There is likely no straightforward solution to solving self-selection bias when conducting research on healthy older adults. As an initial step, recruitment strategies should target a diverse array of older adults in the community, for example, by placing recruitment notices in a wider range of locations, in local/council magazines that target older adults, or potentially visiting community centres or retirement villages to recruit participants. If it is difficult to recruit older adults who might have lower educational attainment or socioeconomic status, perhaps understanding the reasons why older adults participate in research and devising ways to make research participation more accessible to all community dwelling older adults should be a priority for cognitive neuroscientists interested in healthy ageing.

6.2 ALPHA OSCILLATIONS DURING WM PERFORMANCE

As described in Chapter 1, slowing of the alpha rhythm and reductions in alpha power are some of the most prominent hallmarks of brain ageing that can be measured using EEG. Given that alpha oscillatory activity has been shown to support WM performance in younger adults, the aims of Chapters 2, 3 and 5 were to investigate the modulation of alpha oscillations during WM performance in both younger and older adults. In these chapters, it was demonstrated that alpha power is modulated during WM performance in both age groups, but the location, direction and magnitude of this effect depends heavily on task factors.

6.2.1 Age differences

The study contained in Chapter 2 investigated load-dependent modulation of both alpha power and alpha peak frequency. Lower alpha power and peak frequency was observed in older adults during all stages of the task, but a similar pattern of alpha power modulation was present in both age groups— decreases in alpha power with WM load during encoding and decreases in alpha power during the retention period of load-5 trials. However, task-modulation of alpha power and alpha peak frequency did not correlate with WM performance in either age group.

The study described in Chapter 2 provides little evidence for age differences in alpha oscillatory activity during verbal WM performance. A prior study employing a similar, 6-letter modified Sternberg task demonstrated that older adults showed increases in alpha power during the retention period (Proskovec et al., 2016). The increase in alpha power in this study was interpreted to reflect CRUNCH, that is, recruitment of more neural resources (in this case, alpha power) to cope with higher task difficulties (Reuter-Lorenz & Cappell, 2008). One possibility for the lack of age differences beyond the age-related decreases of power and frequency with age, is that the task was not difficult enough to elicit meaningful differences in alpha power or frequency between age groups. Older adults performed as well as, or better, than younger adults in this study, potentially suggesting both age-groups were using similar neural strategies to complete the task.

In Chapter 3, a similar pattern of age differences was observed as in Chapter 2, despite investigating visual WM. This study examined the influence of memory set presentation time and predictive cues on alpha power modulation during visual WM. Given that ageing is associated with poorer top-down modulation in response to predictive cues during WM performance (Bollinger et al., 2011; Gazzaley et al., 2005; Zanto et al., 2010), it was expected that older adults would display no behavioural benefit for the cue denoting presentation time and weaker alpha suppression in preparation of the memory set. Despite older adults demonstrating less alpha suppression in anticipation of the memory set and during the retention period of trials with a short presentation time, there is little evidence to suggest this is because of deficits in top-down modulation due to a lack of behavioural difference between age groups and between conditions. As in Chapter 2, this study provided no evidence that alpha power modulation at any task stage was linked to task performance in either age group.

The only study in this thesis where a clear difference in alpha oscillatory activity between age groups was found was in Chapter 5. In this study, age differences in alpha power modulation in anticipation of distractors during the retention period of visual WM was investigated. While younger adults demonstrated increases in alpha power in anticipation of distractors, with larger increases in alpha power before a strong, relative to a weak distractor, decreases in alpha power before both strong and weak distractors was observed in older adults. If alpha power increases are thought to reflect sensory gating of information (Jensen & Mazaheri, 2010), then an inability for older adults to increase alpha power before a distractor could be indicative of altered top-down modulation. However, a lack of age difference in task performance and the finding that alpha power before the distractor did not correlate with task performance in older adults weakens this claim.

The work contained in this thesis, while confirming the presence of age-related decreases in alpha power and peak frequency, provides little evidence for these changes being implicated in age-related WM deficits. Indeed, this is most likely a reflection of the fact that age differences in WM performance were not detected in any of the studies involving EEG. Though this thesis stands in contrast to the literature linking age-related changes in alpha oscillations to WM deficits, that is not to say that a relationship between the two does not exist, and more research is required to confirm the functional relevance of alpha oscillations during WM performance. However, there are some methodological factors worth considering when investigating changes in alpha activity during WM in older adults.

In Chapter 1, the ‘neural noise’ hypothesis of ageing was introduced (Section 1.6.4) which suggests that with advancing age, a diminished signal to noise ratio in the brain leads to less precise memory representations (Crossman & Szafran, 1956). Recently, it has been suggested that neural noise can be estimated from EEG, with neural noise potentially reflected in the distribution of the power spectral density across the frequency spectrum (Voytek et al., 2015; Voytek & Knight, 2015). When considering the power spectrum in its entirety (rather than examining predefined frequency ranges), the decrease of low frequency power and increase in high-frequency power with age may be due to an increase in 1/f neural noise, causing a flattening of the power spectrum (Hong & Rebec, 2012; Voytek et al., 2015; Voytek & Knight, 2015). Therefore, if the shape of the power spectrum is changing with age due to this ‘aperiodic’ 1/f-like noise, it is important to understand how these changes influence the measurements of oscillatory activity (figure 6.1).

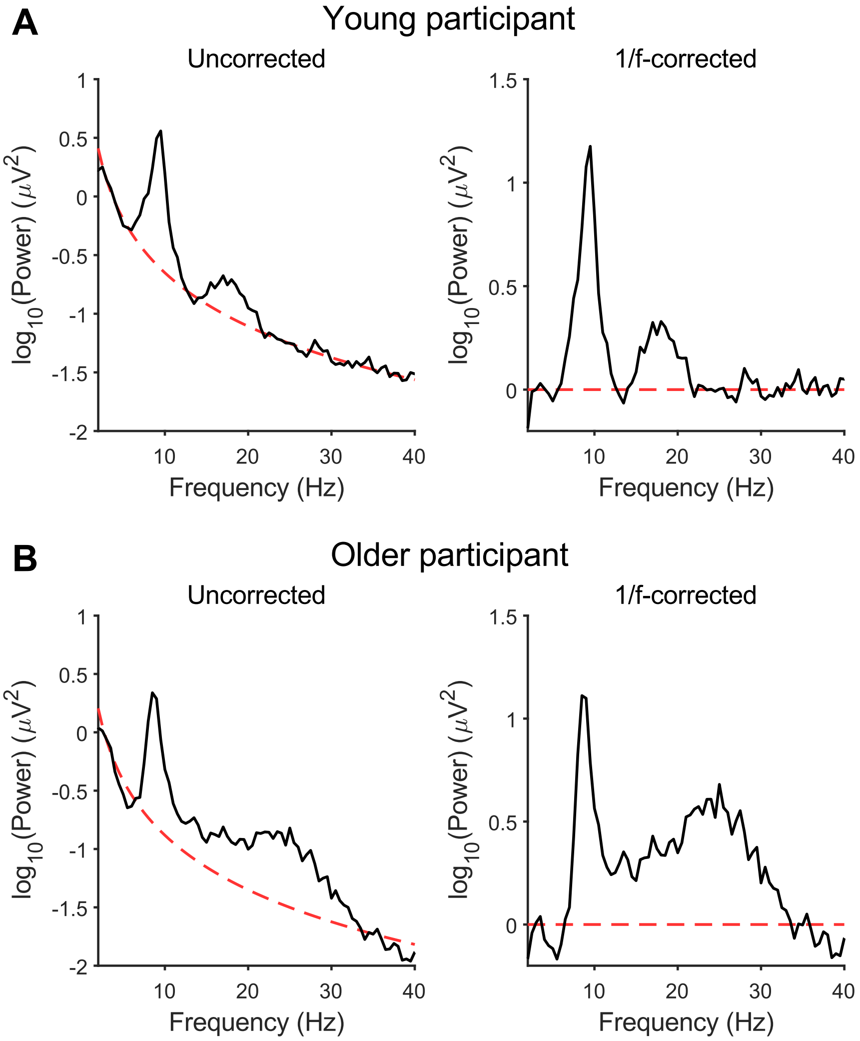

Figure 6.1. Example power spectrum with aperiodic component. *Resting EEG power spectrum from (A) one younger and (B) one older participant. The 1/f-like aperiodic component (dashed red line) was estimated from the original power spectrum (left) and subtracted to provide a 1/f-corrected power spectrum (right). Adapted from figure 1 in Merkin et al. (2021).*

Accordingly, a recent study examining the periodic and aperiodic components of resting EEG in younger and older adults found that after accounting for the aperiodic component, age-related slowing of alpha peak frequency and reductions in alpha power were still present, but the age difference in alpha power between young and older adults was reduced (Donoghue et al., 2020). To expand upon these findings, a study from our group compared resting alpha oscillatory and aperiodic activity in a larger sample of younger and older adults (Merkin et al., 2021). Before correcting for the aperiodic component in this study, older adults showed lower alpha power and peak frequency than younger adults. However, the age difference in alpha power was no longer present when correcting for the aperiodic component. Indeed, the confounding effect of aperiodic activity on task related alpha power has been investigated in younger adults. A recent study investigating the relationship between aperiodic activity, alpha power and processing speed found that alpha power and processing speed were no longer correlated when accounting for aperiodic activity (Ouyang et al., 2019).

In the studies contained in this thesis, the aperiodic component was not corrected for when conducting time-frequency analyses, which brings the results of Chapters 2 and 3 into doubt. In these chapters, the task-related patterns of alpha power modulation were very similar between age groups, but older adults demonstrated lower alpha power in general. It is possible that age differences in the aperiodic component were driving the lower alpha power seen in older compared to younger adults in these studies. The same could be said for the results of Chapter 5, but given the magnitude of difference between younger and older adults in this study, it is unlikely that the aperiodic component can entirely account for the results observed. Nevertheless, it would be interesting to determine whether the magnitude of difference is reduced when accounting for the aperiodic component.

Along with the aperiodic component of the power spectrum, it is also worth considering how the alpha band is defined when investigating age-related changes in alpha power. Many studies involve analyses where alpha is defined as a narrow band (usually 8-12 Hz), and spectral activity is averaged over that range for all participants regardless of age. However, the long reported decrease in alpha peak frequency with age (Klimesch et al., 1993; Lindsley, 1939) suggests that alpha power may fall outside the fixed alpha frequency bands, or activity in theta/beta bands may be included in the alpha window if the age-related slowing of alpha peak frequency is not considered. In Chapter 2, both age- and task-related changes in alpha peak frequency were accounted for by defining the alpha band as +/- 2 Hz of alpha peak frequency (Klimesch, 1999, 1997). The alpha band in Chapter 3 was not individualised as there was no strong hypothesis for frequency bands where condition and age differences were expected. In Chapter 5, the average of all participants and conditions was used to guide time frequency analyses.

There have been several suggestions for how to best capture the alpha band, particularly when investigating age-related changes in alpha. The peak frequency method has been widely applied as an anchor point to determine the frequency band cut-offs for theta, alpha and beta bands, and involves determining alpha peak frequency and using an interval above and below the peak as the alpha band (as seen in Chapter 2) (Capotosto et al., 2009; Klimesch, 1997; Klimesch et al., 2004). Using the peak frequency is limited when there are multiple peaks present, as commonly seen in EEG data. In these cases, basing the alpha band on the centre of gravity frequency is more appropriate, that is, the weighted sum of spectral estimates divided by the total alpha power (Klimesch, 1999). The centre of gravity reflects the central tendency of alpha power and therefore is likely to be a better representation of the average alpha activity. Finally, channel reactivity-based methods (Goljahani et al., 2012) rely on capturing the responsiveness of alpha rhythms to task stimuli, regardless of the presence of peaks in the EEG spectra. Many methods have been suggested to account for the shifting of alpha peak frequency, and while changes in the alpha peak should be accounted for, it is unclear which of these approaches will produce the most valid results when measuring age-related changes in the alpha rhythm. Therefore, more work should be done to investigate the optimal way to capture age-related changes in alpha oscillatory activity.

6.2.2 What is the functional significance of alpha oscillations during WM?

In Chapter 1, the multitude of conflicts in the literature regarding the strength, direction, and location of alpha power modulation during WM performance, and the fact that these patterns depend highly on stimulus type (e.g., verbal or visual) and stimulus presentation method (e.g., sequential, simultaneous, or continuous) were outlined. The work contained in this thesis potentially offers some input on current arguments, while also introducing a range of further questions about the physiological relevance of alpha activity during WM. For the sake of clarity and alignment with the existing literature, the discussion in this section will be limited to EEG data from the younger adults.

The study in Chapter 2 involved a verbal WM task with 1, 3 or 5 letters presented simultaneously. The majority of the research employing similar tasks have reported increases in alpha power during the retention period with increasing load (Jensen et al., 2002; Proskovec et al., 2019; Tuladhar et al., 2007; Wang et al., 2016), with this pattern of alpha modulation interpreted to reflect sensory gating of the visual system to prevent disruption to the WM store. In this study, alpha power was lower in the retention period of load-5 trials compared with load-3 and load-1 trials, and the only condition where both younger and older adults showed increases in alpha power from fixation was load-3. The findings of this study contradict the literature and do not provide evidence for the sensory gating hypothesis, with the decrease in alpha power we observed at load-5 potentially reflecting a strategy in which the visual cortex is engaged to maintain the content of WM.

Studies employing visual WM tasks tend to report a decrease in alpha power during the retention period which strengthens with load–the opposite pattern seen in verbal WM tasks

(Adam et al., 2017; Fukuda et al., 2015; Sauseng et al., 2009). The decrease in alpha power has been interpreted to reflect activation of visual cortical areas to actively maintain the visual WM representations. However, an incidental finding from Chapter 3 places some doubt about functional relevance of alpha power suppression during visual WM retention. In this study, when oscillatory power during the retention periods for trials with short and long presentation times were compared, there were stark differences in alpha and theta power modulation. However, these differences were no longer present when trials were compared from the beginning of encoding, suggesting that the pattern of alpha suppression and increases in theta power are time locked to the memory set rather than the retention period.

The results of Chapter 3 therefore raise questions about the functional relevance of alpha power during visual WM retention. It could be that like the alpha suppression seen with load during the encoding period in Chapter 2, alpha suppression during retention is due to encoding or attention related processes that bleed into the retention period. Given that change detection tasks commonly involve short retention periods of ~1 s in duration, as seen in Fukuda et al. (2015) and Adam et al. (2017), alpha suppression in these studies may reflect encoding related processes. Evidence against this account includes that alpha suppression during retention has been shown to correlate with WM capacity and strengthens with WM load (Fukuda et al., 2015). Though these findings provide evidence for alpha suppression reflecting storage of visual information, the task employed by Fukuda et al. (2015) did not control for visual input during encoding. Therefore, greater alpha suppression with load could simply reflect visual input of more items at the encoding stage, which has then been measured as part of the retention period.

As discussed in Chapter 3, the results of this study can only offer speculation about the role of alpha suppression in WM. However, one suggestion is that alpha suppression that is time locked to the memory set and persists into early retention could reflect WM consolidation—the process by which sensory input is transformed into a stable memory representation (Jolicœur & Dell'Acqua, 1998). WM consolidation was the focus of Chapter 4, and a clear extension of the work in this thesis would be to investigate whether presenting masks after the memory set changes the pattern of alpha power modulation in early retention periods of WM tasks.

As if the results in Chapters 2 and 3 were not difficult enough to interpret within the scope of existing literature, the results of Chapter 5 also ask more questions than they answer about the role of alpha oscillations during WM. Key evidence for the role of alpha power in sensory gating comes from studies investigating distractor inhibition during WM, where increases in alpha power are seen prior to the distractor appearing during the retention period (Bonnefond & Jensen, 2012; Sghirripa et al., 2020). The study described in Chapter 5 provided further evidence for this account, with larger increases in alpha power demonstrated before the onset of strong, relative to weak distractors that seemed to support WM performance in younger adults. However, increases in alpha power in the no distractor condition were also observed, and there were no significant differences in alpha power between the strong and no distractor conditions.

The findings of the no distractor condition in Chapter 5 are confusing in two ways. First, it is currently unclear whether the increase in alpha power in the no distractor condition is due to a general shift in brain state due to the distractor conditions during the task. Second, according to the visual WM literature, alpha power is expected to decrease during retention. If alpha power suppression is time locked to encoding, it is possible that the longer retention period provides more time for alpha to 'recover' after visual input, leading to increases in alpha power that are not observed in short retention periods. Regardless, conducting the no distractor condition in a separate experimental session would be a logical step to clarify these points.

The mixed findings in this thesis, and in the literature, suggests that more replication studies are required in this field. A recent systematic review into oscillatory activity in verbal and visual WM retention periods demonstrated little consensus on the pattern of alpha power modulation, especially in visual WM tasks. For example, of the studies included in the review, 20% of verbal WM studies reported a decrease, and 80% reported an increase in alpha power during retention. However, the proportion in visual WM studies was approximately 40/60%, and the stimulus presentation method (e.g., simultaneous vs sequential) failed to explain the directionality of alpha (Pavlov & Kotchoubey, 2022). As such, it is currently difficult to make definitive statements on the role of alpha power in supporting WM performance.

Based on the findings of Chapters 2, 3 and 5, there are several recommendations worth considering when designing tasks to investigate the neurophysiological underpinnings of WM using EEG. First, though simplistic, many tasks do not balance the amount of visual input at the encoding stage when manipulating WM load. Maintaining equal sensory input would assist in ruling out that alpha suppression is merely due to the number of stimuli seen, and not due to the memory content. Second, employing a consolidation period and pattern mask to rule out the influence of residual sensory trace left by the memory set on oscillatory power during the retention period is recommended. Though it is currently unclear whether this alone would answer any questions regarding the functional relevance of alpha power during WM, disrupting the sensory trace after encoding may aid in creating a clearer delineation between the encoding and retention periods (Woodman & Vogel, 2005). Finally, tasks involving retention periods of longer than 1 s are likely required to understand the time course and functional relevance of alpha power modulation during visual WM.

6.3 IMPLICATIONS AND FUTURE DIRECTIONS

A potential implication for this area of research is to use EEG findings to guide the application of brain stimulation protocols such as transcranial alternating current stimulation (tACS) to entrain oscillatory activity. tACS involves applying a low intensity, sinusoidal electrical current to the brain through electrodes on the scalp and is thought to modulate rhythmic brain activity that can be behaviourally relevant. For example, a study investigating inhibitory abilities in ageing found that applying alpha, but not theta or gamma tACS, significantly improved performance on a WM task with retro cues, and provided causal evidence for the role of alpha oscillations in WM (Borghini et al., 2018). Although age-related differences in alpha power were less apparent during the maintenance tasks described in Chapters 2 and 3, given the stark differences in alpha power observed in Chapter 5, perhaps entraining alpha oscillatory activity could improve distractor inhibition performance in older adults who perform worse than younger adults on the task. Identifying patterns of oscillatory activity that are relevant for task performance in older adults and applying tACS to entrain that activity may be a way to improve cognitive performance with age, as well as determine causal relationships between neural oscillatory activity and behaviour.

A clear extension of the work presented here would be to employ other neuroimaging methods such as fMRI to investigate the neural correlates of WM performance. Much of the research into the cognitive neuroscience theories of cognitive ageing (e.g., frontal lobe hypothesis, top-down modulation, CRUNCH) have been based on research using fMRI due to its high spatial resolution. Despite EEG possessing high temporal resolution, it is limited in spatial resolution and therefore cannot provide insight into the activity of specific brain regions during WM. Concurrent EEG and fMRI, although methodologically demanding, could combine the advantages of both methods and provide a more complete overview of how age-related structural and functional brain changes contribute to WM decline in healthy older adults.

Finally, instead of comparing younger and older adults, a future direction could be to collect data from diverse samples of community dwelling older adults to understand the neurophysiological, cognitive and lifestyle differences between those who demonstrate high WM performance and those who do not. Given the relevance of convenience sampling bias in the studies presented, this would be an intriguing and important extension of the work contained in this thesis.

6.4 CONCLUDING REMARKS

Advancing age is associated with a progressive decline in cognitive function, with WM performance being particularly vulnerable to age-related decline. Though EEG has been used to investigate the neurophysiological underpinnings of WM in younger adults, less research has used EEG to investigate WM performance in older adults. Unexpectedly, the work in this thesis found little evidence for WM decline in older adults and accordingly, few differences in neural activity, as measured by EEG, between age groups. The research in this thesis raises multiple questions about the functional relevance of alpha oscillatory activity in ageing and WM performance, suggesting that more work is required to understand the physiological relevance of neural oscillations in cognitive ageing.

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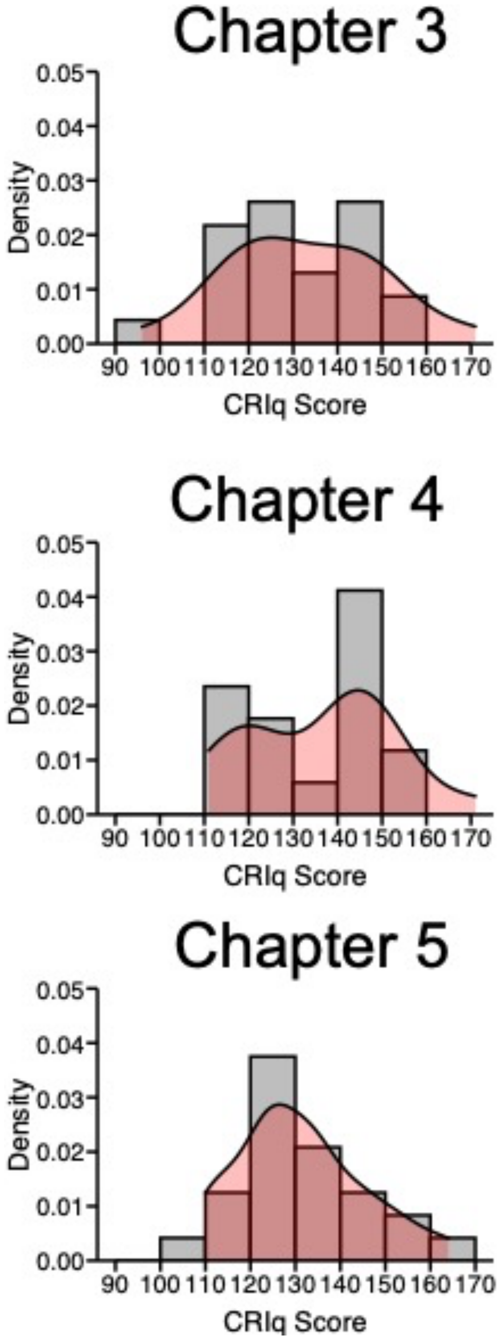
6.6 APPENDIX I: COGNITIVE RESERVE INDEX QUESTIONNAIRE SCORES


Chapter 3

Chapter 4

Chapter 5

Figure 6.2. CRIq Scores. *Histograms of Cognitive Reserve Index Questionnaire (CRIq) scores from Chapters 3, 4 and 5 (the CRIq was not collected in Chapter 2). Scores ranging between 85 to 114 indicate medium, 115 to 130 indicates medium-high, and greater than 130 indicates high cognitive reserve.*

6.7 PUBLICATIONS ARISING FROM THIS THESIS

Sghirripa, S., Graetz, L., Merkin, A., Rogasch, N. C., Semmler, J. G., & Goldsworthy, M. R. (2021). Load-dependent modulation of alpha oscillations during working memory encoding and retention in young and older adults. *Psychophysiology*, *58*(2), e13719. https://doi.org/10.1111/psyp.13719

Sghirripa, S., Graetz, L., Rogasch, N. C., Semmler, J. G., & Goldsworthy, M. R. (2022). Does predictive cueing of presentation time modulate alpha power and facilitate visual working memory performance in younger and older adults? *Brain and Cognition*, *159*, 105861. https://doi.org/10.1016/j.bandc.2022.105861

Sghirripa, S., Semmler, J., & Goldsworthy, M. (2022). Age-Related Changes in Visual Working Memory Consolidation. *Under review*

6.8 OTHER WORK PERFORMED DURING THIS PHD

Sghirripa, S., Graetz, L., Merkin, A., Rogasch, N. C., Ridding, M. C., Semmler, J. G., & Goldsworthy, M. R. (2020). The Role of Alpha Power in the Suppression of Anticipated Distractors During Verbal Working Memory. *Brain Topography*. https://doi.org/10.1007/s10548-020-00810-4

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