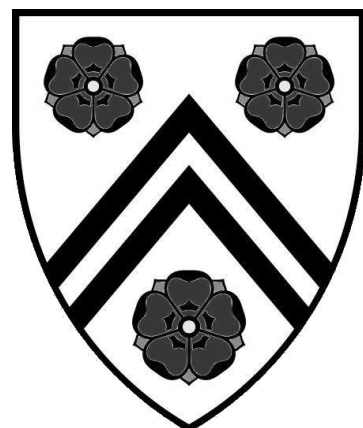
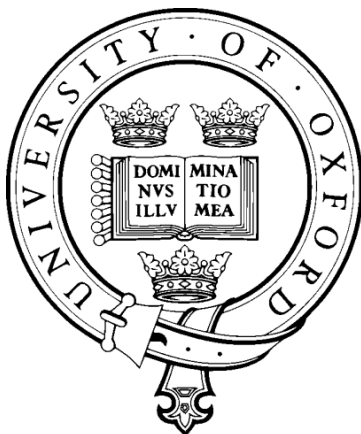


Working Memory in Healthy Ageing

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DPhil Thesis, Trinity Term, 2016



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A dissertation submitted in partial fulfilment of the requirements for the degree of
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ABSTRACT

This thesis is concerned with the age-related changes in working memory (WM), and the inter-individual differences in cognitive and neural mechanisms that correspond to healthy versus poor ageing of WM function. The first half of this thesis focusses on the age-related decline in WM and whether preserved top-down attentional control could mitigate such deficits. In Chapter 2, I present a functional MRI study showing that older adults reliably recruit brain networks that subserve cognitive control, which work in concert with the task relevant sensory areas during effective selective WM. In Chapter 3, I show that older adults retain flexible control over WM representations, and this ability corresponded to the reliable recruitment of neural signals of orienting attention qualitatively similar to those observed in younger adults. Magnetoencephalographic recordings showed that the neural dynamics during orienting attention within WM was predictive of good performance, demonstrating that the more efficient the process of orienting within WM to select the target item, the better the memory representation can be preserved for upcoming behaviour. In the second half of this thesis, I explored whether WM for affective content has a special status in healthy ageing. In Chapter 4, I developed an emotional WM precision task to measure WM abilities for emotional content appropriate for elderly adults. In Chapter 5, I tested a group of young and older adults on WM and perceptual-matching abilities for emotional faces. The results suggest that older adults show a general impairment in task performance, but possibly with some preservation in the ability to maintain emotional content in WM. There were marked differences in how the emotional information was processed between age groups, in which older adults have a tendency to represent negative stimuli as less negative than younger adults in perception and WM, and tended to show a positive interpretation of the valence of more ambiguous emotional stimuli. In Chapter 6, I summarise the findings presented in this thesis, discuss the implications of the key findings, and consider some suggestions for future studies that aim to elucidate the mechanisms of WM in healthy ageing.

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1. Main Introduction

Chapter Abstract

This introduction gives an overview of the changes in cognition and neural function that come with normal ageing, with a focus on working memory (WM) and the control mechanisms that play a role in supporting WM function. A special emphasis is placed on the role of selective attention for WM, and how attention can support WM function. I propose that, although aspects of WM, such as capacity, decline with age, preserved cognitive processes such as attentional control that can support WM function may help mitigate such deficits. In the final section, I outline the scope and structure of the thesis, illustrating the approach taken in this thesis.

1.1. Overview

With each passing day, we experience new sensations, form new memories, and lose old memories. Through this passage of time, we also grow older. One might think: “Though my body gets older, *I* do not change. My mind is who I am”. The brain and mind, which are responsible for the higher faculties of human cognition and arguably define one’s personal identity, do in fact show a great deal of change with age, including declines in performance for cognitively tasks. Although we may become wiser with the passage of time, our biological machinery suffers along the way. Presumably, our knowledge and experience accumulated over the years cannot help with this inevitable decline of biological hardware. However, if we examine the cognitive studies in elderly adults and current theoretical perspectives on healthy ageing, we will find that this is not necessarily the case. There are some older individuals who exhibit poor memory and poor intellectual capacities, but there are others who show exceptional memory, and outstanding social skills. Could there be reasons for these inter-individual differences? Could the highly functioning elders have adopted a better way to cope with cognitive changes in old age? For instance, despite a decline in brain processes that support memory, they could have developed a cognitive strategy for remembering only the most relevant things and therefore exhibit superior memory performance in comparison to their peers.

Working memory (WM), the ability to store information over a short period of time, is an essential cognitive function that supports many aspects of higher cognition and our ability to perform day-to-day tasks (Baddeley & Hitch, 1974; Miyake & Shah, 1999). It also declines with age (Salthouse, 2010). Interestingly, there is high inter-individual variability in memory function even within elderly populations (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012). How do WM mechanisms in the brain change in healthy ageing, and do other processes that support good WM, such as selective attention, also show age-related

declines? Does WM decline across the board, or does the degree of decline depend on the content that is to be maintained, such as its affective valence or motivational relevance to the observer?

In this thesis, I will investigate the cognitive and neural mechanisms that support WM function in healthy ageing, focussing on top-down attentional control functions and emotional content in relation to WM function. In order to test these questions, I conducted behavioural and functional neuroimaging experiments with human volunteers from younger and older groups whilst they perform WM tasks. I will chart the age-related changes in cognition, and examine the inter-individual differences within elderly adults to find the behavioural and neural markers that correspond to successful cognitive ageing. The purpose of these investigations is to understand the cognitive and neural mechanisms of WM that are preserved in healthy ageing, those that deteriorate with age, and the individual differences that correspond to better preservation of cognitive abilities that support healthy cognitive ageing. This thesis comes in two parts with regard to exploration of WM in elderly participants: 1) Studying attentional control over WM and 2) Exploring the role of affective content in WM.

In this introductory section, I will outline the literature relevant to the questions addressed in the experimental chapters of the thesis. First, I will discuss age-related changes in the behavioural and neural markers related to WM and cognitive processes associated with WM. Next, I will describe studies showing that selective attention can enhance WM performance in young adults, which, if preserved in ageing, could be a useful vehicle for the mitigation of WM deficits in older adults. I will also discuss how affective material can affect attention and WM processes, describe some work which suggests that affective material might have a special status for elderly adults, and that WM for such material could show relative

preservation in healthy ageing compared to stimuli that have less personal significance for the observer. The final section of the chapter will outline the structure of the thesis and present an overview of the findings and their significance.

1.2. Cognitive and neural mechanisms of working memory in healthy ageing

1.2.1. Age-related changes in cognition

Most cognitive abilities decline as we grow old. Frustrations about declines in cognition such as memory, motor skills, or learning new material are commonplace in elderly adults. However, cognitive abilities do not all decline in a homogenous fashion with increasing age (Hedden & Gabrieli, 2004). Crystallised intelligence, defined as the knowledge and abilities that have been learnt over years and well practiced, remains stable (Salthouse, 2012). Vocabulary and language abilities also remain intact, and can even show improvements in old age (Hedden & Gabrieli, 2004; Nyberg et al., 2012). In contrast, WM, long-term memory, and the ability to multi-task decline with age (Harada, Natelson Love, & Triebel, 2013; Hedden & Gabrieli, 2004; Nyberg et al., 2012). Fluid intelligence, the ability to think logically and solve problems in novel situations, which is supported by WM and other aspects of flexible cognition, also declines with age (Kievit et al., 2014; Salthouse, 2010). Notably, fluid intelligence correlates with tests that assess day-to-day functioning in society (Salthouse, 2012; Willis & Schaie, 1968), and is likely a key factor that relates to the degree of healthy cognition in ageing.

1.2.2. Working Memory

WM is the cognitive function that enables us to retain information over short periods in the absence of sensory stimulation, which supports our ability to maintain and manipulate information in mind for purposeful behaviour (Baddeley & Hitch, 1974; Miyake & Shah, 1999). In order to accomplish many of our daily cognitive goals, it is wise, and often

necessary, to arrange the task into a sequence of sub-tasks and actions. This requires the short-term storage and deliberation of information in mind specific for the task at hand (e.g. Shallice & Burgess, 1991). Conceptually, WM as a temporary information store is a basic requirement for many high-level cognitive processes, supporting our ability to perform tasks that involve problem solving, multitasking, learning new material, and even encoding into long-term memory. As such, many researchers consider WM a fundamental aspect of cognition (Baddeley & Hitch, 1974; Miyake & Shah, 1999). It is perhaps unsurprising then, that estimates of WM function correlate strongly with measures of fluid intelligence, IQ, academic achievement, and other measures of cognition (Conway, Cowan, Bunting, Theriault, & Minkoff, 2002; Cowan, 2005; Engle, Tuholski, Laughlin, & Conway, 1999; Fukuda, Vogel, Mayr, & Awh, 2010; Kane & Engle, 2002; Unsworth & Engle, 2005). There are also strong correlations between WM measures and tasks that require the maintenance and application of rules (Kane, Bleckley, Conway, & Engle, 2001; Kane & Engle, 2003), which suggests that a deficit in task set or goal maintenance could be due to low WM capacity. Relatedly, WM is compromised in many mental disorders including schizophrenia (J. Lee & Park, 2005), attention deficit hyperactivity disorder (ADHD; Barkley, 1997), and Alzheimer's disease (Baddeley, Bressi, Della Sala, Logie, & Spinnler, 1991).

The amount of information that can be kept in the short-term store, commonly referred to as WM capacity, has been quantified using span measures (e.g. Daneman & Carpenter, 1980; Kane et al., 2004; Shah & Miyake, 1996)) and several variants of the delayed match-to-sample task (e.g. Luck & Vogel, 1997; E. K. Miller, Li, & Desimone, 1991). In span measures, individuals are presented with a sequence of items (e.g. words, letters, digits), and asked to reproduce the items (e.g. vocally) immediately after. Participants can be asked to recall the items in the order they were presented in (forward span), in reverse order (backward span), or in ascending order (sequence span). In delayed-match-to-sample tasks, participants

are presented with a number of stimuli (e.g. coloured squares, spatial locations, oriented bars) to be encoded into WM. The stimuli disappear from the screen and the participant has to retain the item(s) in WM over this maintenance period. At the end of the trial, participants are asked to recall the memory item(s) using a response¹. These tasks have been used widely in neuropsychological batteries and in numerous psychophysical and neuroscientific studies of WM function (e.g. Baddeley & Hitch, 1974; Bays & Husain, 2008; Cowan, 2001; Daneman & Carpenter, 1980; Luck & Vogel, 1997; Ranganath, Cohen, Dam, & D'Esposito, 2004; Todd & Marois, 2004; Vogel & Machizawa, 2004; Wilken & Ma, 2004; Xu & Chun, 2006; W. Zhang & Luck, 2008).

It is worth noting that different researchers have different definitions of the timescale of what is considered WM. In the paradigms noted above, WM is considered as representations actively held in mind, at a relatively short timescale (in the order of seconds). However, WM has also been considered in longer timescales (in the order of minutes), such that items in WM are those that are generally available to the individual from the recent past (e.g. past trials) and can disrupt or improve performance in the current task (e.g. Hasher, Lustig, & Zacks, 2007). In this thesis, my use of WM mostly follows the first definition, except for when discussing the work by Hasher and colleagues (in section 1.2.4. Declines in inhibitory control for working memory).

¹ Paradigms differ in the ways the participant is tested on or reports the item(s). In change-detection tasks, participants are presented with a test array at the end of the trial, which could be the same or different to the initial stimulus array (e.g. one colour in the stimulus array has been changed to a different colour). In another version (partial report), a single test stimulus appears on the screen (e.g. a coloured square), and the participant responds whether this item or its feature was present in the initial stimulus array, or if it was the same or different stimulus to the item in the array at the test stimulus' location. In spatial WM tasks, participants sometimes report the location by pointing at the target location, or making an eye movement toward the location (delayed-saccade task). In orientation memory tasks, participants might be asked to judge whether the orientation of a test bar was tilted clockwise or counter-clockwise relative to the orientation in the initial array, or report the actual orientation using a mouse or keyboard. They are sometimes asked to recall the orientation by clicking on a location on a circle, or adjust a bar on the screen to what they remembered it to be. In colour WM tasks, they might also be asked to recall the colour in memory by clicking on a colour wheel (precision report).

1.2.3. Age-related declines in working memory

Intuitively, the more information an individual can store in WM any given time, the more likely they will have the information for the appropriate course of action. Traditional views support the idea that the larger the capacity the better (e.g. Baddeley, 1986, 1992; Just & Carpenter, 1992), citing evidence that measures of WM capacity are positively correlated with performance on a variety of cognitive tasks as well as IQ and fluid intelligence measures (Conway et al., 2002; Cowan, 2005; Engle et al., 1999; Fukuda et al., 2010; Kane & Engle, 2002). This body of work suggests that the capacity of WM may be a measure of the amount of general cognitive resources, which supports a wide spectrum of cognitive behaviours. This ability is also instrumental in the organisation and enactment of a series of sub-tasks in order to accomplish behavioural goals in daily life (Shallice & Burgess, 1991). WM abilities decline with age, which may partly underlie the reduced ability to cope with day-to-day functioning in some elderly adults. It is therefore unsurprising that WM abilities positively correlate with quality of life in older adults (Davis, Marra, Najafzadeh, & Liu-Ambrose, 2010; Harada et al., 2013).

Early work using cross-sectional studies found that WM function declines with increasing age (e.g. Craik & McDowd, 1987; Craik, 1968, 1977; Parkinson, Lindholm, & Inman, 1982; Parkinson & Perey, 1980; Salthouse & Babcock, 1991; Salthouse, 1990, 1992, 1994; Talland, 1968), which coincides with a decline in grey matter volume in regions of the prefrontal cortex (PFC) (see section 1.3. Age-related changes in brain structure) – some of which are highly implicated in executive functions including WM (Braver & Barch, 2002; Braver & West, 2008; West, 1996; see section 1.4.1. Prefrontal cortex function theory of ageing). Salthouse (1992, 1994, 2010) has suggested that the decline in many cognitive abilities, including WM, can be explained by a decline in ‘processing speed’, which refers to the speed of cognitive processing and motor responses for performing cognitive tasks. Early work (e.g.

Salthouse & Babcock, 1991; Salthouse, 1992, 1994) has suggested that speed (measured by reaction times; RTs) was a better estimator of the decline of WM abilities compared to the construct of 'capacity' (measured by accuracy). However, these studies used span tasks or simple measures of WM that may not have been sensitive to differences in capacity. Furthermore, the construct of 'processing speed' is also confounded with changes in motor abilities with age. Of course, cognitive speed may also be an important factor in determining WM performance in older adults, but measures that are less reliant on speeded responses may be more informative for assessing WM capacity irrespective of motor function.

More recent studies using change-detection and precision tasks have supported previous studies showing declines in WM with increasing age (e.g. Chen, Hale, & Myerson, 2003; Cowan, Naveh-Benjamin, Kilb, & Saults, 2006; Myerson, Emery, White, & Hale, 2003; Park et al., 2002; Peich, Husain, & Bays, 2013). For instance, Peich et al. (2013) used a precision task where participants report the stimulus stored in WM (recalling the precise orientation or colour in memory by adjusting the orientation or colour of a bar), which is a more sensitive test of WM accuracy (Zokaei, Burnett Heyes, Gorgoraptis, Budhdeo, & Husain, 2015) with minimal burden on motor function. They tested 60 participants with a large age range (19 – 77 years), and found that the precision with which WM items were recalled declined with age, and that the probability of incorrectly reporting a distractor item (or 'misbinding') increased with age. Aged monkeys are also impaired in simple spatial WM tasks that require short-term retention of spatial locations (e.g. Arnsten, Cai, Murphy, & Goldman-Rakic, 1994; Bartus, Fleming, & Johnson, 1978; Wang et al., 2011).

Some studies have replicated early work that verbal and visuo-spatial spans decline in healthy ageing, but attributed the impairments to declines in executive function rather than to capacity per se – highlighting that older adults experience greater deficits in span tasks when

there is proactive interference (e.g. Hasher et al., 2007; Hasher, Zacks, & May, 1999; Rowe, Hasher, & Turcotte, 2008, 2010; see section 1.2.4. Declines in inhibitory control for working memory). Indeed, researchers have emphasised the importance of executive function in supporting WM maintenance. In neuropsychological tests, older adults display impairments primarily in tasks related to purported ‘prefrontal’ or executive function (McDowd & Oseas-Kreger, 1991), tasks which also strongly correlate with WM capacity (e.g. Kane et al., 2001; Kane & Engle, 2003). Some researchers have suggested that age-related impairments in WM can be attributed to the general declines in brain regions that support top-down cognitive control (e.g. Braver & Barch, 2002; West, 1996; see section 1.4.1. Prefrontal cortex function theory of ageing).

1.2.4 Declines in inhibitory control for working memory

Lynn Hasher, Rose Zacks, and their colleagues (Hasher et al., 2007, 1999; Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2007) proposed that age-related reductions in WM capacity are specifically owed to age-related declines in inhibitory control. They proposed that stimulus ‘activations’ driven by the external environment are largely automatic and similar across age groups, and only immediately after this activation can individuals apply goal-related executive control to bring relevant information into the focus of attention and inhibit irrelevant information – an ability that changes with age (Hasher et al., 2007).

They outline three concepts related to inhibition, including access, deletion, and restraint. They assume that activation of sensory stimuli is automatic, after which the ‘access’ function of inhibition can determine what enters the focus of attention (Cowan, 1993). When this process is efficient, all task-irrelevant information is suppressed. For instance, in visual-search tasks, individuals are slower to detect targets when distractors are presented, and this distractor effect is pronounced in older adults (Madden, Whiting, Cabeza, & Huettel, 2004;

Plude & Hoyer, 1986; Whiting, Madden, Pierce, & Allen, 2005; J. L. Zacks & Zacks, 1993). Older adults also show greater implicit memory for distractors compared to young adults (Rowe, Valderrama, Hasher, & Lenartowicz, 2006). In the study by Rowe and colleagues (2006), participants were presented with line drawings of objects with irrelevant words overlaid, and were required to respond when they saw an object presented twice. In a subsequent implicit memory task (word-fragment completion task), older adults used a significantly greater proportion of the words presented as distraction relative to the younger adults (Rowe et al., 2006).

Inhibition can also serve to remove irrelevant information from the focus of attention. Irrelevant information can be active because the access function did not efficiently control “leakage” (Hasher et al., 2007). The ‘deletion’ function describes the ability to remove items from WM in the case of ‘leakage’ or at any point information becomes irrelevant, enabling efficient storage of only the goal-relevant information. In a set of studies, they presented participants with garden-path sentences with highly predictable, but missing words which participants were asked to generate (e.g. “She ladled the soup into her _____”, with “bowl” as the highly predictable target word). After several seconds, a word that was less likely but still semantically acceptable appeared (e.g. “lap”). Participants were then given a test where they generated endings to sentences, and older adults used the initially generated words (e.g. “lap”) much more often compared to the young adults, and they interpreted this as a reduced ability to delete the no-longer relevant word inference (Hartman & Hasher, 1991; May & Hasher, 1998; May, Zacks, Hasher, & Multhaup, 1999; also see S. Kim, Hasher, & Zacks, 2007). Studies of directed forgetting also suggest a deficit in older adults to delete irrelevant information (R. T. Zacks, Radvansky, & Hasher, 1996). On each trial, participants were shown individual words, and after several seconds were told to either remember (to-be-remembered; TBR) or forget (to-be-forgotten; TBF) the word. At the end of the block, they

were asked to recall the memory items. Relative to younger adults, older adults recalled more of the TBF items (intrusions) when asked to recall only the TBR items, took longer to reject the TBF items, and recalled more TBF relative to TBR items, suggesting a deficit in removing irrelevant items from memory (R. T. Zacks et al., 1996).

Older adults show declines in WM span tasks that require the retention of sequentially presented items over a short period of time. Hasher and colleagues suggested the reason why older adults seem to have a low span compared to young adults is due to a problem of proactive inference – a deficit in removing items from previously tested lists from memory. When administering span tests, participants are normally asked to recall lists of words, letters, or digits with list lengths of two up to six items, in ascending order of item length. Therefore, when participants first encode items with short lengths, they may retain those items in WM (over minutes), and when they are then tested on long item lists, older adults perform poorly because they are unable to delete items that were presented on previous list from WM. Indeed, they found that when they reversed the test order by administering the long lists first, older adults performed as well as young adults (May et al., 1999). This was replicated in two studies that tested spatial span (WM for spatial locations using a modified Corsi-block task), and also showed that deficits were greater when items were more similar across separate trials (Rowe et al., 2008, 2010). These results suggest that these tasks are influenced by proactive interference (Kane & Engle, 2000; Lustig, May, & Hasher, 2001), and the ability to ‘delete’ irrelevant items from memory is important when assessing WM capacity (Hasher et al., 2007).

Finally, the ‘restraint’ function of inhibition enables individuals to control strong responses, and is what other researchers have called ‘inhibition’ (e.g. Miyake et al., 2000). Older adults show deficits in tasks that require inhibitory control, or ‘restraint’. In the Stroop colour-

naming task, participants have to name the colour of a word stimulus, but ignore the word itself. On the difficult, incongruent trials, the word spells out the name of a colour different to the word's actual colour (e.g. 'Green' printed with blue ink). Older adults show greater deficits on incongruent trials compared to younger adults (Cohn, Dustman, & Bradford, 1984; Comalli, Wapner, & Werner, 1962; Houx, Jolles, & Vreeling, 1993; Spieler, Balota, & Faust, 1996; West & Alain, 2000). They also show deficits in other measures of 'restraint' including performance on stop-signal tasks (May & Hasher, 1998), and anti-saccade tasks (Butler, Zacks, & Henderson, 1999).

Overall, Hasher and colleagues have provided a variety of behavioural evidence that functions related to the inhibition of irrelevant information decline with age, and these deficits seem to have consequences for measures of both WM and longer-term memory.

1.3. Age-related change in brain structure

In this section, I will describe the age-related changes in brain structure reported in post-mortem and in vivo structural imaging studies. Age-related declines seem to be most prominent in the PFC, which is highly implicated in WM and executive control, and will be important when discussing the PFC hypothesis of ageing (see section 1.4.1. Prefrontal cortex function theory of ageing).

1.3.1. Post-mortem studies of age-related changes in brain structure

Post-mortem studies of the human brain have found reductions in brain volume in old age, with an estimate of 6% change in gross brain volume from young age to the seventh decade of life (Haug & Eggers, 1991). Age-related changes in brain volume were found to be heterogeneous across brain regions, with the sharpest declines in the PFC (~10-17%) and the corpus striatum (~8%), with lower declines in the temporal, parietal and occipital lobes (~1%)

(Haug & Eggers, 1991; Haug et al., 1983). Reductions in brain volume have been mainly attributed to a reduction in neuron size, synaptic density, and dendritic regression (Haug, 1985; Uylings, West, Coleman, de Brabander, & Flood, 2000), as well as loss of intralaminar myelin (Courchesne et al., 2000), loss of dendritic arborisation (Jacobs, Driscoll, & Schall, 1997), and, to a lesser extent, cell death (Haug & Eggers, 1991). Cell shrinkage in the PFC begins earlier and is greater than other cortical areas. From the fifth to seventh decade of life, extra-pyramidal cells in the PFC were found to have shrunk by approximately 22%, in contrast to 6% in the parietal cortex, 3% in the orbital prefrontal cortex, and 9% in the primary visual cortex. After the age of 65, cell shrinkage becomes apparent in all brain regions, but still the greater in the PFC (~43%) compared to the parietal (~11%), orbital prefrontal (~25%), and primary visual cortex (~13%) (Haug & Eggers, 1991). Studies of aged monkeys also show similar PFC declines with age (Bachevalier et al., 1991; Peters, Leahu, Moss, & McNally, 1994; Struble, Price, Cork, & Price, 1985), showing dendritic degeneration in upper layers of the PFC and degeneration of myelinated axons in deep cortical layers and in the white matter in old rhesus monkeys (Peters et al., 1994).

1.3.2. In vivo studies of age-related changes in the human brain

In vivo studies of structural changes in the human brain using magnetic resonance imaging (MRI) have found similar decreases in brain volume with age (e.g. Courchesne et al., 2000; Pfefferbaum et al., 1994; Raz et al., 1997; Tisserand, Visser, Van Boxtel, & Jolles, 2000). Grey matter volume reductions begin from late-teenage years, which start to reach a stable level around the sixth decade of life (Bartzokis et al., 2001; Courchesne et al., 2000; Pfefferbaum et al., 1994; Raz et al., 2005; Sullivan, Rosenbloom, Serventi, & Pfefferbaum, 2004). In contrast, white matter changes follow an inverted-U shape, with increases into middle age and a slow decline into old age (Bartzokis et al., 2001; Courchesne et al., 2000; Pfefferbaum et al., 1994; Raz et al., 2005; Sullivan, Rosenbloom, Serventi, & Pfefferbaum,

2004). These age-related changes of grey and white matter are consistent with post-mortem studies in the human brain (A. K. Miller, Alston, & Corsellis, 1980). Changes in white matter integrity are greater in anterior regions (Head, 2004; Pfefferbaum & Sullivan, 2005), which could be due to the greater susceptibility for myelinated fibers in these regions to break down (Bartzokis, 2004). The lateral PFC seems to be the region that shows the greatest decline in healthy ageing (Bartzokis et al., 2001; Good et al., 2001; Jernigan et al., 2001), consistent with findings from post-mortem studies. In more recent studies that used both cross-sectional and longitudinal measures, the PFC and the hippocampi were the regions that most reliably and strongly shrank with age (Fjell et al., 2009; Raz et al., 2005; although see Raz, Ghisletta, Rodrigue, Kennedy, & Lindenberger, 2010 for a shorter longitudinal study reporting statistically reliable changes in the hippocampus in contrast to high between-participant variability in changes in the lateral PFC).

Atrophy of the hippocampus and entorhinal cortex is a key feature of age-related disorders such as dementia (Braak & Braak, 1991; Laakso et al., 1996), and studies have reported reductions in similar structures in individuals with mild cognitive impairment (MCI) (Devanand et al., 2007; Pennanen et al., 2004). Some studies have found age-related decline in these medial temporal lobe structures in healthy populations (e.g. Du et al., 2006; Greenberg et al., 2008; Jernigan et al., 2001), although little to no decline has also been reported in other studies (e.g. Brickman et al., 2008; Good et al., 2001; Sullivan, Marsh, & Pfefferbaum, 2005). It seems that the degree of hippocampal and entorhinal cortex damage depends on the degree of cognitive impairment and brain pathology, whereas the decreases in PFC volume are more consistent with a general decline in normal ageing.

Overall, the general picture suggests that there is significant age-related decline in brain volume in the PFC, which is generally consistent across post-mortem and MRI studies.

1.4. Theories and studies on age-related deficits in WM

1.4.1. Prefrontal cortex function theory of ageing

Prior to the widespread availability of human neuroimaging, neuroscientists already hypothesised the link between the PFC and the impairments in WM and executive function in healthy ageing (Albert & Kaplin, 1980; Parkin & Walter, 1991, 1992). As touched on above, brain volume of the PFC declines with age (Haug & Eggers, 1991; Raz et al., 2005), which coincides with declines in WM capacity and WM-related control functions (Braver & Barch, 2002; West, 1996). Older adults display impairments in neuropsychological tests of purported 'prefrontal' or executive function (McDowd & Oseas-Kreger, 1991), showing notable deficits in inhibitory control similar to patients with prefrontal lesions. Based on a variety of behavioural evidence, researchers hypothesised that age-related changes in cognition, from childhood to old age, could be interpreted by the changes in the efficiency of inhibitory processes supported by the PFC (Dempster, 1991, 1992).

Early evidence that supported the PFC theory of ageing came from patients with prefrontal lesions (e.g. Diamond, 1990a, 1990b; Duncan, Burgess, & Emslie, 1995; Harlow, 1868; Luria, 1980; Stuss & Benson, 1987), who exhibited similar cognitive deficits to those observed in elderly adults. For instance, prefrontal lesions led to disruptions of attention, memory, and planning (Duncan et al., 1995; Luria, 1980; Stuss & Benson, 1987), as well as tasks that involved a sequence of discrete steps (Luria, 1973). After suffering PFC damage, these patients experience difficulties in maintaining items and tasks in WM for goal-oriented behaviour. These patients also suffer from deficits in inhibitory control, experiencing great difficulty in performing the Stroop colour-naming task and the Wisconsin Card Sorting Test (WCST; Duncan, 1995), despite fully understanding the tasks and aware of their incorrect responses (Stuss & Benson, 1987). It has been suggested that prefrontal damage impairs the strength of associations that are active in WM, which leads to an impairment in the ability to

determine the relevance of stimuli and actions to complete goals (Kimberg & Farah, 1993), often termed goal neglect. These patients exhibit problems in perseveration – the tendency to persist in repetitive behaviour even when inappropriate – and distractibility – the tendency to respond to stimuli even when irrelevant to the task (Diamond, 1990b; Fuster, 1989; Knight & Grabowecky, 1995; Luria, 1980; Stuss & Benson, 1987).

A large body of animal work has shown that the PFC is involved in the maintenance of spatial information in WM, typically tested using delayed-response and saccade tasks (Fuster & Alexander, 1971; Goldman-Rakic, 1987, 1995). In a typical delayed-saccade task, a monkey is presented with a brief cue at a particular location (e.g. a visual flash) to maintain over a short delay, and the monkey is subsequently probed to move their eyes to the memorised location for a juice reward. To perform this task, the animal must store a location in mind over a short period without sensory input. Cells in the PFC (frontal eye fields; FEF) preferentially respond to the memory location during maintenance period (Goldman-Rakic, 1987). Lesions to the FEF disrupt performance. Deficits of distractibility and perseveration are reported, in which monkeys are more prone to act before the end of the delay, act on pre-potent habits and perseverative behaviour, and respond to task-irrelevant distractors (Goldman-Rakic, 1987, 1995). Consistent with a role specialized for WM in the dorsolateral PFC (dlPFC), lesions to this area result in errors in memory tasks with delays of one to two seconds, whereas hippocampal lesions produce errors at delays of ten seconds or more (Diamond, 1990a). One study investigated the age-related changes in WM using the delayed-saccade task in young and old monkeys, and found a decrease in the firing rates in the FEF during the WM maintenance period in old monkeys, but no change in firing rate to a sensory cue (Wang et al., 2011).

Similar to patients and animals who experience prefrontal lesions, older adults exhibit goal neglect (De Jong, 2001) and suffer from deficits in inhibitory control, as demonstrated in the Stroop task (e.g. Cohn et al., 1984; Comalli et al., 1962; Houx et al., 1993; Spieler et al., 1996; West & Alain, 2000) and WCST task (Stuss et al., 1982). They also suffer deficits in WM as measured by span tasks (e.g. Lustig et al., 2001; Parkinson & Perey, 1980; Rowe et al., 2008, 2010; Salthouse & Babcock, 1991), change-detection tasks (e.g. Jost, Bryck, Vogel, & Mayr, 2011; Sander, Werkle-Bergner, & Lindenberger, 2011, 2012), and precision tasks (Peich et al., 2013; see section 1.2.3. Age-related declines in working memory). The PFC theory of ageing draws a parallel between behavioral deficits in prefrontal lesion patients and normal elderly adults, and suggests that cognitive deficits, including those related to WM, are attributable to declines in PFC function.

Early evidence for the PFC theory of ageing came from observing age-related deficits in healthy older adults and linking this to observations from behavioural changes in patients with PFC lesions. However, in vivo recordings of PFC activity in healthy older adults performing cognitive tasks provide a more direct test of the hypothesis. Human neuroimaging studies lent some support to these earlier views, showing that the PFC is involved WM maintenance and control over WM representations (e.g. Nobre et al., 2004), and studies have observed a reduction in task-related BOLD (blood-oxygen-level dependent) activity in the PFC of older adults compared to young adults that accompanied impaired WM performance (e.g. Nyberg et al., 2010; Rypma & D'Esposito, 2000). However, the picture has also become more complicated, with other studies finding over-recruitment in older adults (discussed below in section 1.4.3. Compensation and inefficiency of brain mechanisms in ageing). Furthermore, different regions of the PFC are activated during different cognitive tasks, and age-related differences are not necessarily localised to the same prefrontal areas across studies. Given the heterogeneity of neuronal function in the PFC within and across areas (Duncan,

2001; Fusi, Miller, & Rigotti, 2016; E. K. Miller & Cohen, 2001; Rushworth, Noonan, Boorman, Walton, & Behrens, 2011), any theory that claims age-related deficits in healthy ageing are due to ‘general’ declines in PFC function is likely to be *too* general. Age-related declines linked with different aspects of ‘prefrontal’ or executive function are likely to be linked to the degree of decline in the neuronal function in specific PFC areas, and also structural and functional connectivity linking the PFC with different areas for effective cognition. For instance, declines in spatial WM might be related to changes in FEF function (Goldman-Rakic, 1987; Wang et al., 2011), declines in feature-based selection may be due to changes in inferior frontal regions (Baldauf & Desimone, 2014; Bichot, Heard, DeGennaro, & Desimone, 2015), whereas impairments in inhibitory control might relate to changes in the right inferior frontal gyrus (IFG) (Aron & Poldrack, 2006). Some early theories acknowledge this (e.g. Braver & Barch, 2002; West, 1996), and the vagueness in these theories are presumably due to the limited data on the specific regions within the PFC that correspond to age-related behavioural impairments. In the following sections, I will describe several theories and empirical investigations that discuss the key processes that might underlie the age-related deficits in WM, drawing from evidence in behavioural and neuroimaging studies of cognitive ageing.

1.4.2. Inhibitory deficit in ageing: neural evidence

A number of researchers have proposed that age-related deficits in WM can be attributed to declines the ability to inhibit irrelevant information, and avoiding this from interfering with task-relevant information (e.g. Hasher et al., 1999; Hasher & Zacks, 1988; R. T. Zacks, Hasher, & Li, 2000). In the section above, I described the view that age-related declines in cognition can be attributed to declines in purported ‘prefrontal’ or executive functions. These researchers acknowledge that inhibitory control declines with age, but do not claim that it is the key process that underlies the age-related declines in WM (e.g. Braver & Barch, 2002;

West, 1996). In a previous section (1.2.4. Declines in inhibitory control for working memory), I described a behavioural account that proposed age-related declines in inhibitory control is the key factor that underlies age-related declines in WM abilities (Hasher et al., 1999; Hasher & Zacks, 1988; R. T. Zacks et al., 2000). Experiments that have charted the age-related changes in neural processes corresponding to cognitive control, such as inhibition, may be able to lend support to these ideas. I will outline several lines of research that used functional neuroimaging methods that examined the age-related changes in inhibitory processes in order to test the inhibitory deficit hypothesis in ageing.

A number of studies measured brain activity using EEG in groups of younger and older adults, and found changes in behavioural and neural markers of inhibitory control corresponding to healthy ageing (Alain & Woods, 1999; Chao & Knight, 1997; West & Alain, 2000). Chao and Knight (1997) measured event-related potentials (ERPs) in young and older adults during an auditory delayed match-to-sample WM task with and without distractors during the delay, and found that compared to the young group, older adults exhibited greater early evoked responses over the primary auditory cortex, and smaller ERPs in the prefrontal cortex during distractors. The larger ERPs related to the auditory stimuli suggests that older adults were less able to filter out irrelevant stimuli, and the attenuated frontal ERPs might correspond to a reduction in top-down control during the task. The magnitude of the auditory responses was positively correlated with perseverative errors on the WCST task, a putative measure of prefrontal function, suggesting the inability to suppress distractors is a decline in general executive control functions ascribed to the PFC. In another study, participants performed a visual task whilst irrelevant tones were played in the background. The tones were 'standard' tones intermixed with rare 'deviant' tones, which are less expected and generally evoke a greater sensory potential commonly known as the mismatch negativity (MMN; Näätänen, Paavilainen, Rinne, & Alho, 2007). Older adults

showed a reduction in the MMN, in part due to a greater evoked response in the expected (standard) stimuli (Alain & Woods, 1999). The enhancement in the standard tones might be related to a deficit in inhibiting the distractor tones, and the reduction in the MMN response could be related to changes in auditory processing in general. As mentioned above, older adults experience strong deficits in the Stroop colour-naming task. West and Alain (2000) recorded ERPs whilst young and older adults performed a Stroop task. They found that older adults performed worse than the young group, and showed that a decrease in the ERPs related to inhibiting word information on the incongruent trials.

In a series of functional magnetic resonance imaging (fMRI) studies, Gazzaley and colleagues have provided evidence that older adults have a specific deficit in the ability to inhibit irrelevant information, and preserved ability to enhance relevant information during WM encoding (Chadick, Zanto, & Gazzaley, 2014; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Zanto & Gazzaley, 2014). In a typical version of the task, participants are presented with a sequence of face and house stimuli, and instructed to encode selectively either faces or scenes in WM, ignoring stimuli from the other category. At the end of the trial, a test stimulus from the relevant category appears and participants respond whether it was presented in the encoding phase. They have also typically used a passive viewing baseline condition, in which participants were presented with the face and scene stimuli exactly done in the selective WM conditions, but in the absence of any task. To test for attentional enhancement effects, they contrasted neural activity during WM encoding for an attended stimulus (e.g. face stimuli when encoding faces) and compared the brain activity to the passive view conditions for those stimuli (face stimuli in passive view conditions). To test for suppression effects, they contrasted conditions where participants were ignoring stimuli during the WM encoding phase (e.g. face stimuli when encoding houses) with the passive view conditions (face stimuli in passive view conditions). Face stimuli are preferentially processed (elicit greater activity) in

the fusiform gyri (FG; Allison et al., 1994; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995), whereas scene or house stimuli show preferential processing in the parahippocampal gyri (PG; Epstein & Kanwisher, 1998). Furthermore, since activity in these category-sensitive areas can be modulated by attention (O'Craven, Downing, & Kanwisher, 1999; Wojciulik, Kanwisher, & Driver, 1998) they are commonly chosen as regions of interest to test for attentional modulations in cognitive tasks (e.g. Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; Ranganath et al., 2004). In the majority of the ageing studies by Gazzaley and colleagues, they concentrated on the modulation of scene processing in the left PG since it has been shown to be the category-sensitive area most reliably modulated by attention (Gazzaley, Cooney, McEvoy, et al., 2005). In the studies that examined age-related changes of attentional modulation for WM encoding, both younger and older adults exhibited attentional enhancement effects in the left PG, but only the young group showed suppression effects. The degree of suppression in sensory cortex was correlated with WM performance, suggesting selective suppression, or top-down inhibitory control, was the key factor that determined good WM performance (e.g. Chadick et al., 2014; Gazzaley, Cooney, Rissman, et al., 2005; also see Gazzaley et al., 2008)). However, they did not report whether the degree of enhancement, which was significant in older adults, showed any correspondence with performance. One might expect both enhancement and suppressive effects during top-down control (Kastner & Ungerleider, 2000), both of which could be important for behaviour.

1.4.3. Inter-individual differences: what constitutes healthy cognitive ageing?

In contrast to cross-sectional studies comparing groups of younger and older adults, another way to study cognitive ageing is to use an individual-differences approach. There are large inter-individual differences within healthy elderly groups in behaviour (Botwinick, 1978; Krauss, 1980; Welford, 1985), brain structure (e.g. Raz et al., 2010), and functional activity

(Nyberg et al., 2012). Exploring the inter-individual differences in elderly adults could allow us to discover behavioural and neural markers that correspond to healthy versus poor cognitive ageing. In the next two sections, I will describe studies that have used an individual-differences approach to understand healthy cognitive ageing.

1.4.4. Brain maintenance as healthy ageing

To study the individual differences of cognition in ageing, we might first ask: What constitutes healthy cognitive ageing? Intuitively, if an elderly individual performs a task as well as a young adult, then we would likely consider her to be very cognitively healthy. If an elderly adult recruits the same neural mechanisms to a young adult whilst they are performing the same task, then her brain may also be considered to show good cognitive health. Indeed, some researchers have proposed that the ability to maintain a healthy cognitive brain is what defines successful healthy cognitive ageing (e.g. Lindenberger, Burzynska, & Nagel, 2013; Nyberg et al., 2012)

There are large inter-individual differences between elderly adults in the rate of cognitive decline, with some individuals showing sharp declines and others who maintain their cognitive faculties throughout much of old age (Falconer, 1965; Lindenberger et al., 2013; Nolan & Blass, 1992; Nyberg et al., 2012). In light of these inter-individual differences, researchers have proposed that there may exist general mechanisms of ‘protection’ against age-related decline in cognition, such as cognitive and brain ‘reserve’ (Falconer, 1965; Nolan & Blas, 1992). Brain reserve refers to the individual differences in the brain that allow different individuals to cope better than others (Katzman et al., 1988; Satz et al., 1993; Stern, 2009), focussing on how healthy the brain is prior to cognitive decline (e.g. brain size, neuronal count, synaptic density) rather than the degree of age-related brain pathology. Cognitive reserve refers to individual differences in the way people approach tasks that allow

individuals to outperform others (Stern, 2002, 2009). The approach puts the emphasis on how the individual 'reacts' to age-related changes, such as the recruitment of compensatory mechanisms. More recently, researchers have introduced the complementary idea that brain maintenance, or the lack of brain pathology, is what constitutes successful memory ageing (Lindenberger et al., 2013; Nyberg et al., 2012). They propose that differences in brain maintenance – the conditions that promote the preservation of brain structure, function, and neurochemistry – can explain the individual differences in the manifestation of brain changes and pathology in ageing. The key prediction is that individuals that show less deterioration in structural and functional brain properties will show better, or more preserved, cognitive performance.

Various studies have lent support to the idea of brain maintenance. In a longitudinal study, 26 individuals (aged 55-69) were tested with an episodic long-term memory task and scanned with structural and functional MRI in two sessions spaced over six years (Persson et al., 2012). First, they found high inter-individual variability in the longitudinal changes in task-related hippocampal activity. Individuals who showed a decline in memory performance exhibited decreases in the task-related BOLD activity in the hippocampus, whereas those with stable memory performance (no decline) showed no significant changes in hippocampal activity. Nagel et al. (2009) tested younger and older adults using a spatial WM task and showed that older adults, as a group, showed a reduction in changes of neural activity in response to increasing WM load. In support of the brain-maintenance hypothesis, they found that high performing older adults showed more similar activity to the younger adults in response to greater WM loads compared to the low performing older adults. Using a verbal WM task, Nagel et al. (2011) showed similar results where older adults recruited less neural activity related to WM load. BOLD activity and functional connectivity between the left dlPFC and left premotor cortex predicted performance irrespective of age, indicating that it is

the integrity of the network that supports cognitive performance in old age, rather than other mechanisms such as compensatory activity (e.g. Cabeza, 2002; Reuter-Lorenz & Cappell, 2008). Finally, Rieckmann et al. (2011) found that preserved relationships between D1 receptor binding (as measured using PET) in sensorimotor and frontal regions in elderly adults corresponded to good performance comparable with younger adults in an interference resolution task.

Supporting the idea that brain maintenance is key to successful cognitive ageing, researchers have started studying “superagers” – elderly adults over 80 years of age who have unusually high memory abilities (Gefen et al., 2014, 2015; Rogalski et al., 2013). These elderly adults have greater cortical thickness in the anterior cingulate cortex (ACC) than younger elderly adults (50-60 year olds), more von Economo neurons² in the ACC, lower genetic risk for Alzheimer’s disease (lower frequency of the $\epsilon 4$ allele of apolipoprotein E), and lower densities of age-related Alzheimer pathology (Gefen et al., 2015; Rogalski et al., 2013).. Not only do these individuals exhibit superior behavioural performance, they also seem to maintain their cognitive abilities over time. Superagers were tested on a battery of neuropsychological tasks in two sessions and showed stable performance (no decline) in all the tasks over a period of 18 months (Gefen et al., 2014).

1.4.5. Compensation and inefficiency of brain mechanisms in ageing

In a series of studies from different labs, researchers have found marked differences in the patterns of brain activity in elderly adults across different studies. Some find greater activity in older adults compared to younger adults while others that find reduced activity, which accompanies good performance in some cases and poor performance in others. Here, I will

² Von Economo neurons are large spindle neurons, which are prominent in the anterior paralimbic areas including the ACC and insular cortex, and are specific to humans and phylogenetically advanced species.

review these studies, explore some of the reasons for the discrepant results among studies, and describe a theoretical framework that attempts to explain these differences.

A substantial number of fMRI studies have reported *greater* BOLD activity in older adults compared to young adults in response to cognitive tasks (e.g. Cabeza et al., 2004; Cabeza, Anderson, Locantore, & McIntosh, 2002; Dolcos, Rice, & Cabeza, 2002; Grady, McIntosh, & Craik, 2005; Madden, Spaniol, Bucur, & Whiting, 2007; Reuter-Lorenz et al., 2000). These “over-activations”, often localised to areas in the PFC, have been associated with both enhanced (Cabeza et al., 2004; Grady et al., 2005; Morcom, Li, & Rugg, 2007; Park et al., 2003) and impaired (Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Madden et al., 2007; Mitchell, Raye, Johnson, & Greene, 2006) behavioural performance. Accordingly, these studies have interpreted age-associated enhancements in directly opposing ways. When paired with good performance, over-activations are explained as compensatory mechanisms to alleviate the declines in cognitive function when paired with good performance; when paired with poor performance, over-activations are viewed as impairments in efficiency and unnecessary recruitment of neural resources un-related to the task. Other researchers have reported a more bilateral pattern of the PFC in older adults compared to young adults (e.g. Cabeza et al., 2004; Park et al., 2003; Reuter-Lorenz et al., 2000), and proposed that older adults recruit additional neural resources in the other hemisphere in order to compensate for declines in cognitive control – a specific form of over-activation (Cabeza, 2002; hemispheric asymmetry reduction in old adults; HAROLD). In contrast to reports of over-activations or additional activations in older adults, other studies have found reduced PFC activity in older adults during cognitive tasks (e.g. Nyberg et al., 2010; Park et al., 2004; Rypma & D’Esposito, 2000).

More recently, researchers proposed a new model of cognitive ageing that seems to lend a better explanation to these inconsistent data (Reuter-Lorenz & Cappell, 2008; compensation-related utilization of neural circuits hypothesis; CRUNCH). They proposed that older adults show over-activation in the PFC to compensate for age-related cognitive declines, but also suggest that they will show under-activation when they are unable to cope with the task demands. For instance, when older adults perform as well as young adults at low difficulty levels, they should show greater activity in the PFC compared to the young group, reflecting more recruitment of cognitive control mechanisms to produce good task performance (e.g. Madden et al., 2007). However, when task demands surpass the older adults' cognitive abilities, they will show attenuated PFC activity compared to the young adults along with worse behavioural performance (e.g. Cappell, Gmeindl, & Reuter-Lorenz, 2010; Mattay et al., 2006; Schneider-Garces et al., 2010). For instance, Mitchell et al. (2006) found impaired source memory in older adults compared to younger adults, which corresponded to significant recruitment of the left dlPFC activation in young but the older group. In contrast, Morcom et al. (2007) equated source memory performance between age groups and found that young and older adults recruited similar brain regions during the task. Furthermore, older adults showed more widespread and stronger responses in the bilateral anterior PFC and parietal cortex during memory retrieval. Cappell et al. (2010) tested younger and older adults using a verbal WM task with different WM loads (4, 5 and, 7 letters, corresponding to low, medium, and difficult conditions), and found that older adults performed as well as young adults for the medium difficulty trials, which were accompanied by greater right PFC activity. In difficult trials, they performed worse than younger adults and showed reduced activity in the PFC (Cappell et al., 2010; see Mattay et al., 2006 and Schneider-Garces et al., 2010 for similar results). These results are in line with the CRUNCH model, that older adults exhibit greater, compensatory activation when they are able to cope with the cognitive task but show lower activation when they show poor cognitive performance.

How does this model explain reduced performance with over-activations? They do not explicitly discuss this, but they might propose that these over-activations still correspond to compensation by recruiting more brain resources, but performance levels were not sufficiently high to match the younger adults' performance. It seems that interpreting the pattern of activation may not only depend on absolute performance, but also on how well the older adults are coping in the task and the amount of effort exerted in comparison to the young adults. For instance, if young adults find a task easy, whereas the older adults find it difficult but just manageable, you might observe greater recruitment in control regions in older adults (e.g. in visual-search tasks; Madden et al., 2007). However, if younger adults find a task relatively difficult and older adults also find it difficult, you might find similar or weaker activations in the older adults that are just coping, greater activations for those who do as well as the young, and reduced activity for those who fail at performing the task. The exact predictions may be difficult to test (given noise in relatively small samples), but some studies have shown positive correlations between performance and PFC activity in older adults that lend support this idea (e.g. Grady et al., 2005; Nagel et al., 2011).

1.5. Selective attention can support good WM performance

Researchers have often assumed that memory capacity is fixed, and that individuals are able to store approximately 3-4 items in mind as measured by WM paradigms such as change-detection tasks (e.g. Cowan, 2001; Luck & Vogel, 1997). This implies that the short-term retention of information is a rigid process, which cannot be altered. Recent theoretical and empirical work has implicated a key role for selective attention in determining the contents of WM (e.g. Gazzaley & Nobre, 2012; Stokes & Nobre, 2012). In the following, I will outline a body of work that has investigated how selective attention can modulate perceptual processing and WM contents to support good behavioural performance, the neural mechanisms that

underlie these processes, and research that has started to investigate changes in these processes in healthy ageing.

1.5.1. Selective attention for perception and WM: Behaviour

If a friend directs your attention toward a hedge and tells you that there is a prankster there about to surprise us, you will be a lot more prepared to react at his sudden appearance. That is, if you attend to a location where an event of interest will soon occur, you will likely detect it and act much quicker compared to if you did not know where it would occur. Studies of spatial attention have shown that if you present a predictive cue (a pre-cue) which informs you of the location a target will most likely appear (valid cues), individuals are more likely to detect the target or correctly discriminate its identity, compared to trials with no predictive cues or if cues incorrectly directed your attention away from the target (invalid cues) (Posner, 1978, 1980). These cues tell you where the target will most likely occur (usually with 80% or 75% validity; otherwise appear at another location), either by showing you the upcoming target location with a dot, an arrow pointing at the location, or even a symbolic cue that participants learn before hand (e.g. pink square means target will appear on the left, green square means on the right). Much of the behavioural research in attention has been based on this paradigm, which is commonly known as the Posner cueing task (Posner & Petersen, 1990). Studies have also used this elegant yet simple design to interrogate the neural mechanisms of attention in the human brain (e.g. Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta & Shulman, 2002; Gitelman et al., 1999; Nobre et al., 1997).

Researchers adapted the Posner cueing paradigm to WM tasks in order to test whether individuals can use attention to selectively encode items from particular locations or features. Griffin and Nobre (2003) used a change-detection task with spatial cues to test the ability to use top-down selective attention to enhance WM performance (see figure 1.1). On each trial,

they presented participants with an array of four coloured X's, which they had to retain in WM for approximately 2-3 seconds until the end of the trial. In the pre-cue condition, they were presented with a spatial pre-cue which pointed to the location of one of the items that will most likely (80% validity) be tested on at the end of the trial, so that it was possible to focus more on that item during encoding. Shortly following the cue, the stimulus array appears, and after another delay, a single test stimulus appears at the end of the trial and participants judge whether this item was presented in the encoding array (Experiment 1), or whether the item was present in the cued location (Experiment 2 and 3). In the retro-cue condition, participants were first presented with the stimulus array, and following a short delay, a spatial retro-cue appeared which informed them of the item that will most likely be tested at the end of the trial, before the test stimulus appeared. Finally, in the neutral-cue condition, participants had no predictive cues and therefore had to retain all items in memory. In both pre-cue and retro-cues trials, participants showed higher performance on trials with valid cues, slightly poorer accuracy with neutral cues, and even worse performance with invalid cues. These results showed that individuals can use pre-cues to selectively enhance the relevant target in the upcoming array for WM encoding, and use retro-cues to orient attention within WM to enhance the target item and attenuate the representation of the non-target items in memory (also see Landman, Spekreijse, & Lamme, 2003 who provided a similar demonstration of the retro-cue effect in a parallel set of studies). A number of subsequent studies have reliably shown these behavioural enhancements for WM performance using pre-cues and retro-cues (e.g. Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien, Thornton, & Nobre, 2011; Lepsien & Nobre, 2007; A.M. Murray, Nobre, Clark, Cravo, & Stokes, 2013; A.M. Murray, Nobre, & Stokes, 2011; Myers, Walther, Wallis, Stokes, & Nobre, 2015; Nobre et al., 2004; Nobre, Griffin, & Rao, 2007; Rerko & Oberauer, 2013; Rerko, Souza, & Oberauer, 2014; Sligte, Scholte, & Lamme, 2008; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015; Williams, Hong, Kang, Carlisle, & Woodman, 2013; also see

section 1.5.2. Neural mechanisms of spatial attention below for the brain mechanisms related to prospective and retrospective attention in WM).

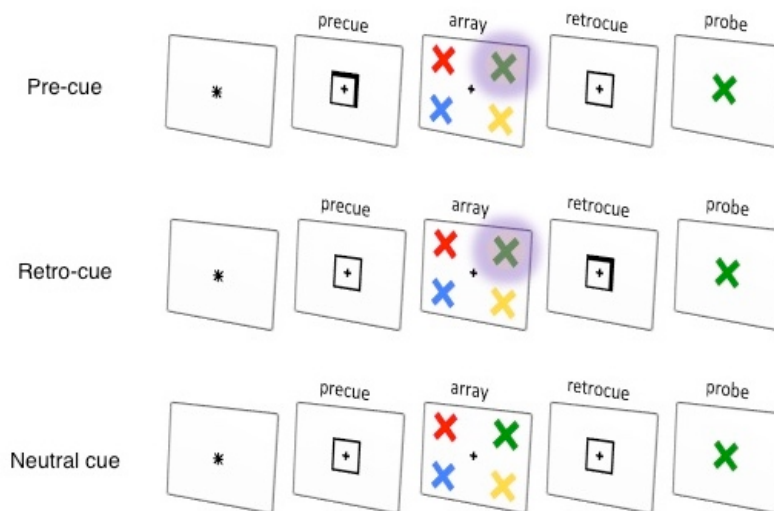


Figure 1.1. Task schematic for a set of conditions from Griffin and Nobre (2003). In the pre-cue condition (top row), a spatially informative cue (80% valid) was presented prior to the stimulus array. In retro-cue trials, the spatially informative cue (80% valid) was presented after the stimulus array. The neutral cue trials, there were no spatially informative cues. At the end of the trial, a probe stimulus appeared at the centre of the screen and participants made a judgement as to whether this stimulus was present in the stimulus array. In a second experiment, the test stimulus appeared at one of the quadrants and participants had to judge whether the stimulus was present at this location. In a third experiment, there were only imperative pre-cues and retro-cues, the test stimulus was presented at the centre of the screen, and participants had to judge whether this stimulus was presented at the cued location. Adapted from Griffin and Nobre (2003).

1.5.2. Neural mechanisms of spatial attention

With the increased availability of functional neuroimaging tools, there is now a plethora of human neuroimaging studies on ‘attention’. I will briefly outline some of the key studies from human neuroimaging and monkey electrophysiology to give an outline of the neural mechanisms involved in selective attention and its role during selection for WM.

Early studies using positron emission tomography (PET) and fMRI investigated the neural mechanisms of attention in humans using the Posner cueing paradigm (e.g. Corbetta et al., 1993; Corbetta & Shulman, 2002; Gitelman et al., 1999; Nobre et al., 1997), and found

robust recruitment of areas in the frontal and parietal cortices in response to spatial attention. These areas included the dlPFC and dorsal premotor cortex (areas 46 and 6, including the frontal eye fields; FEF), middle frontal gyrus (MFG), supplementary eye field (SEF) extending into the ACC, superior parietal lobule (SPL) and inferior parietal cortex (including the intraparietal sulcus; IPS), and sometimes the inferior frontal cortex (IFC) including the frontal operculum (fO) and anterior insula cortex. These have been referred to as the fronto-parietal and cingulo-opercular networks (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Petersen & Posner, 2012). In these tasks, participants typically maintained fixation on a central fixation point and covertly oriented their attention (without eye movements) according to a predictive or instructive cue to a peripheral target location on the left or right of the visual hemifield to detect or discriminate a visual target. Regions of the fronto-parietal network are central to the spatial attention system. Lesions to regions in the network such as the parietal cortex can result in visual extinction or neglect syndrome (with deficits more likely with lesions in the right parietal lobe) in which patients show deficits in the ability to attend to one side of space (Bisiach & Vallar, 1988; Heilman & Van Den Abell, 1980; Kinsbourne, 1977; Rafal, 1994). Lesions to the IFC also can produce neglect (Husain & Kennard, 1996; Mannan et al., 2005). Animal studies have also shown that the dlPFC, FEF, and the lateral intraparietal area (LIP; monkey homologue of human IPS) play key roles in spatial attention and WM (e.g. Buschman & Miller, 2007; Chafee & Goldman-Rakic, 1998, 2000; Constantinidis & Steinmetz, 1996; Fuster & Alexander, 1971; Goldman-Rakic, 1987; E. K. Miller, Erickson, & Desimone, 1996).

Attention can also influence neural processing in sensory cortex. fMRI studies have shown that attention to spatial locations can modulate neural processing in visual cortex in a retinotopic fashion, showing increases in BOLD activity in the attended and decreases in the unattended areas (e.g. Heinze et al., 1994; Kastner, Pinsk, De Weerd, Desimone, &

Ungerleider, 1999; Martinez et al., 1999; Vandenberghe et al., 1997). Electroencephalography (EEG) and magnetoencephalography (MEG) studies have shown similar modulations in visual cortex at a finer timescale (Griffin & Nobre, 2003; Heinze et al., 1994; Hillyard & Anllo-Vento, 1998; Kuo, Rao, Lepsien, & Nobre, 2009; Kuo, Stokes, & Nobre, 2012; Mangun, 1995; Myers et al., 2015; Poch, Campo, & Barnes, 2014; Wallis et al., 2015). Activations in the fronto-parietal network during selective attention are commonly interpreted as control sources, which modulate activity in the sensory regions for biasing perception (Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Kastner & Ungerleider, 2000).

Alpha oscillations (8-14 Hz) found in occipital and parietal cortices measured by EEG and MEG have been implicated in visual attention (e.g. Jensen, Bonnefond, & VanRullen, 2012; Kelly, Gomez-Ramirez, & Foxe, 2009; Klimesch, 2012; Rihs, Michel, & Thut, 2007; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). The alpha oscillation was the first oscillatory brain signal detected in humans using EEG (Berger, 1929). Since the amplitude of alpha oscillations was found to be greater when individuals were at rest or when they closed their eyes, and was strongly attenuated when they were awake and with their eyes open, it was considered the 'idling' rhythm – a neural signature of the brain at rest. More recently, this oscillatory rhythm has been observed in cognitive tasks and in particular has been linked with attention mechanisms (Jensen et al., 2012; Klimesch, 2012). When participants covertly attend to the one side of visual space (e.g. left) in a Posner cueing paradigm, the contralateral (right) visual cortex exhibits a decrease of alpha power relative to the ipsilateral (left) visual cortex, reflecting a spatially-specific modulation of cortical activity in the visual cortex (e.g. Gould, Rushworth, & Nobre, 2011; Kelly et al., 2009; Rihs et al., 2007; Thut et al., 2006; Worden et al., 2000). Alpha power decreases also scale with the number of items in WM (e.g. Fukuda, Mance, & Vogel, 2015; Jensen,

Gelfand, Kounios, & Lisman, 2002). Top-down increases of alpha power, and adjustments in alpha phase, have been proposed to block out distraction if the timing of the distractor is predictable (Bonnefond & Jensen, 2012, 2013). These studies support the idea that alpha oscillations may play an active role in the inhibition of irrelevant information or attention to target locations, which challenges the traditional idea that alpha is the 'idling' rhythm (Jensen et al., 2012).

Findings from human studies are supported by animal work, which has shown robust modulations in neuronal activity by spatial attention in many visual areas, including strong effects in higher-order areas such V4 (Connor, Gallant, Preddie, & Van Essen, 1996; Connor, Preddie, Gallant, & Van Essen, 1997; Haenny, Maunsell, & Schiller, 1988; Luck, Chelazzi, Hillyard, & Desimone, 1997; McAdams & Maunsell, 1999; Moran & Desimone, 1985; Motter, 1993; Reynolds, Chelazzi, & Desimone, 1999; Spitzer, Desimone, & Moran, 1988), but also in earlier visual regions including V1 (Motter, 1993; Roelfsema, Lamme, & Spekreijse, 1998) and V2 (Luck et al., 1997; Motter, 1993).

1.5.3. Neural mechanisms of feature-based attention

Selective attention to features or objects also recruits activity in the fronto-parietal and cingulo-opercular networks (e.g. E.J. Anderson et al., 2007; Bichot et al., 2015; K. K. Kim, Eliassen, Lee, & Kang, 2012; Vallesi, 2014; Weidner, Krummenacher, Reimann, Müller, & Fink, 2009; also see section 1.5.4. Neural mechanisms of spatial and feature-based attention for WM: Control mechanisms). In visual-search tasks, participants are given a template (item or stimulus feature) to keep in mind, and to search for a target item based on the template feature within an array of items. Such tasks involve both spatial and feature-based attention. Search is easy, or 'efficient', when the target is easily identifiable by virtue of salient differences to the distractors, and adding more distractors to the search array does not

increase RTs. Search is more difficult, or ‘inefficient’, when the target and distractors are similar or share stimulus features, and search time increases with the number of distractors (Wolfe & Horowitz, 2004). Several visual-search studies have observed activations in the IFC as well as the dlPFC and FEF (E.J. Anderson et al., 2007; K. K. Kim et al., 2012; Vallesi, 2014; Weidner et al., 2009). E.J. Anderson et al. (2007) found that the FEF was recruited for both efficient and inefficient search, but only the IFG/MFG was activated for the inefficient search trials. Similarly, Vallesi (2014) showed that visual search elicited activity in frontal and parietal regions, but with most robust activation in the right IFG/MFG for difficult trials. K. K. Kim et al. (2012) also found that inefficient search elicited more activity in the frontal and parietal areas, including the IFC. Although visual search involves both spatial and feature-based attention, there is emerging evidence that suggests areas in the IFC are important for feature-based attention from animal electrophysiological studies (e.g. Bichot et al., 2015) and WM studies that involved feature-based attention (see next section 1.5.4. Neural mechanisms of spatial and feature-based attention for WM: Control mechanisms).

Although electrophysiological studies of feature-based attention in prefrontal and parietal brain regions are relatively rare compared to those of spatial attention, several studies have highlighted the importance of cells in the IFC and inferior prefrontal convexity of the PFC for feature-based coding and attention (Baldauf & Desimone, 2014; Bichot et al., 2015; Ninokura, Mushiake, & Tanji, 2004; Wilson, Scalaidhe, & Goldman-Rakic, 1993). Wilson et al. (1993) found that the inferior convexity of the PFC coded for object features more than spatial locations. Ninokura et al. (2004) used a WM task that required monkeys to remember the temporal order of the objects. They found that cells in the more dorsal part of the lateral PFC coded for the temporal order of the objects, whereas the more ventral part of the lateral PFC coded for both the temporal order and the object features (colour/shape), suggesting a role in the integration of features and temporal order. This results parallels the results of a set

of studies in humans where they found that the IFC was involved in feature-based search, and TMS to the IFC mainly disrupted the conjunction task rather than a task that required attention to single features (Jackson, Morgan, Shapiro, Mohr, & Linden, 2011; Morgan, Jackson, Van Koningsbruggen, Shapiro, & Linden, 2013). Bichot et al. (2015) found that cells in the ventral prearcuate (VPA) in the inferior convexity work in concert with the FEF during feature-based attention search. They found that during visual search for a particular object, VPA cells responded to search cues and retained feature-selectivity during the trial, and showed an earlier timecourse related to feature-selection compared to both the FEF and IT cortex. Inactivation of the VPA impaired visual search performance and reduced feature-related activity in the FEF, suggesting the VPA sends signals to the FEF during feature-based visual search. Using MEG in humans, Baldauf and Desimone (2014) showed that the IFG was involved in modulating activity face-sensitive FG during attention to faces and the house-sensitive PG during attention to houses by inducing synchrony between areas in the gamma band (60-90 Hz). They also showed, using DTI, that the FG and PG have strong anatomical connections to areas in the IFC, including the IFG.

A large proportion of feature-based and object-based attention studies have focussed on the modulatory effects in sensory areas that preferentially process particular features or objects. In an early PET study, Corbetta and colleagues (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991) found that attention to colour (and shape), increased the neural response in area V4, which preferentially responds to colour, whereas attention to speed led to greater response in area MT, which responds more to motion. More recent work has replicated these effects in V4 during attention to colour and MT during attention to motion (e.g. Beauchamp, Cox, & DeYoe, 1997; Büchel et al., 1998; Clark et al., 1997; O'Craven et al., 1999). Selective attention to faces, objects, and scenes also enhance the activity in sensory areas that preferentially process these stimuli (e.g. Clark et al., 1997; Haxby et al., 1994; O'Craven et

al., 1999; Wojciulik et al., 1998). For example, O'Craven et al. (1999) used a paradigm where participants viewed a display with semitransparent superimposed faces and houses, and showed that attention to faces elicited greater BOLD activity in the face-sensitive FG, whereas attention to houses elicited greater activity in the house-sensitive PG. Moreover, at certain time points in the experiment, the face or the house stimulus exhibited oscillatory motion, and area MT exhibited greater activity only when the attended stimulus was moving. Animal work has also shown that attention to stimulus features can modulate neuronal activity in V4 and area MT (e.g. Bichot, Rossi, & Desimone, 2005; Chelazzi, Duncan, Miller, & Desimone, 1998; McAdams & Maunsell, 2000; Treue & Martinez Trujillo, 1999) as well as inferior temporal cortex (IT; Chelazzi et al., 1998; Chelazzi, Miller, Duncan, & Desimone, 1993).

1.5.4. Neural mechanisms of spatial and feature-based attention for WM: Control mechanisms

The neural mechanisms recruited during the maintenance of information in WM are closely related to those of attention (Awh & Jonides, 2001). It is notable that many of the tasks that aim to test for selective attention involve a component of WM. For instance, in the Posner cueing task, participants have to retain a spatial location in memory as well as attend to the location. In visual search tasks, individuals keep a search template in WM and try to search for the target item guided by that template. In feature-based attention tasks, participants are asked to keep some feature or object-type in mind, and then deploy attention to those items. fMRI studies have shown similar patterns of brain activity in spatial attention and WM tasks (e.g. Awh et al., 1999; Awh, Anillo-Vento, & Hillyard, 2000). Top-down attention has been therefore been proposed to be tightly linked with WM, with some researchers suggesting that the same neural mechanisms support both attention and WM function (Awh & Jonides, 2001; Postle, 2006).

Top-down attention can modulate sensory representations in WM for guiding behaviour (Gazzaley & Nobre, 2012; Stokes & Nobre, 2012). If individuals are given information on which of the items in a memory array will most likely be relevant for behaviour, they can prioritise and protect those items, whilst ignoring others that are less likely to be useful, and even suppress distractors completely irrelevant to the task (e.g. Griffin & Nobre, 2003; Landman et al., 2003; Nobre et al., 2004, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). In several studies that tested the attentional control over WM representations described above (section 1.5.1. Selective attention for perception and WM: Behaviour), the experimenters also recorded brain activity in order to study the neural mechanisms of prospective attention for WM encoding and retrospective attention for orienting within WM (e.g. Griffin & Nobre, 2003; Nobre et al., 2004, 2007). Nobre et al. (2004) used fMRI to explore the brain areas that were significant recruit for both pre-cues and retro-cues during a WM task. They found large overlap in the activations for spatial attention for WM encoding (pre-cues) and for orienting attention within WM (retro-cues) in areas of the fronto-parietal network including the precentral sulcus/superior frontal sulcus, supramarginal gyrus (SMG), superior parietal gyrus, superior parietal lobule (SPL), and the precuneus. There were also activations that were greater in prospective versus retrospective attention. Pre-cues elicited more activity in the posterior angular gyrus, whereas retro-cues showed more activity in the IFG/anterior insular cortex, posterior inferior frontal sulcus (IFS), middle frontal gyrus (MFG), superior frontal gyrus (SFG), the IPS, and the precuneus. Lepsien et al. (2005) found similar results in a WM task with retro-cues with a number of memory loads, showing robust recruitment of the IFC (including the fO/anterior insular), ACC, and parietal cortex. Kuo et al. (2014) also found retro-cue related activations in areas in the prefrontal cortex (fO/anterior insular, IFS, FEF, SFG, MFG, ACC) and the parietal cortex (SPL, IPS, precuneus). They also showed retinotopically specific attentional

modulation of sensory cortex (V4) and showed that activity in the IFS (but not the FEF or posterior parietal cortex) was coupled with activity in V4. Although they found a strong activation in the fO/anterior insular in response to retro-cues, they unfortunately did not inspect whether this area was coupled with V4. In a meta-analysis of activations for pre-cues and retro-cues, Wallis et al. (2015) reported that both pre-cues and retro-cues activate areas in the fronto-parietal network, but retro-cues additionally recruit the cingulo-opercular networks (including the fO/anterior insular cortex in the IFC and dorsomedial PFC), similar to the initial fMRI study (Nobre et al., 2004). Following up on the fMRI studies that mapped attentional control regions, Wallis et al. (2015) used MEG to study the temporal dynamics of attentional control in brain areas involved in prospective and retrospective spatial attention. They found that the fronto-parietal network was recruited for both cue types, but only the cingulo-opercular network was recruited more for retro-cues. Armed with high-temporal resolution, they observed that after a retro-cue, participants initially engaged the fronto-parietal network – reflecting spatial selection within WM – which was followed by the activations in the cingulo-opercular network, which may play a role in selecting and extracting the feature (orientation in this case) from memory to guide the subsequent action (Dosenbach et al., 2008). It is interesting that the IFC, also involved in feature-based attention (E.J. Anderson et al., 2007; Bichot et al., 2015; Zanto, Rubens, Bollinger, & Gazzaley, 2010; Zanto, Rubens, Thangavel, & Gazzaley, 2011) is activated after a retro-cue. Indeed, spatial retro-cues may involve both spatial orienting followed by feature extraction from that location. The temporally later activation of the IFC (fO/anterior insular) in Wallis et al.'s study (2015) could correspond to the selection and extraction of the stimulus feature from the cued location in WM.

Several studies explored the neural mechanisms involved in orienting attention within WM using face and scene stimuli (Lepsien & Nobre, 2007; Lepsien et al., 2011). On each trial,

participants encoded sequentially presented faces or scenes, and were presented with a cue indicating the object category that would most likely be probed at the end of the trial ('F' or 'S'). In both studies, they found attentional modulation in the face-sensitive FG during attention to scene-sensitive PG during attention to scenes. They also found that retro-cues elicited activity in the fronto-parietal network, the IFS, and fO/anterior insular cortex (Lepsien et al., 2011). In two studies studying orienting attention within WM to faces, houses, and body parts, the researchers found the retrospective cues elicited activity specifically in the fO/anterior insular (Higo, Mars, Boorman, Buch, & Rushworth, 2011; Nelissen, Stokes, Nobre, & Rushworth, 2013), and the BOLD activity in the fO was selectively coupled with the relevant category-sensitive visual areas. Specifically, activity in the fO was coupled with face-sensitive FG during retrospective attention to faces, coupled with house-sensitive PG during attention to houses, and the body-sensitive extrastriate body area (EBA) for attention to body parts (Higo et al., 2011). An additional behavioural experimental with transcranial magnetic stimulation (TMS) to temporarily inactivate the left fO supported a causal role of the fO in feature-based retrospective attention. Using the same behavioural paradigm but examining the patterns of neural activity related to retrospective attention in WM, Nelissen et al. (2013) found that activity in the fO was uniquely correlated with changes in activation patterns in visual cortex.

Areas in the IFC are also involved in feature-based attention during WM encoding. In two studies, Zanto et al. (2010, 2011) used a WM task with pre-cues that instructed participants to attend to colour or motion of a stimulus of moving coloured dots (random dot kinematogram), and showed activation in the right inferior frontal junction (IFJ). They found that BOLD activity in regions in the IFG were selectively coupled with the activity in motion-sensitive MT during attention to motion, and to colour-sensitive V4 when attending to colour. They further substantiated the claim that the right IFG was involved in modulating

the sensory areas for WM, by showing that TMS to this area impaired behavioural performance and reduced the attentional-related modulation of ERPs related to motion and colour processing in posterior areas (Zanto et al., 2011).

1.5.5. Neural mechanisms of spatial and feature-based attention for WM: Modulations on feature and object-sensitive sensory cortex

Attention to particular features or objects can modulate activity in feature and object-sensitive sensory cortex during WM tasks (e.g. Druzgal & D'Esposito, 2001; Gazzaley, Cooney, McEvoy, et al., 2005; Postle, Druzgal, & D'Esposito, 2003; Ranganath, Cohen, et al., 2004; Ranganath, DeGutis, & D'Esposito, 2004). In the preceding section, I already described several studies reported attention-related increases in feature and object-sensitive cortex, and that these effects were coupled with activity in the IFC (Baldauf & Desimone, 2014; Higo et al., 2011; Kuo, Stokes, Murray, & Nobre, 2014; Lepsien et al., 2011; Nelissen et al., 2013; Zanto et al., 2010, 2011).

More recently, researchers have investigated the oscillatory markers of selective attention for WM using EEG and MEG. Similar to studies of selective attention in perceptual tasks, directing spatial attention during WM tasks elicit lateralised signals in the alpha band, showing a decrease of alpha power in visual and parietal cortex contralateral to the direction of attention relative to an increase on the ipsilateral hemisphere. Alpha lateralisation has been shown following pre-cues, where participants prepare to attend to the cued item in the upcoming array, and following retro-cues, where participants orient their attention within WM to prioritise the cued item (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015). Spatial attention effects were specific to the cued location (quadrant of the screen) (Myers et al., 2015; Wallis et al., 2015), similar to the results in fMRI (Kuo et al., 2014). These studies show that individuals can use top-down attention to bias oscillatory activity in sensory cortex

to modulate memory representations and facilitate behavioural performance.

1.5.6. Selective attention for perception and WM in ageing

WM capacity declines with age, which could be related to deficits in the ability to inhibit irrelevant information (Hasher & Zacks, 1988). Since top-down attention can produce robust enhancements in WM in young adults, could deficits in WM performance be mitigated with the strategic deployment of selective attention? By strategically placing more weight on a subset of items, this reduces the WM load burden, and enables the protection of only the most relevant items in WM for behavioural performance.

A number of studies have shown that older adults can use pre-cues to improve visual detection and discrimination performance (e.g. Greenwood, Parasuraman, & Haxby, 1993; Nagamatsu, Carolan, Liu-Ambrose, & Handy, 2011; Nissen & Corkin, 1985; Ryan, Shen, & Reingold, 2006; Tales, Muir, Bayer, & Snowden, 2002; Tellinghuisen, Zimba, & Robin, 1996). Nissen and Corkin (1985) tested younger and older adults using a visual detection task with pre-cues, and found that both groups showed cueing benefits for valid compared to neutral cues, and cueing costs for invalid cues compared to neutral cues. Interestingly, older adults showed greater cueing benefits and costs, suggesting that they were more reliant on the cues. Tales et al. (2002) tested younger and older adults as well as patients with Alzheimer's disease (AD) in detection and discrimination tasks with both endogenous and exogenous pre-cues. Endogenous cues are pre-cues that predict of the target item location, so that they can use top-down control to prepare for the target at that location (the cues as described above). Exogenous cues are pre-cues that are not spatially predictive, but that capture automatic, or reflexive spatial attention. Since they are not spatially predictive, participants should not use top-down control to prepare for targets at any location, but the automatic capture of attention would still improve performance at those locations and impair performance at the uncued

locations. They found that younger and older adults showed similar cueing benefits with both exogenous and endogenous cues, whereas the AD patients showed a greater validity effect than the healthy younger and older adults for exogenous cues. In visual-search tasks with a pre-cue that provided information about the target location, older adults showed slightly impaired, but similar patterns of behavioural performance to young adults (Madden et al., 2004; Whiting et al., 2005). The relative preservation of top-down control in visual search corresponded to greater activity in the fronto-parietal network compared to younger adults (Madden et al., 2007), suggesting a greater recruitment of control regions to support good behavioural performance.

Older adults can use feature or object-based pre-cues to some extent to enhance the processing of relevant information during WM encoding (Chadick et al., 2014; Gazzaley, Cooney, Rissman, et al., 2005; Gazzaley et al., 2008). In these studies, older adults were able to utilise cues (attend faces or attend scenes) to selectively encode items into WM, shown by the greater activity in the category-sensitive regions in visual cortex during WM encoding (relative to a passive view condition and ignoring the stimuli). Although these studies have primarily investigated the effects of top-down control on the modulation of sensory areas, the behavioural performance in older adults are usually quite high, and the degree of this modulation is correlated with behavioural performance (Chadick et al., 2014; Gazzaley, Cooney, Rissman, et al., 2005).

Studies are beginning to test whether the ability to use retro-cues to orient attention within WM is impaired with ageing. Two studies have reported a deficit in spatial orienting within WM (Duarte et al., 2013; Newsome et al., 2015) and one showed preserved feature-based orienting within WM (Gilchrist, Duarte, & Verhaeghen, 2015). Duarte et al. (2013) tested younger and older adults on a colour change-detection task with spatial retro-cues whilst they

recorded EEG from the scalp. Participants were first presented with a pre-cue informing participants to encode items on the left or right side of the screen, which was followed by an array of eight coloured squares, four on the left and the other four on the right side of the screen. After a short maintenance period, either a spatial retro-cue (100% valid) was presented which pointed to the item that will be tested at the end of the trial, or no cue was presented. At the end of the trial, a coloured square appeared at the centre of the screen and participants judged whether the colour was presented in the attended side of the memory array. They found that there was a retro-cue benefit for the younger adults in terms of hit rate but not for older adults. Using EEG, they measured the contralateral delay activity (CDA) that has been suggested to correspond to the number of items held in WM (Vogel & Machizawa, 2004). If participants used the retro-cue to preferentially maintain the cued item over the other items, the CDA should decrease, corresponding a reduced number of items retained in memory (Kuo et al., 2012). They found that younger adults showed a reduction of the CDA after retro-cues, whereas in older adults, the CDA started reducing even prior to the retro-cue. This suggests that WM maintenance was already declining prior to the retro-cue, indicating that older adults may not have benefitted from the cue due to a compromised representation of the WM items by the presentation of the retro-cue. Newsome et al. (2015) found similar behavioural evidence that older adults could not use a spatial retro-cue to improve WM performance. In contrast to these studies, Gilchrist et al. (2015) found that older adults could orient attention within WM to enhance performance with a feature retro-cue. Younger and older adults were presented with arrays of coloured shapes, and after a short delay, a feature retro-cue appeared, which informed participants of the feature (shape or colour) of the items in WM that will be tested at the end of the trial. Both age groups showed accuracy benefits from feature-based retro-cues compared with neutral cues. In Chapter 3, I present a study with a large sample of older adults that examines the ability to orient spatial attention within WM in healthy ageing using an individual-differences approach.

1.5.7. Control mechanisms for WM function in healthy ageing

Age-related deficits in WM capacity are likely to stem from a variety of reasons, such as problems with inhibiting task-irrelevant material, deficits in executive control, or simply the ability to maintain task-relevant information over short periods of time. Researchers in the psychology and cognitive neuroscience of ageing have used several approaches to study WM deficits in old age. However, there are relatively few well-powered functional neuroimaging studies with large numbers of older adults, and perhaps more surprisingly, very little work has tested for the relative preservation or decline in attentional processes that could help support good WM performance.

Some researchers have proposed that age-related declines in WM are related to deficits in the suppression task-irrelevant information, based on several relatively low-powered functional imaging studies. Gazzaley and colleagues suggested that WM deficits in older adults can be attributed to an age-related decline in the ability to suppress task-irrelevant information, indexed by a reduction in the suppression of neural responses in task-irrelevant sensory areas (in fMRI). Importantly, there was a correlation between the degree of suppression and WM performance. Although there was a difference in the suppression effects and age groups, and a hint of a relationship between the neural suppression effects and certain measures of WM performance (high-performing older adults versus low-performing older adults; Gazzaley, Cooney, Rissman, et al., 2005), the sample sizes were relatively low (16 older adults in Gazzaley, Cooney, Rissman, et al., 2005, and 20 older adults in Chadick et al., 2014). Considering the noisy measurements from fMRI, plus the high inter-individual variability in older adults, it is worth reconsidering the general question with larger sample sizes. Furthermore, they used a region-of-interest approach to look only at the left PG for attentional effects, which was somewhat justified from a previous study (Gazzaley, Cooney, McEvoy, et al., 2005), possibly to compensate for their lack of statistical power due to a small

sample size. In Chapter 2, I present an fMRI study with a large sample of older adults (70 participants) to test if older adults can use attention to selective encode stimuli into WM, and if there are reliable attentional modulation effects in the PG and FG in both hemispheres, as well as attentional-control networks. I also explore the relationship of attentional modulation in these areas with WM performance (indexed by digit span). Finally, I explore other brain areas that are functionally coupled with attentional modulation in these category-sensitive sensory areas (since they are notoriously hard to detect with small samples), looking at the influences from purported top-down control areas in the PFC.

Hasher and colleagues (Hasher & Zacks, 1988) suggest a related account by which WM deficits in older adults are related to the inability to suppress irrelevant items in mind, such as items presented in the recent past. However, these tasks do not specifically test whether top-down attentional control can be utilised to support WM performance, such as explicit cues that signify what items to strategically attend to or ignore. In Chapter 3, I present a WM study with retro-cues to test whether older adults can orient attention within WM to select the relevant item and ignore the irrelevant items for good WM performance, and chart the neural dynamics of attentional orienting using MEG.

Few studies have systematically assessed whether older individuals can exert flexible control over their WM capacity to enhance performance, and virtually none have used more sensitive behavioural paradigms (designed specifically to test the cognitive ability; WM) and well-powered neuroimaging studies. As described above, top-down attention can enhance WM encoding and protect memories from interference in cognitive tasks. Top-down attentional control may be relatively preserved in healthy ageing, suggesting that older adults might be able to use cues to enhance task-relevant representations and inhibit irrelevant distracting information to enhance WM performance. The degree of preservation of attentional control

mechanisms that help mitigate deficits in WM might be an important factor that determines the degree of healthy cognitive ageing.

In my thesis, I plan use well-powered functional neuroimaging and behavioural studies (large sample sizes) to ascertain if older adults retain the attentional control mechanisms that modulate sensory brain areas according to task demands and to support WM performance. Utilising these large samples, which are relatively rare in the literature, I will also test the inter-individual differences within elderly adults in order to find behavioural and neural markers that correspond to healthy cognitive ageing.

1.6. Affective material draws attention and modulates WM performance

The ability to keep information in WM exhibits marked declines in ageing – but is this always the case? In addition to attention-related prioritisation, stimulus content also affects the way sensory information is processed. The ability to keep things in WM might therefore depend on the stimulus features and personal relevance of the memory items. For example, there might be a benefit in WM abilities for objects that are more ecologically valid and motivationally salient for older adults. Interestingly, affective processing does not exhibit a simple steady decline like other cognitive functions in ageing (Grady, 2008; Hedden & Gabrieli, 2004; Mather, 2012). Elderly adults are relatively unimpaired at performing certain tasks with emotional content (e.g. Calder et al., 2003; Keightley, Winocur, Burianova, Hongwanishkul, & Grady, 2006; Mammarella, Borella, Carretti, Leonardi, & Fairfield, 2013; Mikels, Larkin, Reuter-Lorenz, & Cartensen, 2005; although see Ruffman, Henry, Livingstone, & Phillips, 2008, for some deficits in emotional recognition) and selectively attend to the emotional parts of their lives as much as, or even more than, younger adults (Carstensen, Fung, & Charles, 2003). Could older adults have relatively preserved abilities for the short-term maintenance of emotional information? And could the individual differences

in the WM ability for different affective contents depend on cognitive health (general cognitive function, non-emotional WM) or emotional health (mood) in ageing?

In the following, I will review studies that explored the effect of emotional content on cognition in young adults and in healthy ageing, and motivate why it is interesting to study WM for emotional content in elderly adults.

1.6.1. Affective material affects attention and WM

Stimuli with affective content can modulate attentional allocation and neural processing (Compton, 2003; Vuilleumier, 2005; Vuilleumier & Driver, 2007; Yiend, 2010). They can lead to benefits or costs in behaviour (E. Fox & Damjanovic, 2006; Holmes, Green, & Vuilleumier, 2005; Lipp & Derakshan, 2005; Öhman, Flykt, & Esteves, 2001; Phelps, Ling, & Carrasco, 2006; Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Vuilleumier, Armony, Driver, & Dolan, 2001), with effects varying according to traits related to anxiety (e.g. Bradley, Mogg, Falla, & Hamilton, 1998; Bradley, Mogg, White, Groom, & de Bono, 1999; E. Fox, Russo, Bowles, & Dutton, 2001; E. Fox, Russo, & Dutton, 2002; Mathews & MacLeod, 2005; Yiend & Mathews, 2001) and depression (Bradley, Mogg, & Lee, 1997; Donaldson, Lam, & Mathews, 2007; Gotlib, Krasnoperova, Neubauer Yue, & Joormann, 2004; Joormann & Gotlib, 2007; Leyman, De Raedt, Schacht, & Koster, 2007; Mogg, Bradley, & Williams, 1995). Many studies have supported the idea that young adults tend to preferentially process negative information over neutral or positive information across cognitive domains, which could be linked to innate survival mechanisms (Rozin & Royzman, 2001; (Rozin & Royzman, 2001; also see Baumeister et al., 2001; Cacioppo & Berntson, 1994; Cacioppo et al., 1997, 1999). Indeed, it would be evolutionarily advantageous to be alert when encountering a fear-inducing stimulus, such as a snake (Damasio & Carvalho, 2013; LeDoux, 2003; Pessoa & Adolphs, 2010; Phelps, 2006).

In one study, Öhman, Flykt, et al. (2001) showed that young participants were faster at finding a target (a discrepant image that did not belong to the category of the other items in the display) when it was a fear-related compared to a non-fear-related target (in a display of spiders, snakes, flowers or mushrooms). Spider and snake-phobic individuals further showed a greater reaction-time benefit when the target belonged to the category of their own phobia. Lipp and Derakshan (2005) conducted an attentional dot-probe task with pictures of spiders, snakes, flowers and mushrooms to test attentional allocation to spatial locations with fear-related stimuli. Participants partook in a standard attentional dot-probe task, in which they were briefly shown two images on the left and right of the screen (e.g. snake on the left and flower on the right), and were required to report the location of a dot 'probe' stimulus (left or right) subsequently presented at one of the image locations. The idea is that a fear-related stimulus will attract more attention than a neutral stimulus, and so a dot probe presented at the location previously occupied by the fear-related stimulus (e.g. snake) should be processed faster than a probe presented at the location of the neutral stimulus (e.g. flower). This attentional facilitation or 'bias' for emotional stimuli is quantified by taking the reaction time for the probe detection following a fearful stimulus (with a neutral stimulus on the other side) minus the probe detection reaction time following a neutral stimulus (with a fear-related stimulus on the other side). The authors found that all participants exhibited speeded reaction times for probes that replaced pictures of spiders, but with an even greater facilitation in spider-phobic individuals (although they did not find the same effect in snake-phobic individuals). Others have similarly shown a facilitation of discriminating oriented bars or gratings following presentations of negative stimuli, in the form of reaction-time benefits (Pourtois et al., 2004) and increases in contrast sensitivity (Phelps et al., 2006).

Finally, some studies have found that performance on WM tasks for negative (threatening and fear-related) stimuli is enhanced in healthy young adults (e.g. Jackson, Linden, & Raymond, 2014; Jackson, Wolf, Johnston, Raymond, & Linden, 2008; Jackson, Wu, Linden, & Raymond, 2009; Mikels, Reuter-Lorenz, Beyer, & Fredrickson, 2008). For instance, Jackson et al. (2009) tested WM capacity for maintaining facial identities in WM, in which the emotional expressions were irrelevant to the task, and found that the number of angry faces that could be remembered was greater than the number of happy or neutral face identities. Overall, these studies indicate that emotional – in particular fear-related or threatening – stimuli can attract attention and facilitate perceptual processing to prepare to act upon or remember things identified to be behaviourally significant.

1.6.2. Affective processing in elderly adults

Older adults also show benefits in attention and memory tasks for emotional stimuli (D'Argembeau & van der Linden, 2004; Hartley, Ravich, Stringer, & Wiley, 2013; Mammarella et al., 2013; Mather & Knight, 2006; Mikels et al., 2005; Rösler et al., 2005). For instance, threat detection seems to be unimpaired in older adults (Mather & Knight, 2006; Rösler et al., 2005). In one study, young and old adults were asked to detect a discrepant emotional expression in a set of schematic faces (e.g. an angry face in an array of neutral faces; Mather & Knight, 2006, using the paradigm in Öhman, Lundqvist, & Esteves, 2001). Both young and old adults were faster at detecting an angry face in an array of faces with neutral expressions compared to detecting the non-threatening (sad, happy) emotional expressions. Rösler et al. (2005) also found that both young and old participants attended to emotional stimuli more than neutral stimuli, with slightly less sustained attention (looking time) to negative stimuli in older adults. Furthermore, the amygdala – a brain structure involved in processing emotional stimuli – has been reported to show relatively little structural decline or changes in functional response to emotional information in old age (Good et al.,

2001; Mather et al., 2004).

A few studies that have tested for WM abilities for affective content in healthy ageing have found WM benefits for emotional stimuli. For example, Mammarella et al. (2013) found a significant age-related deficit of WM for non-emotional words, but WM for emotional words (positive and negative) was no different to that in young adults. D'Argembeau and van der Linden (2004) found that older adults were impaired at recalling the identity of a set of previously presented faces (after a five-minute delay), but showed equivalent performance to younger adults for identifying the emotional expression (angry or happy) of a recalled face. Hartley et al. (2013) found similar results using a change-detection task. They asked participants to remember faces (one, two, or three) over a short delay period and judged whether a face presented at the end of the trial matched one of the faces in the memory array in emotional expression (experiment 1) or identity (experiment 2). Older adults performed as well as young adults in remembering the emotional expression but were significantly worse at the recalling the identity.

Interestingly, older adults exhibit a tendency to focus on positive over negative information (Carstensen & Mikels, 2005; Charles, Mather, & Carstensen, 2003; Grady, Hongwanishkul, Keightley, Lee, & Hasher, 2007; Mather & Carstensen, 2005; Mikels et al., 2005; Reed, Chan, & Mikels, 2014). Researchers have proposed the idea that older adults exhibit a general 'positivity' bias, preferentially attending to positive stimuli and recalling positive memories (e.g. Carstensen & Mikels, 2005; Charles et al., 2003; Mather & Carstensen, 2005), whereas younger adults show a 'negativity bias' (e.g. Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Cacioppo & Berntson, 1994; Cacioppo, Gardner, & Berntson, 1997, 1999; Rozin & Royzman, 2001). The original idea, the socio-emotional selectivity

theory, stated that since older adults have less concerns about the future and greater appreciation for the fragility of life, they concentrate more on positive information and emotional meaning in life (Carstensen et al., 2003). The evidence that supported this idea initially came from observational methods and questionnaire measures. More recent work has attempted to use behavioural measures from cognitive psychology to test if the theory applies to more basic cognitive processes (Carstensen & Mikels, 2005; Mather & Carstensen, 2005).

In one study, Charles et al. (2003) found that older adults showed a reduction in the number of negative images that were recalled in a memory task, suggesting a reduced negative bias but not a positive bias for memory. In a dot-probe task, Mather and Carstensen (2003) found that older adults exhibited a bias away from negative faces (when paired with a neutral face distractor), whereas there was no significant attentional bias in the young adults. In one experiment, older adults showed a bias toward positive faces (paired with a neutral face), but this was not replicated in the second experiment. In both experiments, they asked participants to perform a recognition memory task, in which they were presented with a series of faces and were asked to judge whether they had seen them before in the dot-probe task. Old adults showed better memory for happy faces relative to negative faces. This suggests a reduced negative bias in attention but a positive bias for memory in older adults. Three studies have suggested that older adults have a benefit for emotional content in WM, regardless of valence (D'Argembeau & van der Linden, 2004; Hartley et al., 2013; Mammarella et al., 2013), suggesting no valence-specific bias. Finally, one study found that older adults showed better WM performance compared to young adults for positive images, and worse for negative images (Mikels et al., 2005), suggesting that older adults have both a positive bias and a reduced negative bias in WM. However, not all studies show results that support this theory (Murphy & Isaacowitz, 2008). As mentioned above, both young and old showed comparable reaction-time benefits to threat-related information (Mather & Knight, 2006; Rösler et al., 2005), and benefits in WM for both positive and negative stimuli relative to neutral stimuli in

older adults (Hartley et al., 2013; Mammarella et al., 2013).

1.6.3. Working memory for affective content in healthy ageing

The studies described suggest that WM for emotional content might be relatively preserved in healthy ageing, and elderly adults may have a particular preference for positive information. However, studies that investigate the changes in emotional processing, in particular for WM, are scarce. Moreover the existing studies are inconclusive. Part of the reason for this might be due the tasks used which give behavioural measures that might not be best suited for testing for age differences. Most of the studies that examined differences in attention and WM in younger and older adults use speeded reaction-time tasks, where behavioural measures are usually limited to accuracy (e.g. proportion correct) and reaction times. For reasons of fatigue and motor problems, these measures may not be ideal for an elderly population. Furthermore, these behavioural measures may not be ideally suited for testing memory for emotional information, since there is no straightforward way to characterise the degree to which individuals remembered the emotional information (e.g. how negative did they perceive or remember the stimulus?).

There are only a limited number of studies that have tested whether WM for emotional content changes in old age, and the tasks available have not been designed to test these questions and therefore are unsatisfactory in several respects (described above). To fill this gap in the literature, I will develop a new experimental paradigm that is better suited for testing age-related changes in emotional processing, and examine emotional processing in WM and perception in healthy ageing. I will develop a task that can provide a sensitive measure of behavioural accuracy for emotional WM and emotional perception, and test for age-related changes of affective processing in healthy ageing. I aim to test whether older adults really

show a benefit with maintaining emotional material in WM and if this benefit is specific to positive or negative information. I also aim to test whether there is a positive bias in older adults compared to younger adults, if there is a reduced negative bias, or if there is in fact no change with age with maintaining affective material in WM. Finally, I will also test whether inter-individual differences in affective processing in WM relate to mood traits measured by self-report questionnaires.

1.6 Scope of the thesis

This thesis examines several aspects of WM function in healthy ageing, including the neural mechanisms of top-down control that support WM function and the effect of emotional content on WM performance. The introduction reviewed the relevant behavioural and neuroscientific literature of WM, attention, the relationship between attention and WM, and age-related changes in cognition, brain structure, and cognitive brain function. In Chapter 2, I present an fMRI study that investigates the changes in attentional control for WM encoding in healthy ageing, and examines the individual differences in brain activity that corresponds to healthy cognitive ageing of attentional control. In Chapter 3, I present an MEG study that explores the ability orient attention within WM using retro-cues in healthy ageing, and examines the neural dynamics that correspond to healthy cognitive ageing of flexible control over WM. In Chapter 4, I present a series of experiments showing the development of a task to measure emotional WM and perceptual function. In Chapter 5, I present an experiment with a large group of younger and older adults to test for the age-related changes of WM for affective content in healthy ageing. Finally, in Chapter 6, I consider the findings from this thesis and discuss the broad implications of the results. I will discuss the behavioural and neural mechanisms of WM that decline with age, and those that show relative preservation in ageing that can be utilised to support declines in other cognitive domains. I consider the advantages of large sample sizes and testing for inter-individual

differences in behaviour in groups of elderly adults to discover behavioural and neural markers that correspond to healthy cognitive ageing. Finally, I also discuss the shortcomings of the work in this thesis and what future studies can do to improve the scientific investigation of cognitive ageing.

2. Top-down control for selective working memory in healthy ageing

Chapter Abstract

WM abilities exhibit significant decline as we age. Selective encoding of only the most relevant items in the environment is advantageous for the maintenance of memory representations, and such strategic deployment of attention could help enhance WM abilities in older adults. In the current experiment, I studied a large sample of older adults (N = 70) using a selective WM task to assess the neural mechanisms of selective attention for WM encoding in ageing, and the individual differences in brain activity that correspond to healthy ageing of WM function. Older adults showed significant attentional modulation of bilateral category-sensitive visual areas during selective encoding of face and house stimuli into WM, extending the results from previous studies. Activity in regions in the IFC was functionally coupled with the task relevant category-sensitive visual areas during selective attention, whereas areas in the default-mode network were coupled with the task irrelevant category-sensitive visual areas, reflecting preserved functional brain networks that support selective WM in healthy ageing. Finally, the older adults within this elderly cohort (old-old) recruited a larger region of the IFC to modulate the task relevant category-sensitive visual areas, which, paired with matched behavioural performance with the younger elderly adults (young-old), suggests that the old-old adults recruited a larger region of the control regions for top-down modulation of sensory cortex to support good cognitive behaviour.

Introduction

WM is an important cognition function that enables us to store information over short periods to guide purposeful behaviour (Baddeley & Hitch, 1974; Miyake & Shah, 1999). Consequently, deficits in WM can lead to adverse effects for other cognitive domains, and ultimately, to impairments in effective cognition in everyday life. The ability to hold items in WM declines with normal ageing (Chen et al., 2003; Iachini, Iavarone, Senese, Ruotolo, & Ruggiero, 2009; Park et al., 2002; Parkinson & Perey, 1980; Peich et al., 2013; Salthouse & Babcock, 1991; Salthouse, 1992, 1994), which coincide with age-related changes in anatomy and functional activity during WM tasks in the human brain (Braver & West, 2008; Hedden & Gabrieli, 2004; Li, Lindenberger, & Frensch, 2000; Li & Lindenberger, 1999; Nyberg et al., 2012; Raz et al., 2005; West, 1996). Notably, quality of life in old age is positively associated with WM and executive functions (Davis et al., 2010; Harada et al., 2013). It is therefore important to understand the neural mechanisms that are impaired or preserved in healthy ageing, and whether top-down control can help reduce age-related deficits in WM.

A significant body of research has shown that WM can be improved by using top-down attention to proactively guide selection of relevant items to be encoded in WM and avoid distraction (e.g. Gazzaley & Nobre, 2012; Stokes & Nobre, 2012; Vogel & Machizawa, 2004; Vogel et al., 2005). Various studies have suggested that healthy elderly adults experience significant declines in their ability to use selective attention to guide the encoding of relevant material and suppress irrelevant items for WM (e.g. Fabiani, Low, Wee, Sable, & Gratton, 2006; Gazzaley, Cooney, Rissman, et al., 2005; Jost et al., 2011; McNab et al., 2015; Peich et al., 2013; Sander et al., 2011, 2012; Werkle-Bergner, Freunberger, Sander, Lindenberger, & Klimesch, 2012; also see Hasher & Zacks 1988; Hasher et al., 1999), which are associated with age-related changes in anatomy and neural activity in purported cognitive control regions of the PFC (Braver & West, 2008; Chadick et al., 2014; Chao & Knight, 1997;

Nagel et al., 2011; Raz et al., 2005; Rypma & D'Esposito, 2000). Some researchers have suggested that age-related declines in WM stem from a specific deficit in the ability to inhibit irrelevant information (Chadick et al., 2014; Gazzaley, Cooney, Rissman, et al., 2005; Gazzaley et al., 2008; Hasher et al., 1999; Hasher & Zacks, 1988), whereas the ability to use attention to enhance sensory representations remains intact (Chadick et al., 2014; Gazzaley, Cooney, Rissman, et al., 2005). However, these studies only concentrated on one brain area (the left PG) and were relatively underpowered (16 in Gazzaley, Cooney, Rissman, et al., 2005, 20 in Chadick et al., 2014). Some studies have found that older adults show relatively preserved abilities in using selective attention to suppress distractors and enhance perception (e.g. Nissen & Corkin, 1985; Tales et al., 2002), visual search (Madden et al., 2007, 2004; Whiting et al., 2005), and WM (e.g. Gilchrist et al., 2015; see Chapter 3). In this respect, the neural mechanisms that underlie preserved versus impaired WM functions in healthy ageing are not entirely clear.

Studying individual differences in behavioural performance and neural activity during WM tasks might provide hints for the mechanisms that are preserved in healthy ageing. Older adults often show increased BOLD activity in the PFC compared to young adults during successful cognition (Cappell et al., 2010; Grady et al., 2005; Grady, 2008; Madden et al., 2007; Mattay et al., 2006), suggesting stronger recruitment of cognitive control mechanisms to perform the same task. Notably, there are large inter-individual differences even within elderly groups (Nyberg et al., 2012). Older adults who are less affected by the detrimental effects of cognitive ageing sometimes show brain activity more similar to young adults (e.g. Gazzaley, Cooney, Rissman, et al., 2005; Nagel et al., 2009), recruit compensatory mechanisms such as enhanced neural activity in the PFC (Grady et al., 2005; Madden et al., 2007), or display a more bilateral pattern of activation in the PFC (e.g. Cabeza, 2002; Dolcos et al., 2002; Madden et al., 2004; Reuter-Lorenz et al., 2000), whereas those who suffer from

age-related decline show reduced recruitment of purported control areas in the PFC (e.g. Cappell et al., 2010; Mattay et al., 2006; Rypma & D'Esposito, 2000).

In the current study, I tested a large sample of elderly adults using a selective WM task to study top-down control for the prioritisation of task-relevant information and filtering of distractors for WM encoding in healthy ageing. Specifically, I aimed to test whether elderly adults retained the ability to use top-down control to recruit cognitive control networks shown in younger populations (Dosenbach et al., 2008; Petersen & Posner, 2012) to modulate the relevant category-sensitive visual areas (bilateral FG and PG, opposed to only the left PG in other studies), and to investigate age-related changes in these top-down processes. I chose to recruit a large group of elderly adults in order to avoid the nuisance variables that contribute to comparisons of different age groups (e.g., motivation, fatigue, exposure to computer technology, etc.). Considering the high inter-individual variability in cognitive abilities even within healthy elderly adults (Nyberg et al., 2012), I aimed to study a large group of elderly adults to test for the mechanisms that relate to successful ageing.

I found that elderly adults were able to employ top-down control to enhance sensory processing in category-sensitive visual areas, and the degree to which elderly individuals were able to modulate these areas was positively correlated with general WM abilities indexed by digit span. During selective WM encoding, elderly adults recruited cognitive control networks qualitatively similar to those recruited by young adults during attention and WM tasks. Furthermore, areas in the left IFC including the fO were functionally coupled with the relevant category-sensitive visual, whereas areas in the default-mode network (DMN) were coupled with the irrelevant category-sensitive visual areas. Finally, the coupling strength in areas in the left IFC were positively correlated with age, suggesting that the older individuals

within this elderly group may have recruited compensatory mechanisms in the IFC specifically to modulate sensory cortex to support high WM performance.

Methods

Participants

Eighty-one healthy older adults (aged 60-87) were recruited from the community via local media and public advertisements. Of these, 77 participants were able to complete the current experiment. Two participants were not scanned due to claustrophobia, and a further five participants were excluded from the analysis due to cortical abnormalities observed in their T1-structural scans.

The remaining 70 participants (42 female) were 60-87 years old (mean 68.5 ± 0.85 years), had 16.0 ± 0.44 years of education. All participants were fluent in English, had normal or corrected-to-normal vision and hearing, and scored >26 on the Mini-Mental State Examination (MMSE, Folstein et al., 1975). None of the participants had any current diagnosed psychiatric or neurological disorder, and none were taking psychoactive medication.

Stimuli and Apparatus

The stimuli used in the task consisted of digital, colour photographs of faces and houses standardized to 350 x 350 pixels. The face images were photographs of individuals of different ages (including children, young, middle-aged and elderly adults) and different ethnicities, and the photographs did not undergo any editing apart from resizing. Only faces with neutral or positive expressions were selected. The house images were photographs of houses with a range of styles and colours, which also did not undergo any editing apart from resizing. The nature of the task did not require standardisation of the images, and I chose to use images that were as natural and pleasant as possible to keep the elderly participants

engaged with the task. All images were obtained via the Creative Commons licence on Flickr, and a full list of photo references was made available to the participants. Seventy-two stimuli were used in the main task (36 faces, 36 houses), and a separate set of 24 stimuli (12 faces, 12 houses) was used in the practice session. See figure S2.1 and S2.2 for a full set of the images used in the main task and figure S2.3 for the images used in the practice task.

The task was programmed and run in Presentation® software (version 16.2, www.neurobs.com). The task was presented using a computer display with a spatial resolution of 1024 x 768 pixels and a refresh rate of 60 Hz, which was projected onto a screen in the scanner room and reflected onto an angled mirror inside the scanner (horizontal length of 26° in visual angle).

Task design

A selective WM task was used to test top-down control for WM encoding in healthy ageing. In each block, participants were presented with an instruction cue followed by a sequence of images consisting of faces and houses presented at the centre of the screen. According to the instruction cue, they attended to either the face or house stimuli, and were required to make a response whenever they saw an image presented a second time (stimulus repetition) in the attended category. The repetition could happen at different times within the block and could be preceded by intervening items of the other category (see below for details).

In each block, participants viewed a stream of face and house stimuli with reminder cues. At the start of the block, instructions were presented on the screen (2000 ms) which indicated if the upcoming block required attention to faces (on screen: “REPEATED FACES”) or to houses (on screen: “REPEATED HOUSES”). Prior to each stimulus presentation, a reminder cue (“F” or “H”) was presented at the centre of the screen (2000 ms) to ensure participants were aware of the task block they were in, followed by the face or house stimulus

(1000 ms). Each block consisted of a stream of ten trials of the reminder cue (“F” or “H”) paired with a face/house stimulus. Participants monitored the sequential stream of visual stimuli, and made a left mouse click when they detected a previously presented stimulus in the attended category.

For each stimulus, its associated target (stimulus repeat) could be presented after one to three intervening stimuli, or not shown at all. This was true for both the attended and ignored stimulus categories, even though no response was required for a stimulus repeat in the ignored category. Participants were not explicitly informed of these details. Intervening stimuli were either face or house images with equal probability.

There were 18 trials each in the attend face, ignore face, attend house, and ignore house conditions with novel stimuli (total of 72 trials), and 12 trials each in the attend face, ignore face, attend house, and ignore house conditions with repeated stimuli (total of 48 trials), giving a total of 120 trials. Stimuli presented in the attended blocks were never presented in the ignore blocks (e.g. face stimuli in attend-face blocks were not presented in the ignore-face blocks), and vice versa.

Experimental procedure

At the beginning of the session, the experimenter provided a demonstration of the task accompanied with verbal instructions from a prewritten script. Participants proceeded to perform the task in a practice session, which consisted of two attend-faces and two attend-houses blocks. The experimenter provided verbal feedback on their performance. Once the experimenter was satisfied that the participant understood the task, the participant entered the scanner and proceeded with the task.

For the main experiment, participants completed six attend-faces blocks and six attend-houses blocks in alternating order. In each block, there were ten trials, followed by 14 seconds (s) of rest, where participants maintained central fixation. Eye movements were not monitored.

Behavioural data analysis

To characterise behavioural performance on the task for each block type, I computed the hit rate, false alarms, and inverse efficiency scores (IES) for each block condition. Hit rate was computed as the number of responses when a target stimulus was presented (repeated stimulus in the attended category) divided by the total number of target stimuli. False alarms were the number of responses when the target stimulus was not present. Inverse efficiency scores were computed by taking the mean correct reaction times divided by the hit rate.

Paired t-tests were used to test for differences between conditions, and Cohen's d was used to determine effect sizes (Cohen, 1988). Correlations were conducted by computing Spearman's rank correlation coefficients. Correlations with age were performed with years of education and gender as covariates of no interest.

Statistical analyses for behavioural performance were performed using Matlab R2015a, Matlab's Statistics Toolbox, and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann et al., 2015).

Neuropsychological Tests

Participants underwent an extensive neuropsychological battery and questionnaires separate to the current experiment (for full list, see Appendix: Neuropsychological Tests and

Questionnaires). Individual differences in the ability to filter task-irrelevant distractors and enhance task-relevant items have been linked to WM capacity (e.g. Vogel & Machizawa, 2004). Therefore, the ability of enhance target categories (faces/houses) during selective WM encoding was hypothesised to correlate with digit-span scores, a standard measure of WM capacity. Since there are three scores, I used an aggregate score by computing the mean of the forward, backward, and sequence digit span. I used Spearman's rank correlations to test for an association between digit span and neural measures. Age, years of education and gender were considered as covariates of no interest.

Digit Span Forward

For the digit span forward task, the experimenter read out sequences of digits from the digit span list at the rate of one digit per second. The participant repeated the sequence of numbers in the same order vocalized by the experimenter to the best of their ability. After a sequence was repeated correctly, the following sequence was increased by one digit. If the participant made a mistake for two consecutive attempts, the following sequence length was decreased by one digit. The final digit span was determined as the maximum length of the list which the participant recalled five out of six correctly. Six lists per span condition were presented.

Digit Span Backward

The procedure for the digit span backward task was essentially identical to the forward span task, but the participant had to repeat the sequence of numbers in reverse order, i.e. from the number the experimenter vocalized last to the first in the sequence.

Digit Span Sequence

The procedure for the digit span sequence was similar to the forward and backward span tasks, but in this case, the participant had to vocalize the numbers in ascending order.

MRI acquisition

Structural and functional MRI data were acquired on a 3T Siemens TIM Trio System (Siemens, Erlangen, Germany) at the Oxford Centre for Magnetic Resonance Imaging (OCMR), using a 32-channel head coil. An EPI-BOLD contrast image with a total of 32 slices was acquired with 3 mm³ voxel size, repetition time (TR) = 2000 milliseconds (ms), and echo time (TE) = 30 ms. Flip angle was set to 78°. A fieldmap image was acquired to correct for signal distortions and compensate for signal loss. Fieldmap parameters were as follows: 3.5 mm³ voxel size, TR = 488 ms, first TE = 5.19 ms, second TE = 7.65 ms. A high-resolution whole-brain T1-weighted structural image (MPRAGE) was acquired in each participant for registration purposes, with resolution of 1 mm³ voxel size, TE = 4.7 ms, and TR = 2040 ms. For each participant, a resting-state scan and a different task scan were also acquired, which do not form part of this investigation.

fMRI analyses

fMRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB Software Library, *Oxford Centre for Functional Magnetic Resonance Imaging of the Brain, Oxford University, Oxford, United Kingdom*, <http://www.fmrib.ox.ac.uk/fsl>). Pre-processing consisted of head-motion correction (MCFLIRT; Jenkinson, Bannister, Brady, & Smith, 2002), brain extraction (FSL's Brain Extraction Tool; Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM (full width at half maximum) 8 mm, intensity normalisation, and high-pass temporal filtering set at 275 s. Images were unwarped using B-0 fieldmaps (Jenkinson, 2003, 2004). Functional data were registered to standard space using FSL's Boundary-Based

Registration (BBR) and non-linear registration tools (Andersson, Jenkinson, & Smith, 2007; Greve & Fischl, 2009; Jenkinson et al., 2002; Jenkinson & Smith, 2001)

Time-series analysis was carried out using FMRIB's Improved Linear Model (FILM) with local autocorrelation correction (Woolrich, Ripley, Brady, & Smith, 2001). Data were analysed using the general linear model. Ten explanatory variables (EVs) were used to model the task events: Face Attend Novel (FA; Novel Face Stimulus in Attend-Faces Block), Face Ignore Novel (FI; Novel Face Stimulus in Attend-Houses Block), House Attend Novel (HA; Novel House Stimulus in Attend-Houses Block), House Ignore Novel (HI; Novel House Stimulus in Attend-Faces Block), Face Attend Repeat (Repeated Face Stimulus in Attend-Faces Block), Face Ignore Repeat (Repeated Face Stimulus in Attend-Houses Block), House Attend Repeat (Repeated House Stimulus in Attend-Houses Block), House Ignore Repeat (repeated House Stimulus in Attend-Faces Block), Instructions, Incorrect Trials. 'Instructions' modelled the initial instruction screen which informed participants of the current block type. 'Incorrect Trials' included misses and false alarms. All 'Repeat' conditions were not used in the task analyses to avoid artefacts and confounds related to motor responses and potential motor responses. Time points affected by large head movements remaining after motion correction were identified by FSL's Motion Outliers tool, and were included in the model as confound regressors.

Eight contrasts were used. To localise brain areas that preferentially processed face stimuli in the bilateral fusiform gyri (FG), I tested for regions that evoked greater BOLD activity for face stimuli compared house stimuli (FA & FI > HA & HI). To localise brain areas that preferentially processed house stimuli in the parahippocampal gyri (PG), I tested for regions that evoked greater activity for house stimuli compared face stimuli (HA & HI > FA & FI; see Region-of-interest analyses section for details of the procedure). To test for areas that showed attentional modulation for face stimuli, I contrasted Face Attend with Face Ignore

(FA > FI). For house stimuli, I contrasted House Attend with House Ignore (HA > HI). I also tested for areas that were more active in the Ignore conditions (FI > FA) and (HI > HA). To test for the effect of selective attention for categories (irrespective of stimulus category), I contrasted attend-face blocks and attend-house blocks (FA & HI > HA & FI, HA & FI > FA & HI).

Group-level analyses were carried out using FMRIB's Local Analysis of Mixed Effects (FLAME, Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). Z (Gaussianised T/F) statistic images were thresholded using clusters with $z > 2.3$ and a corrected cluster significance threshold of $p = 0.05$ (Worsley, 2001). To test for individual differences in attentional modulation of neural activity that corresponded to WM and age, I included digit span (aggregate measure) and age as regressors. Years of education and gender were included as regressors of no interest. Grey matter images were extracted from each participant's structural scan (T1) using FAST (Y. Zhang, Brady, & Smith, 2001) and added to the model as a covariate to account for voxel-wise differences in grey matter.

Region-of-interest analyses

In order to test for attentional modulation in category-sensitive areas, I first localised the face-sensitive fusiform gyri (FG; Allison et al., 1994; Puce et al., 1995; Kanwisher et al., 1997) and place-sensitive parahippocampal gyri (PG; Epstein & Kanwisher, 1998) in each participant. To do this, I extracted the MNI coordinates of the peak BOLD signal (z -statistic at the group-level; see figure S2.4) in the inferior temporal lobe from the faces versus houses contrast and the houses versus faces contrast (one ROI in each hemisphere for each contrast, giving a total of four ROIs). I created masks (17 mm³ cubes) centred on the peak in each region of interest in standard MNI space, which were then transformed into single-subject space. There was no spatial overlap between the masks for the two regions of interest. Within

each mask, I extracted the coordinates with the peak activity from each participant's z-statistic image for the relevant contrast using FSL's Cluster function, which I defined as the individual participants' left and right FG and PG.

I constructed spherical masks (5 mm^3) centred on the single-participant defined FGs and extracted the mean beta weights from each mask in the FA and FI conditions. Another pair of spherical masks was constructed around the single-participant defined PGs and I extracted the mean beta estimates from the mask in the HA and HI conditions. I compared the beta values from the FG in the FA versus the FI conditions, and compared the beta values from the PG in the HA versus the HI conditions using paired t-tests. To test if the degree of top-down modulation in house-sensitive regions was different to face-sensitive regions, I performed a repeated-measures ANOVA with factors Category (modulation in FG, modulation in PG) and Hemisphere (left, right). Correlations of attentional modulation (betas in the attend minus ignore conditions in each relevant bilateral ROI) with digit span were tested using Spearman's rank correlation coefficients, with age, education, and gender as covariates of no interest. Spearman's rank correlation was used to test the relationship between attentional modulation and age, with education and gender as covariates of no interest. Participants were excluded from individual analyses if the extracted BOLD activity was greater than three standard deviations from the group mean in a given condition. This led to exclusion of one participant in the left FG in the ignore faces condition, one participant in the right PG in the attend houses condition, and one participant in the right FG in the ignore houses condition. Results were equivalent after outlier exclusion.

Psychophysical interaction (PPI) analyses

To investigate the brain areas that were functionally coupled with category-sensitive visual areas during feature-based attention, I performed psychophysical interaction analyses (Friston

et al., 1997) . FSL was used to implement the PPI analyses using standard procedures (O'Reilly, Woolrich, Behrens, Smith, & Johansen-Berg, 2012).

I tested for areas that showed greater coupling with the bilateral FG when encoding faces that were attended versus ignored (FA > FI). I performed the same analysis for bilateral PG for attended versus ignored house stimuli (HA > HI). I also tested for the areas that were more coupled with the PG and FG for attend-face blocks versus attend-house blocks (FA & HI > HA & FI, HA & FI > FA & HI).

For each PPI analysis, I used four regressors: 1) The contrast between the conditions (e.g. FA – FI); 2) the timecourse from the seed ROI (e.g. bilateral FG); 3) the vector product of the first two regressors, representing the PPI; and 4) Both conditions (e.g. FA + FI). The fourth regressor was included to model the shared variance of the two regressors that would not be modelled by the contrast itself. For each analysis, I also included all other task regressors apart from the relevant conditions (in this case, FA and FI; see O'Reilly et al., 2012; <http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/PPIFAQ>).

Group-level analyses were performed as above, with age and digit span as regressors, and years of education and gender as regressors of no interest.

To test whether the correlation of age with coupling strength in the left IFV was mainly driven by brain areas surrounding the peak of the connectivity effect in the left fO (see fMRI Results), I created a 3 mm³ mask at the peak of the PPI effect, and a mask of the brain regions surrounding the peak by creating a spherical mask (25 mm³) centred on the left fO peak with an empty centre by subtracting it from another spherical mask (15 mm³). I then extracted the mean beta estimates from these areas to correlate with age. In order to test the

unique contribution of the coupling strength in the areas surrounding the left fO correlating with age compared to the centre of the left fO peak, I used linear regression with age as the observed variable and coupling strength in the peak in the lfO and coupling strength in the surrounding areas as predictor variables, with years of education and gender as variables of no interest. All variables were rank-transformed in order to be comparable to Spearman's rank correlations used in other analyses. I compared the strength of the coupling strength between areas using a paired t-test.

I performed several hypothesis-driven comparisons testing the degree of laterality in the recruitment of PFC in healthy ageing. Previous researchers have suggested that young adults recruit the right PFC more during cognitive tasks, whereas older adults show more bilateral recruitment to compensate for age-related decline of cognitive abilities (e.g. Cabeza et al., 2002; Grady, 2008; Reuter-Lorenz & Capell, 2008). I extracted the beta estimates in the left and right fO in several attention contrasts during encoding house stimuli (which showed the most robust fO/IFC activation) using 3 mm³ spherical masks centred on coordinates in a previous study that showed robust fO modulation for feature-based attention (Higo et al., 2011). BOLD activity and PPI beta estimates were extracted from these areas for the HA > HI contrast (house stimuli, attend houses > house stimuli, attend faces), as well as for the attend houses greater than attend faces contrast (all stimuli in house blocks > all stimuli in face blocks). These beta estimates were compared to baseline (one-sample t-test) or between different brain regions using paired t-tests.

Behavioural Results

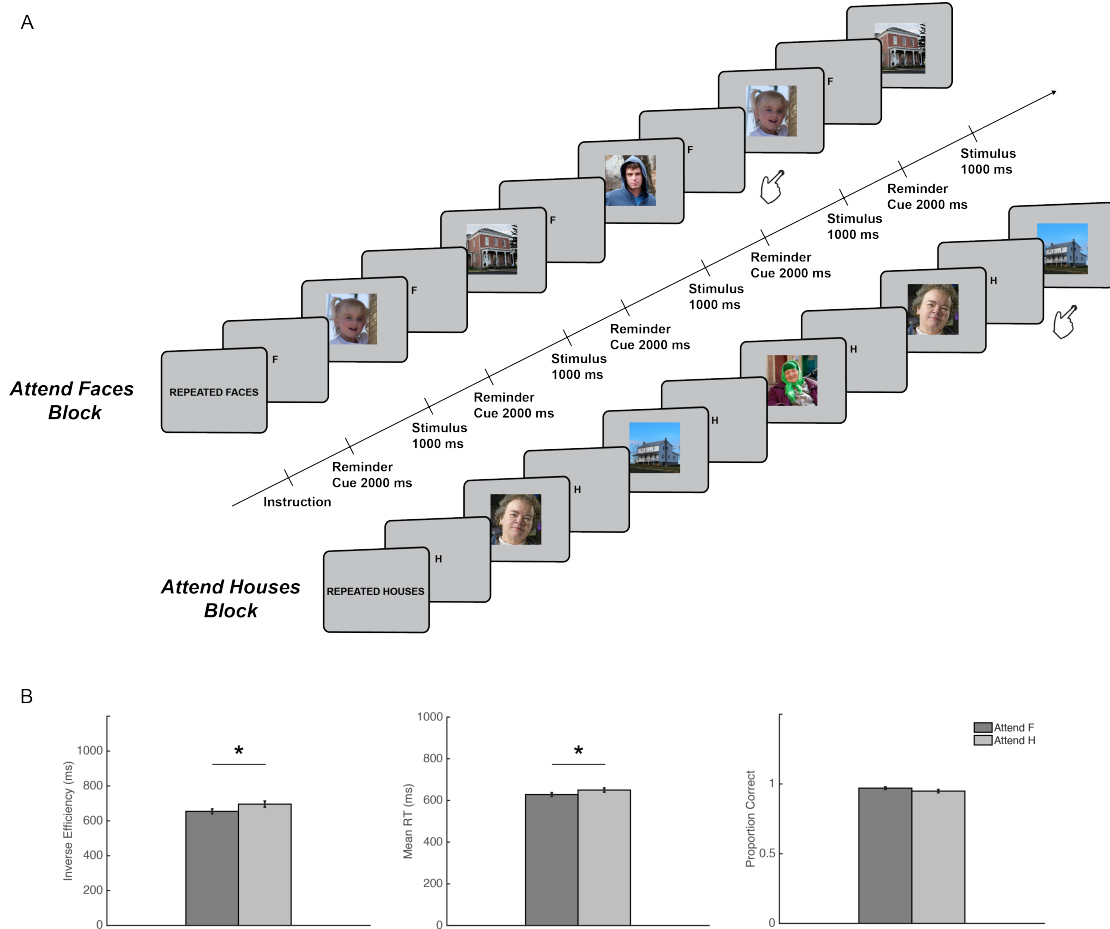


Figure 2.1. Task schematic and behavioural results. A) Selective working memory task. In each block, participants attended to face or house stimuli according to the instruction cue, and monitored a sequence of 10 face and house stimuli presented at the centre of the screen. In the 'attend faces' blocks (top), participants encoded the face stimuli into WM and made a response when they saw a previously presented face stimulus reappear, ignoring the house stimuli. In the 'attend houses' blocks (bottom), participants encoded house stimuli into WM and made a response when they saw a previously presented house reappear, ignoring the face stimuli. Prior to each face/house stimulus, a letter ("F" or "H") is presented at the centre of the screen reminding the participant of the current block type. B) Inverse efficiency scores (left), mean RT (middle) and proportion correct (right) for face responses and house responses. Dark grey bars correspond to responses in face blocks, light grey bars correspond to responses in house blocks. * designates $p < 0.05$.

Participants' performance was near ceiling for both attend-faces (hit rate: 0.97 ± 0.01 ; false alarms: 1.41 ± 0.24) and attend-houses (hit rate: 0.95 ± 0.01 ; false alarms: 1.33 ± 0.22) blocks, with comparable reaction times (attend-face blocks mean RT: 628 ± 8.93 ms; attend-house blocks mean RT: 650 ± 9.96 ms). Performance was better in face blocks relative to house blocks (IES for faces: 654 ± 13.8 ms; IES for houses: 696 ± 17.3 ms; $t(69) = -2.35$, $p = 0.02$,

effect size: -0.32; see figure 2.1B, left), consistent with the idea that faces draw more attention than other stimuli (Hershler & Hochstein, 2005; Langton, Law, Burton, & Schweinberger, 2008). Behavioural performance (IES) was not significantly correlated with age for face targets ($r = 0.02$, $p = 0.89$), house targets ($r = -0.08$, $p = 0.51$), nor the difference between face targets and house targets ($r = 0.13$, $p = 0.29$).

fMRI Results

Top-down modulation of category-sensitive visual areas during selective WM encoding in healthy ageing

Older adults were able to use top-down attention to modulate category-sensitive visual cortex according to task demands. Specifically, there was greater BOLD activity whilst participants were encoding houses into WM (house stimulus, attend-house blocks) relative to ignoring distractor houses (house stimulus, attend-face blocks) in bilateral PG (left: $t(69) = 5.69$, $p = 2.78 \times 10^{-7}$, effect size: 0.50; right: $t(68) = 5.74$, $p = 2.42 \times 10^{-7}$, effect size: 0.42; no difference between hemispheres: $t(68) = 1.56$, $p = 0.13$, effect size: 0.16; figure 2.2A, left). The degree of top-down modulation in the PG was positively correlated with digit span ($r = 0.34$, $p = 0.005$; figure 2.2C, right), but not with age ($r = -0.01$, $p = 0.93$). There was also more activity whilst participants were encoding faces into WM (face stimulus, attend-face blocks) relative to ignoring distractor faces (face stimulus, attend-house blocks) in bilateral FG (left: $t(68) = 5.95$, $p = 1.03 \times 10^{-7}$, effect size: 0.38; right: $t(68) = 3.53$, $p = 0.0007$, effect size: 0.34; no difference between hemispheres; $t(69) = 0.93$, $p = 0.35$, effect size: 0.12; figure 2.2A, right). There was no significant difference between attentional modulation in the face-sensitive and house-sensitive areas (Category attention: $F(1,66) = 0.07$, $p = 0.79$, $np^2 = 0.001$; Hemisphere: $F(1,66) = 2.98$, $p = 0.09$, $np^2 = 0.04$; Category attention by Hemisphere interaction: $F(1,66) = 0.08$, $p = 0.78$, $np^2 = 0.001$).

Whole-brain analyses revealed that older adults recruited a broad range of brain areas during top-down attention for WM (house attention: cluster-corrected $p = 5.61 \times 10^{-45}$, figure 2.2A; face attention: cluster-corrected p 's $< 7.8 \times 10^{-5}$, figure 2.2B), including regions in the fronto-parietal network, cingulo-opercular network (Petersen & Posner, 2012; Dosenbach et al., 2007), and bilateral thalamus and the basal ganglia (caudate and putamen). Prominent peaks occurred in the left IFC, anterior cingulate cortex, middle/superior frontal gyrus, and inferior temporal cortex (see table S2.1 and 2.2 for cluster peaks and their MNI coordinates). Consistent with the ROI analyses, category-sensitive visual areas were modulated by attention according to task condition, and the modulation in bilateral PG during WM encoding for houses significantly co-varied with digit span (cluster-corrected p 's < 0.025 ; figure 2.2C, left; table S2.3) but not with age.

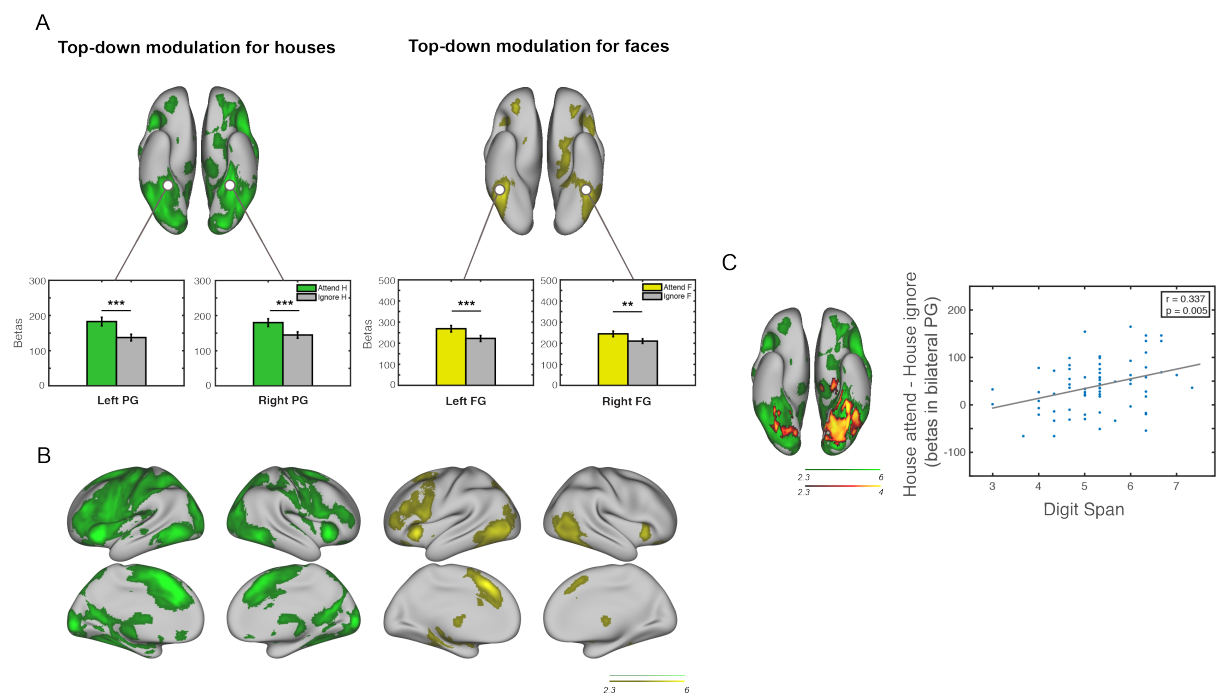


Figure 2.2. Attentional modulation in category-sensitive visual cortex, fronto-parietal and operculo-cingulate networks, and correlation of attentional modulation with WM digit span. A) Attentional modulation in category-sensitive visual cortex. Left: BOLD activity in the parahippocampal gyri (PG) was significantly modulated by selective attention to houses. Green clusters show areas that were more active during house stimuli in the attend-house blocks (WM encoding) relative to house stimuli in the attend-face blocks (ignoring). The circles designate the approximate location of the left and right PG at the group level, and the lines connect to bar plots showing beta estimates (arbitrary units) for the attend houses (green; house stimulus, attend-house blocks) and ignore houses (grey; house stimulus, attend-face blocks) conditions from the participant-defined PGs. Right: BOLD activity in the fusiform gyri (FG) was modulated by selective attention for houses. Yellow clusters

show areas that were more active during face stimuli in the attend-face blocks (WM encoding) relative to face stimuli in the attend-house blocks (ignoring). The circles designate the approximate location of the left and right FG at the group level, and the lines connect to bar plots showing beta estimates (arbitrary units) for the attend faces (yellow; face stimulus, attend-face blocks) and ignore faces (grey; face stimulus, attend-house blocks) conditions from the participant-defined FGs. *** designates $p < 0.000001$, ** $p = 0.0007$. B) Whole-brain analyses showing significant modulation in areas in the fronto-parietal network and cingulo-opercular network during selective encoding for houses (left; cluster-corrected $p = 5.61 \times 10^{-45}$) and faces (right; cluster-corrected p 's $< 7.8 \times 10^{-5}$). C) Degree of modulation in the inferior temporal cortex (including the PG) during selective encoding of house stimuli was positively correlated with digit span. Left: Whole-brain analysis showing areas modulated by attention as shown in A (green), overlaid with areas that positively covaried with digit span (red; cluster-corrected p 's < 0.025). Right: Scatterplot of BOLD beta estimates extracted from participant-defined bilateral PG (betas in house attend – betas in house ignore) plot as a function of digit span. All clusters displayed are significant clusters from whole-brain analyses, thresholded at $p < 0.05$, cluster-corrected (see Methods). Clusters displayed on the brains are z-statistic images.

The left frontal operculum/IFC is involved in top-down control over category-sensitive visual cortex during WM encoding for houses

To investigate the brain areas involved in top-down control over sensory information during WM encoding, I tested for brain areas that were functionally coupled with category-sensitive visual cortex during WM encoding (psychophysical interaction (PPI); Friston et al., 1997). The left fO/IFG, central opercular cortex, and precentral gyrus were coupled with activity in bilateral PG during encoding house stimuli into WM relative to ignoring distractor houses (figure 2.3; cluster-corrected $p = 5.36 \times 10^{-7}$; table S2.4), consistent with previous feature-based attention-WM studies in young adults showing coupling between category-sensitive visual cortex and bilateral fO (Higo et al., 2011; Nelissen et al., 2013), and feature-sensitive regions (V4/MT) with a similar region the right IFC (Zanto et al., 2010; Zanto et al., 2011).

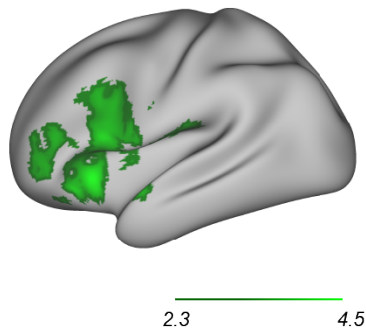


Figure 2.3. *The left IFC is selectively coupled with the PG during selective encoding of house stimuli versus filtering of house distractors. The left fO, inferior frontal gyrus pars operculus, central opercular cortex, and precentral gyrus were coupled with activity in bilateral PG during selective encoding of house stimuli (house stimulus, attend-house blocks > house stimulus, attend-face blocks; cluster-corrected $p = 5.36 \times 10^{-7}$). The cluster displayed is a significant cluster from whole-brain analyses, thresholded at $p < 0.05$, cluster-corrected (see Methods). Cluster displayed on the brain is a z-statistic image.*

Stronger recruitment of the fronto-parietal and cingulo-opercular network related to task difficulty

Faces capture attention and can be difficult to suppress when acting as distractors (e.g. Hershler & Hochstein, 2005; Langton et al., 2008), reflected here in the superior behavioural performance in WM for face compared to house stimuli. This suggests that participants may have exercised greater cognitive effort and recruited more neural activity in task-related areas during selective attention for encoding house stimuli into WM compared with encoding face stimuli. Indeed, during selective attention for house stimuli (all stimuli from the attend-house blocks > all stimuli from the attend-face blocks) the left fO, caudate, putamen, supplemental motor area, ACC, medial prefrontal, parietal, and visual cortices were more active (cluster-corrected p 's < 0.0028, figure 2.4A; table S2.5), whereas during selective attention for face stimuli (all stimuli from the attend-face blocks > attend-house blocks), only the precuneus – an area of the default-mode network (Raichle et al., 2001) – exhibited greater activity (cluster-corrected $p = 0.035$; figure 2.4B; table S2.6).

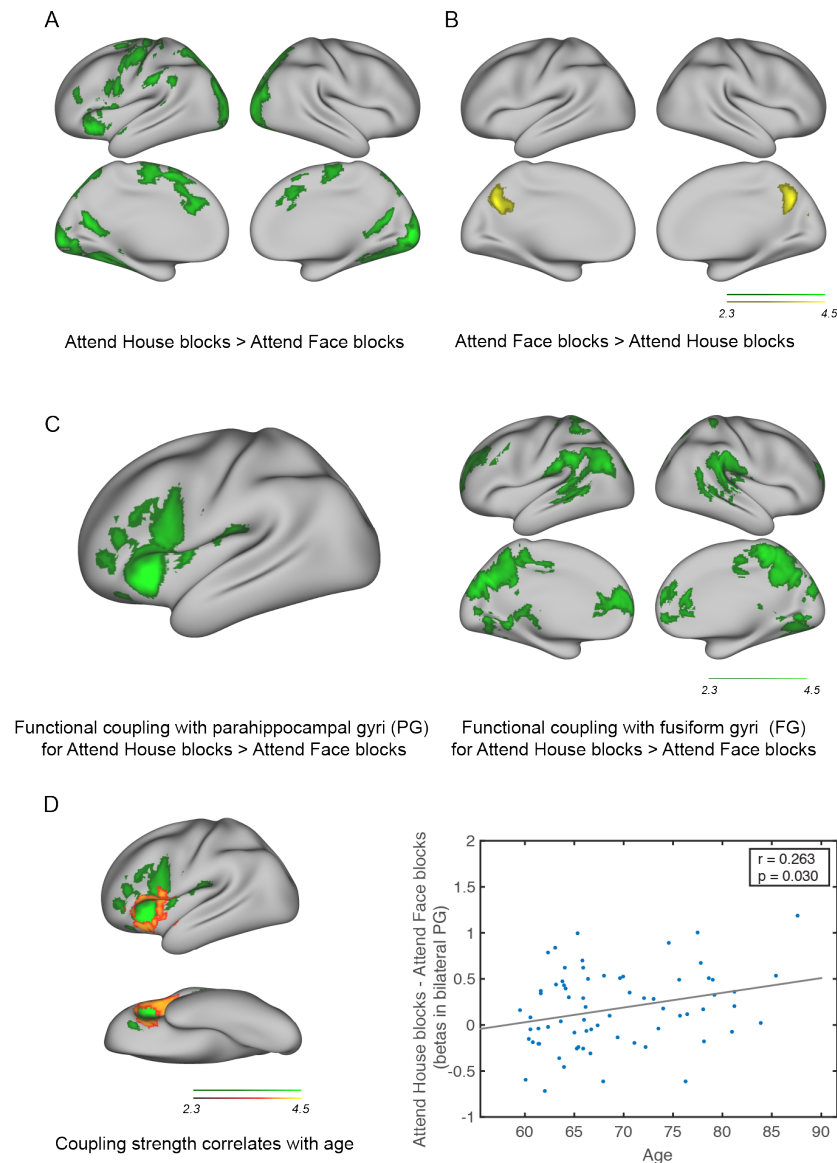


Figure 2.4. Neural activity and functional coupling (psychophysical interaction) during attention to stimulus categories for WM encoding. A) Selective encoding for houses whilst filtering distractor faces elicited activity in inferior frontal, anterior cingulate, parietal, and visual cortices (all stimuli in house blocks > all stimuli in face blocks; cluster-corrected p 's < 0.0028). B) Selective encoding for faces whilst filtering distractor houses elicited activity in the precuneus (all stimuli in face blocks > stimuli in the house blocks; cluster-corrected $p = 0.035$). C) The IFC is selectively coupled with the relevant category-sensitive visual areas (PG), and the default-mode network is coupled with the irrelevant visual areas (FG) during selective encoding of house stimuli. Left: The left frontal operculum (lFO), inferior frontal gyrus (IFG), insular, and parts of the caudate and putamen were coupled with activity in bilateral PG during selective encoding of house stimuli (all stimuli in the attend-house blocks > all stimuli in the attend-face blocks). Right: Areas in the default-mode network (medial PFC, precuneus, temporal-parietal regions) were coupled with the FG during selective encoding of house stimuli. D) Functional connectivity strength between category-sensitive visual cortices and areas surrounding the left fO were positively correlated with age. Left: The green cluster shows the inferior frontal areas that were functionally coupled with the PG (as presented in C, left), and the red cluster shows the areas that were positively correlated with age. Right: Scatterplot showing a positive correlation between age and functional connectivity strength for attention for houses versus attention for faces for visualisation (betas extracted using a mask of the significant age-correlation)

cluster). All clusters displayed are significant clusters from whole-brain analyses, thresholded at $p < 0.05$, cluster-corrected (see Methods). Clusters displayed on the brains are z-statistic images.

Category-sensitive visual cortex was selectively coupled with task-related versus rest-related brain areas during selective attention for WM

Next, I tested for brain areas that were functionally coupled with category-sensitive visual cortex during selective attention for WM. Bilateral PG was significantly coupled with the left fO/IFG, left central opercular cortex, as well as the left caudate and putamen during attention to houses relative to attention to faces (all stimuli in attend-house blocks > all stimuli in attend-face blocks; cluster-corrected $p = 8.94 \times 10^{-7}$; figure 2.4C, left; table S2.7), whereas activity in the bilateral FG was significantly coupled with areas in the default-mode network, including the precuneus, medial PFC (including rostral ACC, paracingulate gyrus), temporal-parietal regions (bilateral middle temporal gyrus, superior temporal gyrus, parietal operculum, supramarginal gyrus, angular gyrus), as well as bilateral lingual gyri (cluster-corrected p 's < 0.0001, figure 2.4C, right; table S2.8).

There was a similar but weak pattern of connectivity for the attend-faces blocks compared to the attend-houses blocks (all stimuli in attend-face blocks > all stimuli in attend-house blocks), in which the left fO showed a trend for coupling with the FG (uncorrected $z = 1.5$; figure S2.5), whilst the precuneus was significantly coupled with the PG (cluster-corrected $p = 0.029$; figure S2.5; table S2.10).

Old-old adults recruit a spatially more distributed region in the left fO/IFC during top-down control over category-sensitive cortices

Coupling strength between the PG and regions around the left fO/IFC during attention to houses relative to attention to faces was positively correlated with age (cluster-corrected $p = 0.008$; figure 2.4D, left, red cluster; table S2.9). Although this cluster overlapped with the

main effect of connectivity, the correlation with age was *surrounding* the peak of the connectivity effect in the left fO. Indeed, regressing the coupling strength at the peak and the surrounding brain regions on age revealed that coupling at the peak was not significantly associated with age ($b = -0.06$, $p = 0.66$), whereas the coupling strength surrounding the peak was ($b = 0.55$, $p = 0.029$). Note that the lack of an association with age with the coupling strength at the peak was not due to less signal (coupling strength) or more noise compared to the age-correlation cluster surrounding the peak, since the coupling strength was actually greater in the peak compared to the surrounding cluster ($t(69) = 4.69$, $p = 4.69 \times 10^{-6}$, effect size: 0.40). BOLD activity from the peak ($b = 0.09$, $p = 0.57$) or the surrounding regions ($b = -0.12$, $p = 0.42$) were not correlated with age.

Left-lateralised responses in the PFC in healthy ageing

Some researchers have suggested that young adults recruit the right PFC during cognitive tasks, whereas older adults also recruit areas in the left PFC whilst performing the same task, possibly to compensate for age-related decline of purported cognitive control areas (Cabeza et al., 2002; Grady, 2008; Reuter-Lorenz & Capell, 2008). The group results suggest that activity in prefrontal regions are left lateralised, whereas the attentional modulation in category-sensitive visual areas are largely similar across hemispheres and do not correlate with age in this elderly group. In order to test the degree of laterality in prefrontal regions, I used an ROI approach to test if there was a reduced lateralisation, or left lateralisation in this group of older adults (see Methods).

Bilateral fO was recruited during encoding house stimuli into WM relative to ignoring houses (house stimuli, attend-house blocks > house stimuli, attend-face blocks; left: $t(69) = 5.52$, $p = 5.59 \times 10^{-7}$, effect size: 0.66; right: $t(69) = 2.14$, $p = 0.03$, effect size: 0.26), and activity in the left fO was greater than in the right ($t(69) = 2.77$, $p = 0.007$, effect size: 0.29). There was

significant coupling between bilateral PG and the left fO for selective encoding of house stimuli relative to ignoring houses ($t(69) = 3.90$, $p = 0.0002$, effect size: 0.47), a trend for the right fO ($t(69) = 1.65$, $p = 0.10$, effect size: 0.20), but the coupling strength was not significantly different between areas ($t(69) = 0.94$, $p = 0.35$, effect size: 0.13).

For the general effect of selective attention for houses (all stimuli in attend-houses blocks > all stimuli in attend-faces blocks), left fO was significantly recruited ($t(69) = 3.34$, $p = 0.001$, effect size: 0.40), the right fO only showed a trend ($t(69) = 1.61$, $p = 0.11$, effect size: 0.19), but there was no significant difference between the left and right fO ($t(69) = 0.79$, $p = 0.43$, effect size: 0.08). There was significant functional coupling between the bilateral PG and the left fO ($t(69) = 4.27$, $p = 6.14 \times 10^{-5}$, effect size: 0.51) but not with the right fO ($t(69) = 0.70$, $p = 0.49$, effect size: 0.08), and the coupling was greater in the left compared to the right ($t(69) = 2.49$, $p = 0.015$, effect size: 0.33).

Discussion

I tested a large sample of elderly participants on a selective WM task and found that the neural mechanisms of top-down control for WM are relatively preserved in healthy ageing. Category-sensitive visual areas were selectively modulated according to the attended category, and the degree of modulation in house-sensitive PG was positively correlated with digit span measures. Cognitive control networks were strongly recruited during selective WM encoding. Control regions in the left IFC were selectively coupled with the relevant category-sensitive visual areas (PG) during selective attention to stimuli in the associated category, during which the DMN was coupled with the irrelevant category-sensitive visual areas. The older individuals within this elderly group recruited a more spatially distributed region in the IFC to modulate sensory cortex for successful selective WM performance, suggesting that they employed compensatory neural resources to lessen age-related cognitive declines. Finally, I found that activity in the PFC was mostly left lateralised, in contrast to theories of cognitive

ageing that suggest older adults recruit bilateral activation of PFC to compensate for age-related declines.

Older adults were able to use top-down control to modulate category-sensitive visual areas during WM encoding and filtering distractors from entering memory. I replicated the finding that older adults are able to modulate the left PG during selective WM (attend versus ignore; Chadick et al., 2014; Gazzaley et al., 2005), but also show that the right PG, and bilateral FG are significantly modulated by top-down attention in older adults. This indicates that older adults retain the ability to selectively enhance the sensory representations of relevant stimuli for selective WM encoding. Previous studies have suggested that older adults exhibit deficits in inhibition during selective attention and memory tasks (e.g. Alain & Woods, 1999; Chao & Knight, 1997; Fabiani et al., 2006; Gazzaley, Cooney, Rissman, et al., 2005; Hasher & Zacks, 1988; McNab et al., 2015; West & Alain, 2000; R. T. Zacks et al., 2000, 1996). In the current study, older adults showed preserved abilities of top-down modulation over sensory areas, which did not appear to correlate with age within this elderly age group. However, I did not explicitly test for suppression in my task, such as using a passive view condition (Chadick et al., 2014; Gazzaley et al., 2005) or whether there was enhanced memory for stimuli in the ignored category, which would hint toward impaired inhibitory processes (faces presented in the house block or houses presented in the face blocks; e.g. see Campbell, Hasher, & Thomas, 2010; Gerard, Zacks, Hasher, & Radvansky, 1991; S. Kim et al., 2007; R. T. Zacks et al., 1996). In the future, it would be interesting to include tests of implicit and explicit memory of the attended and ignored stimuli after the scanning session to test the inhibition hypothesis in ageing (Hasher & Zacks, 1988) and how performance on these tests corresponds to the degree of top-down modulation in sensory cortex. Nevertheless, this study shows that older adults exhibit robust modulation of category-sensitive visual areas,

suggesting relative preservation of top-down mechanisms for selective WM encoding, without referring to the mechanisms of enhancement or inhibition.

Attentional modulation in the PG was positively correlated with digit span – a general measure of WM capacity – suggesting that the ability to use top-down control to modulate sensory processing is linked with WM capacity in older adults. These results support the idea that selective attention is closely related to, and even actively involved in WM maintenance processes (Awh & Jonides, 2001; D’Esposito & Postle, 2015; Gazzaley & Nobre, 2012; Postle, 2006; Stokes & Nobre, 2012; also see Sander, Lindenberger, & Werkle-Bergner, 2012 for a review focussed on ageing). Notably, individual differences in top-down modulation were not correlated with age within this elderly group. A few studies have reported inter-individual differences in top-down suppression within elderly groups (e.g. Chadick et al., 2014; Gazzaley et al. 2005). Gazzaley et al. (2005) found that older adults showed significantly greater activity in the left PG during encoding scenes into WM relative to a passive viewing baseline, but did not show suppression of activity for ignore relative to the passive viewing condition (whereas young adults did). The degree of suppression (ignore scenes > passive view scenes) was negatively correlated with performance on face trials, where the high performing elderly adults showed top-down suppression similar to the young adults (also see Chadick et al., 2014 for a similar result). However, they did not report whether the top-down enhancement is correlated with performance during WM for scenes. In the current study, there was a robust correlation between the degree of top-down modulation in the PG for house stimuli (encoding versus ignoring houses) and general WM capacity measured by digit span. Although it was not possible to disentangle whether this relationship was due to top-down enhancement of targets or suppression of distractors, previous work suggests that it could result from a deficit in suppressing irrelevant stimuli in healthy ageing (Chadick et al., 2014; Gazzaley et al., 2005).

Older adults exhibited preserved brain mechanisms for top-down control during feature-based selective WM. They recruited brain areas in the fronto-parietal and cingulo-opercular networks during selective encoding for houses (encoding versus ignoring house stimuli), and faces (encoding versus ignoring face stimuli), which was qualitatively similar to attention and control networks recruited by young adults (Dosenbach et al., 2008; Petersen & Posner, 2012), and by both young and old adults during successful visual search (Madden et al., 2007). Activity in the left IFC was functionally coupled with house-sensitive PG during selective WM for houses, suggesting a role of the IFC in feature-based attention for WM. The left fO, situated within the IFC, was one of the key areas activated in the task and showed strong functional coupling with sensory areas during selective WM, replicating previous feature-based attention studies in young adults (Higo et al., 2011; Nelissen et al., 2013). A more superior region in the right IFG, which was also activated in the current study, was selectively coupled with motion and colour-sensitive visual areas during feature-based attention (Zanto et al., 2010, 2011; also see Baldauf & Desimone, 2014). In the current study, although coupling between frontal and sensory cortices were lateralised to the left IFC, an ROI approach revealed similar effects in the right fO (also see figure S2.5 for uncorrected images showing similar results). Recent animal work has provided substantial support that the IFC plays a key causal role in feature-based attention (Bichot et al., 2015).

Task-relevant brain networks were selectively coupled to the relevant category-sensitive visual areas whilst the rest-related network (DMN) was coupled to irrelevant category-sensitive visual areas during selective WM in older adults, indicating preserved functional network integrity for top-down control in healthy ageing. The fronto-parietal and cingulo-opercular networks were recruited during attention to houses (attend house blocks > attend face blocks), whereas only the precuneus – a region associated with the DMN (M. D. Fox et al., 2005;

Raichle et al., 2001) and is deactivated during cognitive tasks (Shulman et al., 1997) – exhibited greater activity during attention to faces (attend face blocks > attend house blocks), consistent with more cognitive effort during encoding houses and ignoring faces compared with encoding faces and ignoring houses. During selective attention for houses, the house-sensitive visual areas (PG) were functionally coupled with the left IFC (similar to selective WM for house stimuli), whereas the face-sensitive areas (FG) were functionally coupled with regions of the default-mode network, including the precuneus, medial PFC, and temporo-parietal cortex. During attention to faces, activity in the house-sensitive PG was similarly coupled with areas in the default-mode network. There was a hint that the face-sensitive FG was coupled with the IFC, but this did not survive the statistical significance threshold, consistent with the behavioural and univariate BOLD results which suggested that attention to faces required less cognitive effort, and thus less demand on prefrontal control areas to modulate sensory cortex. It was particularly intriguing to find that activity in the task-relevant category-sensitive visual areas was coupled with brain regions in the IFC, whereas activity in the task-irrelevant visual areas was coupled with the DMN. The DMN is a network of brain areas including regions of the posterior cingulate cortex (PCC), precuneus, medial PFC, orbital frontal gyrus, ACC, inferior-lateral temporal cortex, and lateral parietal cortex, which are recruited and show coupled activity during rest (M. D. Fox et al., 2005; Raichle et al., 2001). Similar brain regions, including the PCC, precuneus, medial PFC, and temporo-parietal junction shows deactivation during cognitive tasks compared with rest (Shulman et al., 1997), and the magnitude of deactivation scales linearly with task difficulty (McKiernan, D'Angelo, Kaufman, & Binder, 2006; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Singh & Fawcett, 2008), WM load (Mayer, Roebroek, Maurer, & Linden, 2010; McKiernan et al., 2003; Todd, Fougine, & Marois, 2005; Tomasi, Ernst, Caparelli, & Chang, 2006), and behavioural performance (Anticevic, Repovs, Shulman, & Barch, 2010; Hampson, Driesen, Skudlarski, Gore, & Constable, 2006; Shulman, Astafiev, McAvoy,

D'Avossa, & Corbetta, 2007). One study showed significant deactivations in areas in the precuneus and the medial PFC in older adults, and that these areas showed less deactivation compared to young adults (Chadick et al., 2014). These studies suggest that deactivations in DMN regions might play an active role during selective attention and WM processes. In the current study, I found that the fronto-parietal and cingulo-opercular networks were recruited during selective WM encoding, with the left IFC playing a role in top-down modulation of the task-relevant category-sensitive visual cortex. Brain areas in the DMN were selectively coupled with the irrelevant category-sensitive visual areas, suggesting selective suppression of the irrelevant sensory areas during WM encoding. These results suggest that the brain selectively recruits different networks for the relevant versus irrelevant sensory areas in order to selectively enhance target stimuli for WM encoding and filter distractors from entering memory. In contrast to previous work suggesting age-related cognitive control deficits and impaired PFC function, I found that older adults exhibited preserved neural mechanisms of top-down control, showing robust recruitment of task-relevant networks and selective coupling between task and rest-related networks for modulating sensory cortex during selective WM encoding.

The older adults within this elderly group recruited a larger region of the IFC to effectively modulate sensory cortex for selective WM encoding, possibly reflecting compensatory processes for age-related declines in cognitive control. The coupling strength between areas in the left IFC and the relevant category-sensitive visual areas (PG) during selective attention for houses was positively correlated with age, indicating that the older adults in this elderly group (old-old) recruited more neural activity in the IFC to modulate sensory cortex. Crucially, only the degree of functional coupling was related to age, and not the magnitude of the BOLD response in either brain area, meaning that the additional activity recruited in the IFC was *specifically* for the modulation of the relevant category-sensitive visual areas during

WM encoding. On close inspection, the areas that showed this positive correlation with age in the IFC were *surrounding* the left fO – a region implicated in feature-based attention (Higo et al., 2011; Nelissen et al., 2013) and exhibited the strongest effect of functional coupling with sensory cortex in the current study. This means that the old-old adults showed greater coupling between sensory cortex and a larger – or spatially more distributed – region of the IFC. Previous studies have observed greater activations in older adults compared with young adults, which were associated with both impaired and matched performance with young adults (e.g. Cappell et al., 2010; Gutchess et al., 2005; Madden et al., 2007; Mattay et al., 2006; Morcom et al., 2007; Schneider-Garces et al., 2010). A theoretical model proposed by Reuter-Lorenz and colleagues (Reuter-Lorenz & Cappell, 2008; compensation-related utilization of neural circuits hypothesis; CRUNCH) suggests that older adults show “over-activation” in the PFC to compensate for age-related cognitive declines, but “under-activation” when they are unable to cope with high task demands. They proposed that when older adults perform as well as young adults at low difficulty levels, they show greater activity in the PFC compared to the young group, reflecting more recruitment of cognitive control mechanisms to produce good task performance. However, when task demands outreach the older adults’ cognitive abilities, they exhibit reduced PFC activity compared to the young adults, which accompanies poor task performance (e.g. Cappell et al., 2010; Mattay et al., 2006; Schneider-Garces et al., 2010). In this study, the old-old adults recruited a larger region of the IFC to modulate visual cortex compared with the younger elderly adults. Since the old-old adults performed as well the younger elderly adults, this is consistent with the idea that they recruited more neural resources in the IFC to support behaviour. One study showed that functional coupling between the PFC and pre-motor cortex, as well as BOLD activity in both areas, was positively correlated with performance in an n-back task in both young and older adults, suggesting the integrity of the functional network supports successful WM performance (Nagel et al., 2011). In future work, it would be interesting to include several

task-difficulty conditions to test if old-old adults would show reduced functional coupling between PFC and sensory areas in more difficult conditions which correspond to impaired behavioural performance.

The current study suggests that older adults recruit the left IFC more than the right IFC during selective WM, but I did not find evidence for a reduction in asymmetry in prefrontal recruitment in older adults. Some researchers have suggested that older adults recruit bilateral PFC in order to compensate for age-related decline in cognitive control, compared to young adults who only recruit unilateral PFC when performing the same task (Cabeza, 2002; hemispheric asymmetry reduction in old adults; HAROLD). The evidence has come from a range of different tasks including WM tasks (Cabeza, 2004; Dolcos et al., 2002; Park et al., 2003; Reuter-Lorenz et al., 2000; although see Cappell et al., 2010; Grady et al., 2005). In the current study, activations in the PFC were bilateral, stronger on the left, or lateralised to the left. If it was possible to compare with a younger group that exhibited more unilateral PFC activations, there may have been age differences in laterality. However, if this was the case, one might expect that the young-old adults in the current elderly group would show greater unilateral activation in the PFC compared to the old-old adults, which was not the case. Furthermore, the data suggest strong lateralisation to the left, rather than bilateral activation of the PFC. One possibility for greater activation in the left IFC during selective WM could have been due to a greater reliance on verbal strategies in older populations. Overall, my results suggest that older adults show a more left-lateralised recruitment of the PFC during a selective WM task, rather than a bilateral pattern.

In sum, older adults engaged cognitive control networks in concert with the relevant sensory areas and recruited the DMN with irrelevant sensory areas for effective selective WM. Older adults within this elderly group engaged compensatory activity to modulate sensory cortex,

and matched behavioural performance with their younger elderly counterparts. The current study shows that older adults retain preserved neural mechanisms for selective WM, and suggests that, as individuals grow older, they can employ additional neural resources to strengthen relevant brain networks to support successful cognition. Studying inter-individual variability of the neural mechanisms linked with cognitive behaviour in large groups of elderly adults might be an effective way to study the neural mechanisms that underlie successful cognitive ageing. Future studies should keep exploring the neural markers associated with both successful and impaired cognitive behaviour to map out the mechanisms that underlie healthy versus poor cognitive ageing.

In conclusion, I found that the neural mechanisms for selective WM were relatively preserved in healthy ageing, and that, as individuals grow older and experience age-related decline, they can employ additional neural resources to strengthen relevant brain networks to support successful cognition. This group of older adults exhibited impressive flexibility and selectivity in brain function, recruiting cognitive control networks in concert with the relevant sensory areas and the rest-related DMN with irrelevant sensory areas for effective selective WM. The older adults within this elderly group engaged compensatory activity specifically to modulate sensory cortex during selective WM, and produced matched behavioural performance to their younger elderly counterparts. Studying inter-individual variability of the neural markers in large groups of elderly adults might be an effective way to study the neural mechanisms that underlie successful cognitive ageing. Future studies should continue to explore the neural markers associated with both successful and impaired cognitive behaviour to map out the mechanisms that underlie healthy versus poor cognitive ageing.

3. Flexible control over visual representations within working memory in healthy ageing

Chapter Abstract³

In this chapter, I tested whether older individuals benefit from flexible orienting of attention within WM to mitigate age-related deficits in short-term memory maintenance, and how the individual differences in neural activity corresponded to good behavioural performance. I measured MEG in older adults performing a WM precision task with cues during the maintenance period that retroactively predicted the location of the relevant items for performance (retro-cues). Older adults' WM performance significantly benefitted from retro-cues. Whereas WM maintenance declined with age, retro-cues conferred strong attentional benefits. A model-based analysis revealed an increase in the probability of recalling the target, a lowered probability of retrieving incorrect items or guessing, and an improvement in memory precision. Magnetoencephalographic recordings showed that retro-cues induced a transient lateralisation of alpha (8-14 Hz) and beta (15-30 Hz) oscillatory power. Interestingly, shorter durations of alpha/beta lateralisation following retro-cues predicted larger cueing benefits, reinforcing recent ideas about the dynamic nature of access to WM representations. The results suggest that older adults retain flexible control over WM, but individual differences in control correspond to differences in neural dynamics, possibly reflecting the degree of preservation of dynamic attentional control in healthy ageing.

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Introduction

WM is essential for much of higher-order cognition. As such, deficits in WM may have adverse effects for other cognitive domains, leading to deficits in effective decision-making, planning, and long-term memory. A growing body of research suggests that selective attention is critical to support effective WM, by enabling selection and maintenance of relevant items in the face of competing distractors (Gazzaley & Nobre, 2012; Stokes & Nobre, 2012; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). In addition, it has been shown that it is possible to orient attention after WM encoding to prioritise or update information being maintained in WM (Griffin & Nobre, 2003; Landman et al., 2003).

WM functions decline with ageing (Chen, Hale, & Myerson, 2003; Iachini, Iavarone, Senese, Ruotolo, & Ruggiero, 2009; Nagel et al., 2009; Park et al., 2002; Peich, Husain, & Bays, 2013; Rypma & D'Esposito, 2000; Salthouse & Babcock, 1991; Salthouse, 1992, 1994; Werkle-Bergner, Freunberger, Sander, Lindenberger, & Klimesch, 2012), which may have important deleterious consequences for other cognitive functions. It is important, therefore, to understand which aspects of WM are compromised, and the extent to which top-down attentional control may be able to mitigate deficits. Several studies have demonstrated that healthy elderly adults experience significant declines in their ability to use selective attention to guide the encoding of relevant material and suppress irrelevant items during WM encoding (Gazzaley et al. 2005, 2008; Zanto et al. 2010; Gazzaley 2013; see also Hasher and Zacks 1988; Hasher et al. 1999). A number of previous investigations have tested for the effects of attention on WM in elderly adults, and have reported deficits in modulating expectation and encoding of stimuli for effective WM performance (Fabiani et al., 2006; Gazzaley, Cooney, Rissman, et al., 2005; Gazzaley et al., 2008; Jost et al., 2011; Peich et al., 2013; Sander, Werkle-Bergner, et al., 2012). These studies leave open the important question of whether

healthy ageing also compromises the ability to exert flexible attentional control *after* encoding, in order to prioritise the maintenance or retrieval of certain elements over others.

Prior work has shown that the ability to orient attention within WM can be tested by presenting cues during the WM maintenance interval that provides retrospective information about which items are likely to be relevant to guide subsequent performance (“retro-cues”; Griffin & Nobre 2003). Retro-cues lead to reliable performance benefits in young adults (Griffin & Nobre, 2003; Landman et al., 2003; Makovski, 2012; Nobre, et al., 2007; Nobre, 2004; Rerko & Oberauer, 2013; Rerko et al., 2014; Sligte, et al., 2008; Williams et al., 2013). Preserved abilities to orient attention within WM would mean that, in contrast to preparatory attentional control during WM encoding, retrospective attentional control remains relatively intact in healthy ageing.

In the current experiment, I tested whether elderly participants are able to exert flexible control over WM contents. I recruited a large sample of older adults to test for differences in the ability to orient attention to the contents of WM, and to investigate the neural correlates of spared versus impaired WM control. By capitalising on variability within a homogenous cohort of older participants, I aimed to circumvent the inevitable extraneous nuisance variables that can contribute to comparisons of different age groups (e.g., motivation, fatigue, exposure to computer technology, medication, etc.). Furthermore, investigating individual differences within an elderly age group can tell us about the mechanisms that relate to successful ageing. To my knowledge, two studies have tested the effectiveness of retro-cues in elderly participants (Duarte et al., 2013; Newsome et al., 2015), and both showed a significant impairment with healthy ageing. I revisited this question by combining retro-cues with a WM precision task that enabled us to measure benefits in memory recall and in the quality of WM representations. I used a model-based analysis to explore whether putative

retro-cue benefits arise from either an increased probability to retrieve relevant items or an increase in the precision of representations.

I recorded neural activity during task performance using MEG in order to chart the temporal dynamics of oscillatory markers of orienting attention within WM. Similar to the effects observed when spatial attention is deployed in perceptual tasks (Gould, et al., 2011; Kelly et al., 2009; Rihs et al., 2007; Thut et al., 2006; Worden et al., 2000), a robust marker for the deployment of spatial attention within WM is the systematic decrease in the power of alpha oscillations contralateral to the location of the cued WM item (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015). In contrast to the sustained desynchronisation found after anticipatory attention shifts, modulations of alpha power during internal shifts of attention to items within WM appear to be more transient (Myers et al. 2015; Wallis et al. 2015). These rapid dynamics may reflect a transient process of changing excitability in — or access to — sensory cortex (Myers et al. 2015; Wallis et al. 2015).

I found that, as a group, elderly participants benefited significantly from retro-cues. The behavioural benefits were mainly associated with an increased probability of retrieving the attended item and decreased guessing or confusion with other items. Neural markers of orienting attention in working memory were similar to those described for younger populations (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015). At the individual level, the dynamics of the oscillatory markers were strongly predictive of performance benefits arising from flexible control over WM.

Methods

Participants

The study received ethical approval from the Central University Research Ethics Committee of the University of Oxford. All participants provided written informed consent, and were compensated for their time and travel expenses.

Eighty-one healthy older adults (aged 60-87) were recruited from the community via local media and public advertisements. Of these, 75 participants were able to complete the current experiment. Reasons for withdrawing from the study included difficulty with travelling to the assessment centre or instances of poor health. One further participant was unable to perform the task above chance level and therefore was excluded from the analysis (see section on Behavioural Data Analysis). The remaining 74 participants (42 female) were 60-87 years old (mean 68.8 ± 0.82 years), had 16 ± 0.47 years of education. All participants were fluent in English, had normal or corrected-to-normal vision and hearing, and scored >26 on the Mini-Mental State Examination (MMSE, Folstein et al. 1975). None of the participants had any current diagnosed psychiatric or neurological disorder, and none were taking psychoactive medication.

Data from 61 participants were used in the MEG analysis (aged 60-87 years; mean 69.22 ± 0.92 S.E.M.; 16.1 ± 0.52 years of education; 32 females). Five participants were excluded because the structural MRI scans revealed significant cortical atrophy. Seven further participants were excluded because the MEG data contained excessive artefacts, and were consequently discarded before any processing (this included one participant who responded randomly in the task; see Behavioural Data Analysis). Data from one further participant were not saved due to a technical failure.

WM Precision Retro-cueing Task

The main experimental task tested the number and quality of representations that individuals could maintain in working memory, as well as their ability to orient attention within WM flexibly to prioritise relevant items. A WM precision task (W. Zhang & Luck, 2008) was combined with a retro-cueing manipulation (Griffin & Nobre, 2003). Figure 1A provides a schematic of the task.

On each trial, participants encoded an array of four 'orientation' items into WM, and were subsequently probed to recall one item after a delay. On spatial retro-cue trials, the location of the relevant item was indicated by a 100% predictive spatial cue during the delay interval. Spatial retro-cues appeared 700 ms after disappearance of the stimulus array. On neutral retro-cue trials, the cue provided no spatial information about the item to be probed.

Trials were self-initiated. A 'GO' screen signalled that participants could initiate the trial by pressing a button on a MEG-compatible response pad. A red fixation point followed (150 ms in duration) alerting the participant of the upcoming stimulus array. The WM array appeared after 850 ms, and remained visible for 600 ms. Four orientation stimuli were positioned in the four quadrants (centred at 4.8° horizontally, and 4.8° vertically from fixation). Each array stimulus consisted of an oriented bar (2.32° in length, 0.16° in width), with a disc (0.72° diameter) at its centre. Spatial or neutral retro-cues appeared after a delay of 700 ms. In half the trials, the cue indicated the location of the item that would subsequently be probed (100% validity). In the other trials, the cue provided no predictive information about the location to be probed. Cues were made up of a small black square (0.96° by 0.96°) presented centrally for 500 ms. In spatial retro-cue trials, two sides were coloured white, forming an arrow pointing to one quadrant location. In neutral retro-cue trials, no sides were coloured. After another 1500-ms delay, a probe bar appeared in one of the screen quadrants in a random orientation. Participants used the response pad to adjust the orientation of the probe stimulus so that it

matched the orientation of the remembered item previously presented at that location. The pad contained two buttons; one button rotated the item clockwise and the other button counter-clockwise. Participants used their right hand to adjust the orientation, and then made a separate button-press response with the left hand to confirm their response. The maximum allowed recall time was 8500 ms. After the confirmatory button press, the actual orientation of the memory-array stimulus was overlaid over the participant's recall, providing feedback (200 ms duration). The inter-trial interval from the feedback to the 'GO' screen was 50 ms.

The task was programmed in Matlab v.7.10 (MathWorks) and presented using the Psychophysics Toolbox v.3.0 package (Brainard, 1997). Stimuli were back-projected (Panasonic PT D7700E) onto a screen at a viewing distance of 120 cm with a spatial resolution of 1280 by 1024 pixels and a refresh rate of 60 Hz.

Experimental Procedure

Participants completed a practise session in a 'mock' MEG scanner before completing the experiment in the MEG scanner room. The practice session was used to familiarise the participant with the scanning environment and with the response demands of the task. The experimenter provided verbal instructions about the task using a slide show to illustrate the stimuli and experimental procedure. The 'mock' scanner contained the same scanner layout, projector, and response pads as the MEG scanner room.

During the practise session, participants completed a visual matching task with oriented bars (2.88° length, 0.24° width, disc diameter 0.88°) to ensure participants understood the task and response method, and to verify that their visual acuity was sufficiently good to complete the task. In each trial, an oriented bar was presented at the top half and another at the bottom half of the screen. Participants had to adjust the orientation of the bottom bar to match the

orientation of the bar above. All participants completed 24 trials. The stimuli were the same as those in the main experiment, except that the stimuli in the visual matching practice were larger.

Once participants were proficient at judging stimulus orientation and using the response pads to provide accurate responses, they completed practice trials of the main WM-precision task described above. In a first set of 24 trials, no cues were presented. Retro-cues were introduced in a second set of 24 trials. In this set, only valid spatial retro-cues were used. In a final set of 24 trials, both valid spatial retro-cues and neutral cues were intermixed randomly, as they would appear in the main task. This preparation procedure took approximately 20 minutes.

After setting up participants for MEG recordings, the main experimental task was completed in the MEG scanner. Participants completed six blocks of 40 trials, resulting in 240 trials (120 trials in the spatial and neutral retro-cue conditions). Spatial and neutral retro-cue trials were randomly intermixed within each block. Each spatial location was cued and probed with equal probability. Participants were asked to fixate on the centre of the screen throughout each trial until the probe appeared. They were free to move their eyes while they adjusted the orientation of the probe stimulus and until they initiated the subsequent trial.

Behavioural Data Analysis

The aim of the data analysis was to characterise the number of items older adults could maintain in WM, the precision of their representations, and their ability to orient attention to cued items in WM. I quantified various components that contribute to WM performance. Accuracy (reciprocal of the circular standard deviation of the recall error distribution; $1/\sigma$) was calculated for each participant (Bays & Husain, 2008), measuring the variability in the recall

error⁴. It is important to point out that this measure does not distinguish between types of errors such as inaccurate responses and random guesses. Therefore, to model different sources of error, a mixture model was applied (Bays, Catalao, & Husain, 2009; W. Zhang & Luck, 2008), which attributes the distribution of recalls to a mixture of three separate components: the probability of responding to the target, responding to a non-target, and responding at random (guessing). Orientations are assumed to be recalled with Gaussian variability. The model is described by the following equation:

$$p(\hat{\theta}) = \alpha \Phi_{\kappa}(\hat{\theta} - \theta) + \beta \frac{1}{m} \sum_i^m \Phi_{\kappa}(\hat{\theta} - \varphi_i) + \gamma \frac{1}{2\pi} \quad (1)$$

where θ is the actual orientation of the target, $\hat{\theta}$ is the reported orientation, Φ_{κ} is the von Mises distribution (circular analogue of the Gaussian) describing recall variability with mean zero and precision parameter κ (precision). The probability of reporting the target is given by α , the probability of mistakenly reporting a non-target is given by β , and $\varphi_1, \varphi_2, \dots, \varphi_m$ are the orientations of the m non-target items. The probability of responding randomly (guess rate) is given by $\gamma = 1 - \alpha - \beta$. Maximum-likelihood estimates of each parameter (α , β , γ , and κ) were obtained for each participant and condition (spatial retro-cue, neutral retro-cue) by using an expectation–maximisation algorithm. To ensure that a global maximum was found for the model fit, the optimisation procedure was repeated multiple times using various initial parameter values. These parameter estimates were compared between the spatial and neutral retro-cue conditions using paired t-tests.

Effect size (Cohen’s d) was computed to test the magnitude of the retro-cue benefit (the difference between spatial and neutral retro-cue conditions). Modelling and statistical

⁴ As described in Bays et al. 2009, a correction was applied in which the standard deviation for circular data was taken subtracting the value expected by chance (values taken from a uniform distribution).

analyses were conducted in Matlab R2013a, Matlab's Statistics Toolbox and IBM SPSS Statistics 21.

The Rayleigh's test was used to determine whether the response errors for each participant were distributed non-uniformly around a circle. One participant was removed from the analysis because the Rayleigh's test was non-significant ($p = 0.12$), for both spatial and neutral retro-cue conditions, reflecting a random distribution of responses.

Correlations with behavioural data were conducted by computing Spearman's rank correlation coefficients. Correlational analyses were performed between age and accuracy ($1/\sigma$) in the neutral retro-cue condition and retro-cue benefit (spatial retro-cue minus neutral retro-cue). Correlation coefficients were transformed into z-scores using Fisher's r-to-z transformation and compared to test for significant differences (Cohen & Cohen, 1983).

MEG scan

MEG data were acquired using an Elekta Neuromag 306-channel system (204 planar gradiometers, 102 magnetometers) with a sampling rate of 1000 Hz. A band-pass filter of 0.03 – 330 Hz was applied during acquisition. Eye movements were monitored on-line with a MEG-compatible eye-tracker (EyeLink 1000, SR Research, Ontario, Canada) recording at 500 Hz. If participants broke fixation during trials, I reminded them to refrain from moving their eyes in the next break. The electrocardiogram and the vertical and horizontal electrooculograms (EOG) were also recorded. Head position was monitored during the experiment with emitting coils affixed to the participant's head. The positions of these coils were digitised using a Polhemus 3D tracking system (Polhemus, EastTrach 3D). The Polhemus probe was used to obtain a set of ~100 points to record the shape of the participant's head.

Each participant completed six task blocks with 40 trials each. These were collected during two to four successive MEG recording sessions lasting approximately 25 minutes each, depending on the duration of breaks and reaction times of individual participants.

MEG analysis

MEG data were analysed using custom-written MATLAB scripts, the in-house OHBA Software Library (OSL), SPM8 (Litvak et al., 2011), and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). The epoch of interest used for the analyses was the period between the retro-cue and the onset of the probe stimulus.

MEG Pre-Processing

The continuous MEG data were visually inspected to remove channels with high levels of noise. Elekta's Maxfilter Signal Space Separation (SSS) algorithm was then applied to attenuate signals originating outside the head. The algorithm decomposes the data into a set of spherical harmonic basis functions and rejects components estimated to come from outside a sphere defined around the head. The data are then re-projected onto the MEG sensors. This final step also compensates for head movements by transforming the position of the interim representation relative to the sensors before re-projecting the data.

Continuous data were down-sampled to 250 Hz and band-pass filtered between 1 and 100 Hz. These data were cut into 3.5-s epochs running from the onset of the WM array to the onset of the probe stimulus. Resulting epochs were visually inspected for artefacts. EOG traces were used to identify trials containing saccades. Trials with abnormal variance in the MEG signal or saccades during the WM maintenance period were excluded from subsequent analysis. Eyeblink components were detected over the whole continuous dataset and regressed

out using independent component analysis. Only planar gradiometers were used for the MEG analysis. The total number of trials excluded from the MEG analysis was 594 out of 7320 trials, or 8.11% (spatial retro-cue condition). On average, 10.2 ± 3.4 trials were excluded for each participant. The number of exclusions did not differ between trials with left (5.0 ± 1.7) and right (5.2 ± 1.7) retro-cues.

Time-Frequency Analysis

I computed a time-frequency representation (TFR) of power using a Fourier transform over sliding time windows in 40-ms steps. The width of the sliding time window was variable in duration: for each frequency, the window width was four cycles long. The time-domain signal was multiplied with a Hanning taper of equal length. Estimates were obtained at frequencies from 4 to 35 Hz in 1-Hz steps.

The power spectra for each cue condition were averaged over trials. The power time-series in the planar gradiometers were combined (Cartesian sum), resulting in a 102-channel combined planar gradiometer map of power in sensor space. For each participant, I contrasted the power spectra in the left versus the right spatial retro-cue conditions, normalised by the power of both conditions:

$$\frac{Left}{Left+Right} - \frac{Right}{Left+Right} \quad (2)$$

Across the group, I tested for significant lateralisation of brain activity according to spatial cues using paired t-tests, and used spatial cluster permutation statistics to control for multiple comparisons. Sensor-space cluster permutation statistics were computed by permuting cue condition labels (left and right spatial retro-cue conditions) using Fieldtrip's `ft_freqstatistics` (10,000 iterations). Clusters were formed in space (sensors) and time, averaging over the

alpha band (8-14 Hz) and the beta band (15-30 Hz) separately, and tested for significance against the permuted distribution. Control analyses were also performed in the theta band (4-7 Hz).

In order to verify that distinct alpha-band and beta-band peaks were observable in this elderly cohort, and that they conformed to the conventional frequency ranges used in my analyses, I plotted the spectral distribution of power over sensors showing maximal alpha and beta lateralisation. Topographic analyses (TANOVAs, see Murray et al. 2008) were used to compare the topographies of alpha-band and beta-band lateralisation in the period after the retro-cue. The difference between two topographies was computed by taking the square root of the sum of squared differences between conditions at each sensor, normalised by the variance across all sensors. This value was compared against a permutation distribution derived through computing values with randomly shuffled condition labels over 10,000 iterations.

Attentional modulation index and correlating with behaviour

To explore the relationship between neural activity and the deployment of retrospective attention, I characterised the time course of alpha lateralisation by computing an attentional modulation index (AMI) for each participant. To generate the AMI, I selected sensors involved in retrospective attention using a cluster-based analysis, and then subtracted average alpha power activity in the sensors ipsilateral to the attended hemifield (positive) from the sensors contralateral to the attended hemifield (negative), where a higher AMI meant more alpha lateralisation and a lower AMI meant less alpha lateralisation. In order to select sensors in an unbiased way, I used a leave-one-out method, and tested for differences between the normalised (as before) left and right cue conditions in the alpha band using paired t-tests and cluster permutation statistics during the delay period after the retro-cue (as above, but with

100 iterations) for 60 out of 61 participants. I used the significant sensors to calculate the AMI for the left-out participant, and repeated the procedure for all participants. For each left-out participant, one positive (left) and one negative (right) cluster were identified. Clusters were highly overlapping across participants. The same analysis was conducted in the beta band. I tested the significance of the AMI using one-sample t-tests over time points after cue offset and used cluster-based permutation testing (10,000 iterations) to correct for multiple comparisons across time, with a cluster-forming threshold (and a cluster mass significance threshold) of $p < 0.05$.

In order to compare the dynamics of neural effects in individuals with high versus low cueing benefit, I split the participants into two groups based on the size of the behavioural retro-cue benefit in each participant (spatial minus neutral retro-cue accuracy, $1/\sigma$, median split). I confirmed that there were no differences in the numbers of excluded trials between the two groups (mean high-performers = 9.1 ± 5.1 , mean low-performers = 10.0 ± 4.5 ; $t(56.8) = -0.14$, $p = 0.89$). Initially, splitting the data led to a significant difference in age (independent samples t-test between groups: $t(49.8) = -2.43$, $p = 0.02$). Therefore I performed the median split on the residuals of a regression of age against performance (independent samples t-test between groups: $t(50.9) = -1.7$, $p = 0.1$).

To compare the time course of lateralisation between groups, I split the duration of significant alpha AMI at the group level into three bins, giving an early, middle and late lateralisation period. Differences in groups for the early, middle and late periods of alpha and beta modulation were tested using mixed ANCOVAs, regressing out the effect of age. Mauchly's test was used to test for sphericity of the data. For both ANCOVAs, the assumption of sphericity was violated, therefore degrees of freedom were corrected using

Huynh-Feldt estimates of sphericity, according to the recommendation to use the Huynh-Feldt correction when the epsilon parameter is greater than 0.75 (Girden, 1992).

To supplement the tertiles analysis and ensure that any difference in lateralisation time course did not reflect the choice of arbitrary time points, I also performed a cluster-based analysis. A mixed one-way analysis of variance (ANOVA) tested for the effects of Group (high retro-cue benefits, low retro-cue benefits), Frequency (alpha AMI, beta AMI), and Group x Frequency interactions at each time point in the maintenance period after cue offset, and cluster-based permutation testing was used to control for multiple comparisons across time with a cluster-forming threshold of $p < 0.05$ and 10,000 iterations. To test for the effect of Group, group labels were randomly permuted, and the sum of the largest cluster of F values over time (with $p < 0.05$) was saved to build up a null distribution. The same procedure was performed to test for the effect of Frequency, permuting the frequency labels but keeping Group constant. Finally, I permuted both Group and Frequency and built up a null distribution to test for the interaction effect (Anderson & Ter Braak, 2003). I compared the original results with the right side of the null distributions (one-tailed test) because only an effect that is significantly greater than the permutation distribution of F values would be interpretable.

Behavioural Results

Main Experiment

As a group, the elderly participants were able to use spatial retro-cues to improve working-memory performance (accuracy for spatial retro-cue: 0.67 ± 0.04 ; neutral retro-cue 0.35 ± 0.02 ; $t(73) = 11.4$, $p = 7.24 \times 10^{-18}$; effect size (Cohen's d): 1.17; figure 1B-C). There was a significant negative correlation of accuracy on neutral retro-cue trials with age ($r = -0.24$, $p = 0.038$; figure 1D), but no relationship between the ability to use a spatial retro-cue to improve WM accuracy and age (spatial retro-cue accuracy minus neutral cue accuracy: $r = -0.036$, $p = 0.76$; figure 1E). In order to compare the extent to which each effect correlated with age

when any common variance in performance across the conditions was removed, I repeated the analyses using partial correlations. Accuracy on neutral trials still showed a negative correlation with age when partialling out the effects of retro-cueing ($r = -0.21, p = 0.006$), and retro-cueing benefits showed no relation to age when partialling out the performance on neutral-cue trials ($r = 0.003, p = 0.98$). When compared directly using Fisher's r -to- z transform, these correlation coefficients differed significantly ($z = 2.00, p = 0.046$).

The pattern of behavioural results was not significantly affected by whether participants were taking calcium-channel blockers (15 of 74 participants) or had a previous history of depression (11 of 74 participants).

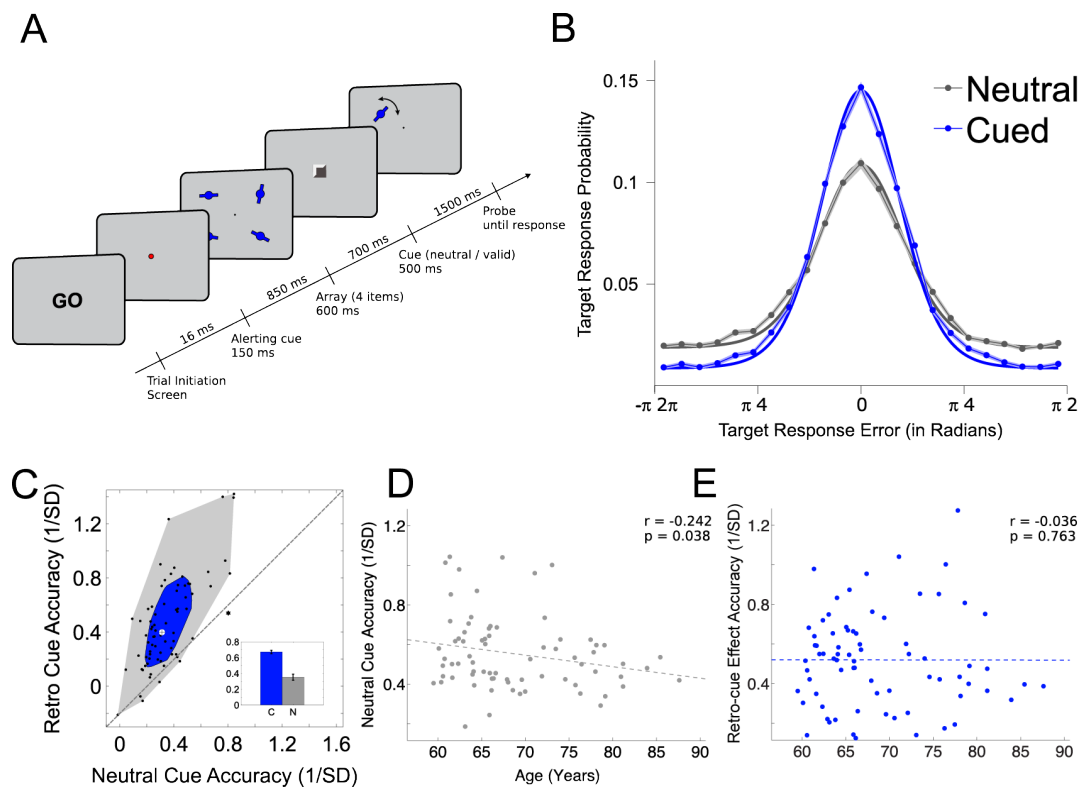


Figure 1. Task schematic and behavioural results for 74 participants. *A*) Task schematic. Participants pressed a button to initiate each trial at the “GO” screen. Participants encoded four orientation stimuli into WM. After a fixed delay of 700 ms, a retro-cue appeared. In half the trials, a spatial retro-cue (100% valid) appeared, indicating the location of the item that would subsequently be probed. In the other trials, a neutral retro-cue provided no predictive information about the location to be probed. After another fixed delay of 1500 ms, a randomly oriented probe bar appeared in one of the quadrants. Participants indicated the orientation of the item at that location in the memory array by rotating the bar and confirmed with a button press. After responding, the correct orientation of the memory-array item was overlaid as feedback (not shown here). *B*) Response error

distributions centred on the target for spatial and neutral retro-cue conditions. The mean error is plotted at each bin and connected by the lines for the spatial (blue) and neutral (grey) retro-cue condition and the shading shows the standard error of the mean. The smooth lines show the model fit (weighted mixture of the von Mises and uniform distribution). X-axis shows response error in radians, y-axis is the response error probability. C) Scatter and bag plot and bar plot showing the effect of the spatial retro-cue on WM behavioural measures. The small bar-plot insert shows WM accuracy for the spatial (blue) and neutral (grey) cue conditions (** $p < 0.0001$). For the scatter and bag plot, dots represent individual participants, x-axis is accuracy on neutral retro-cue conditions and the y-axis is accuracy on spatial retro-cue conditions. Dots above the diagonal represent participants who exhibited an increase in WM accuracy in the retro-cue conditions relative to the neutral-cue conditions and dots below the diagonal represent a decrease in accuracy in the retro-cue relative to neutral-cue conditions. The inner blue bag includes 50% of the data with the largest depth, the outer grey polygon contains all other non-outlier data points, and the Xs outside of the shaded areas represent outliers. The cross at the center of the bag plot represents the center of mass of the bivariate distribution of empirical data (Rousseeuw, Ruts, & Tukey, 1999). D-E) Age was negatively correlated with accuracy in the neutral cue condition (D) but not with retro-cue benefit (E). Correlation values are Spearman's rank correlation coefficients.

The mixture-model analysis revealed that this effect was attributable to an increase in the probability of reporting a target ($t(73) = 10.1$, $p = 1.78 \times 10^{-15}$; effect size: 1.3; figure 2A), a decreased probability of mistakenly reporting a non-target ($t(73) = -6.85$, $p = 1.93 \times 10^{-9}$; effect size: -1.64; figure 2B), and a decrease in guess rate ($t(73) = -2.78$, $p = 0.007$; effect size: 0.5; figure 2C). The measure of precision in the mixture model (concentration parameter κ) was also significantly modulated by a retro-cue, though the effect size was small ($t(73) = 2.18$, $p = 0.032$; effect size: 0.32; figure 2D). The 61 participants who were submitted to the MEG analysis showed a similar pattern of behavioural performance except that precision was no longer significantly modulated by the cue. Statistical values for the subset of participants were: accuracy for spatial retro-cue (0.68 ± 0.04 ; neutral retro-cue 0.35 ± 0.02 ; $t(60) = 11.4$, $p = 1.34 \times 10^{-15}$; effect size: 1.24), probability for target ($t(60) = 10.1$, $p = 4.4 \times 10^{-15}$; effect size: 2.00), probability for non-target ($t(60) = -6.85$, $p = 1.7 \times 10^{-7}$; effect size: -1.52), guess rate ($t(60) = -2.78$, $p = 7.0 \times 10^{-4}$; effect size: -1.07); precision ($t(60) = 1.11$, $p = 0.27$; effect size: 0.17).

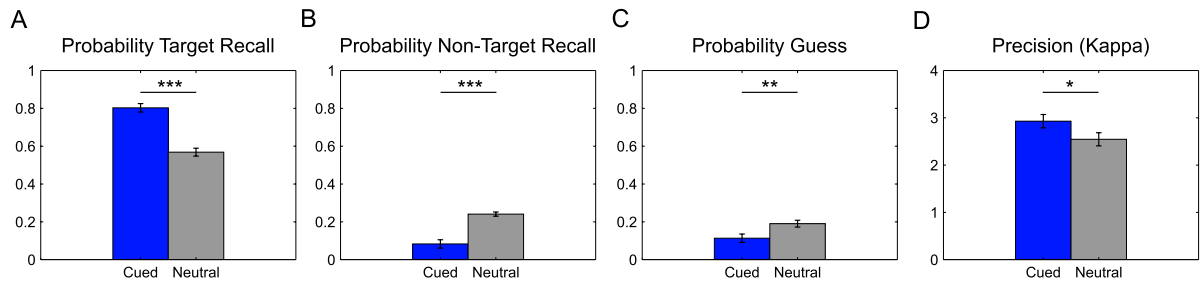


Figure 2. Significant retro-cue benefits in WM components from the mixture model analysis for 74 participants. The probability of target recall (A), and precision (D) were significantly higher in the retro-cue relative to the neutral-cue condition, and the probability of non-target (B) and guess responses (C) were significantly lower in the retro-cue relative to the neutral-cue condition. *** $p < 0.00001$; ** $p < 0.01$; * $p < 0.05$.

MEG Results

Alpha power lateralisation during retroactive attention

Retroactive attention to spatial locations in working memory elicits a pattern of lateralised alpha power activity in posterior cortex in younger adults in both MEG (Poch et al. 2014; Wallis et al. 2015) and EEG (Myers et al. 2015). Here I tested for an alpha lateralisation effect related to retroactive attention in older adults. I performed a sensor-space analysis comparing alpha-band power (8-14 Hz) after left retro cues versus right retro cues. Performing a cluster permutation test revealed a significant negative cluster (figure 3A, 3B top panel) over right sensors from 200 ms to 800 ms after cue offset ($p = 7.0 \times 10^{-4}$) and a significant positive cluster over left sensors from 240 ms to 800 after cue offset ($p = 6.0 \times 10^{-4}$). I noted that the distribution of the alpha effects in the left hemisphere extended more anteriorly than is typically reported, including central and frontal sensors (c.f. Foxe, Murphy, & De Sanctis, 2014).

I performed the same analysis on the beta band (15-30 Hz) and found a significant negative cluster over right sensors from 8 ms to 440 ms after cue offset ($p < 1.0 \times 10^{-4}$) and a significant positive cluster over left sensors from 120 ms to 840 ms after cue offset ($p = 4.0 \times 10^{-4}$) (figure

3A, 3B bottom panel). I also performed the same analysis on the theta band (4-7 Hz) and found no significant effects.

Plots of the raw spectral power at the sensors with maximal alpha-band and beta-band AMI (Figure 3C) confirmed that their peak distributions were similar to the conventional frequency ranges used for analysis. Power in the alpha band peaked at 11 Hz over lateral posterior sensors, while power in the beta band peaked at 19 Hz over lateral central sensors. A comparison of the topographies associated with alpha-band vs. beta-band lateralisation using a TANOVA (see Murray et al., 2008) in the period after the retro-cue (8 to 800 ms) showed them to be significantly different ($p < 1.0 \times 10^{-4}$). A similar analysis confined to the periods of strongest alpha lateralisation (240 to 800 ms) and beta lateralisation (120 to 440 ms) found similar results ($p < 1.0 \times 10^{-4}$).

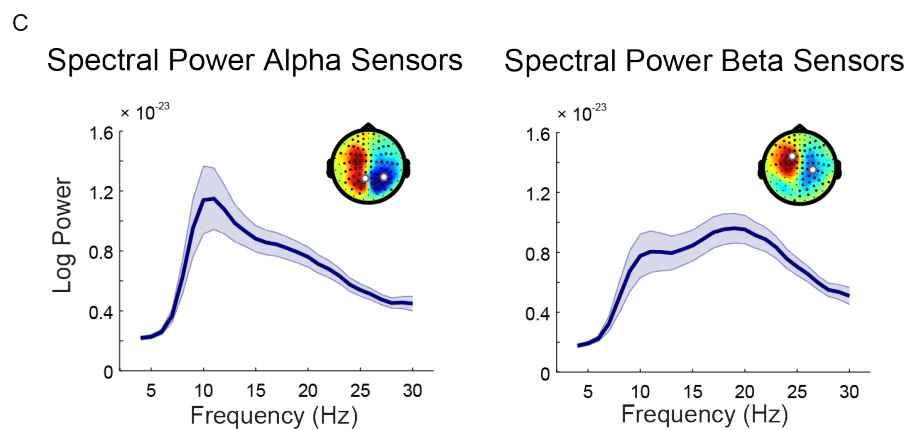
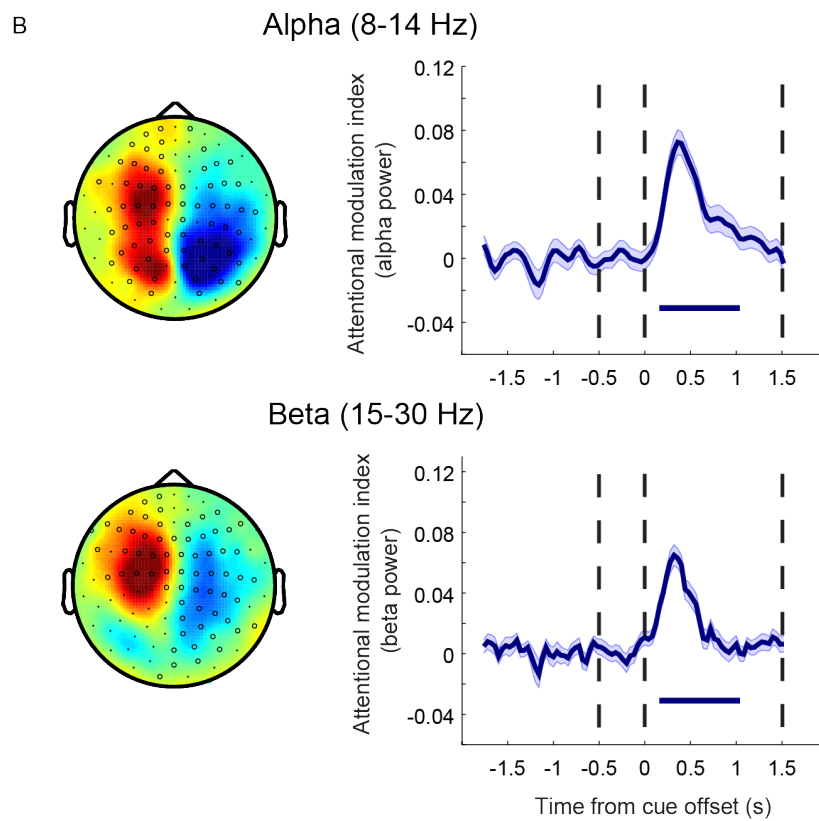
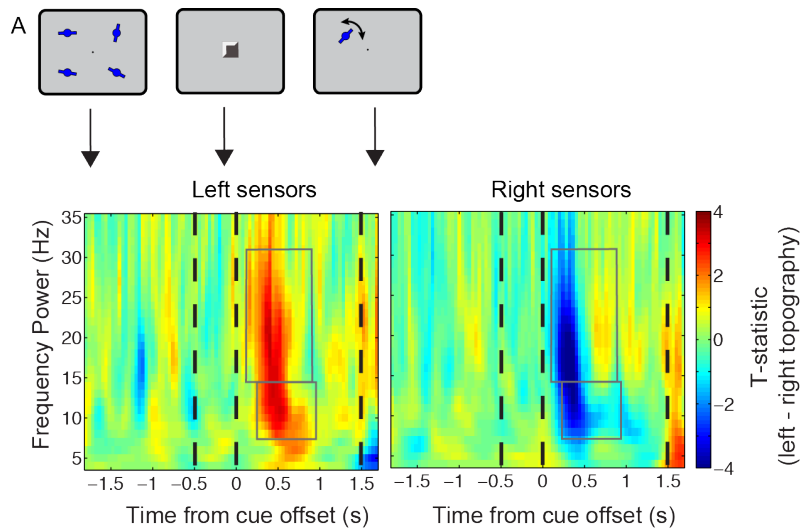


Figure 3. Alpha and beta lateralisation. A) Time course of alpha (8–14 Hz) and beta (15–30 Hz) power lateralisation from sensors for the left minus right retro-cue contrast. Left: Increase of event-related synchronisation (ERS) of alpha/beta power on the ipsilateral hemisphere to the attended side following a retro-cue. Right: Decrease of ERS of alpha/beta power on the contralateral hemisphere to the attended side following a retro-cue. Grey boxes denote significant increase/decrease in lateralisation for alpha and beta bands. X-axis is time from cue offset; y-axis is frequency power. B) Left: Topography of alpha (top) and beta (bottom) power for the left minus right retro-cue contrast at 120 ms to 800 ms (alpha) and 8 to 840 ms (beta) after cue offset. Right: Time course of alpha (top) and beta (bottom) attention modulation index (AMI). The AMI is the average of the ipsilateral sensors minus average of the contralateral sensors' alpha or beta power, respectively (sensor selection via a leave-one-out method; see Methods). X-axis is time from cue offset; y-axis is AMI. The bar below the AMI denotes significant lateralisation compared to zero (both alpha and beta AMI: $p < 1.0 \times 10^{-4}$ cluster-corrected over time). C) Spectral power for peak alpha and beta lateralisation sensors. Mean log power for each frequency from 4 to 30 Hz in 1 Hz steps at sensors that exhibited peak modulation during the period of significant alpha lateralisation (120 ms to 800 ms; left) and beta lateralisation (8 ms to 840 ms; right) averaged over left and right retro-cue conditions, showing separate alpha and beta spectral peaks.

Temporal dynamics of alpha lateralisation predict WM performance

In order to test what aspects of neural activity predicted the ability to benefit from spatial cues, I performed a median split based on the behavioural retro-cue benefit (controlled for age) for WM accuracy, and then contrasted alpha lateralisation between groups using the attentional modulation index (AMI; see Methods). I was particularly interested in whether the strength and timing of the alpha AMI predicted performance. At the group level, alpha lateralisation reflected in the AMI was statistically significant from 160 ms to 1000 ms after cue offset ($p < 1.0 \times 10^{-4}$). To characterise the time course of lateralisation between groups, I split the duration of significant alpha AMI at the group level into three equal bins to form an early (160 to 360 ms), middle, (480 to 680 ms), and late (800 to 1000 ms after cue offset) lateralisation period, leaving out the two time points between each time period. A mixed ANCOVA with within-subject factor Time Bin (Early, Middle and Late), between-subject factor Group (High and Low retro-cue benefit), and age as a covariate was used to test the amount of alpha AMI over the early, middle and late time periods between groups (figure 4A). This revealed a significant interaction ($F(1.77, 100.6) = 4.47, p = 0.017, \eta^2 = 0.73$), but no main effect of Time Bin ($F(1.77, 100.6) = 1.53, p = 0.3, \eta^2 = 0.03$) or Group ($F(1,57) = 0.314, p = 0.58, \eta^2 = 0.005$). The interaction was due to significantly less degree of AMI in

the high relative to low performers in the Late epoch ($t(57.8) = -2.79$, $p = 0.007$, effect size: -0.72), but not in the Early ($t(58) = 1.06$, $p = 0.3$, effect size: 0.27) or the Middle ($t(57.7) = 0.8$, $p = 0.43$, effect size: 0.21) epoch.

I conducted the same analysis on the beta AMI to explore whether the group differences were exclusive to the alpha band (figure 4B). A mixed ANCOVA with within-subject factor Time (Early, Middle and Late) and between-subject factor Group (High and Low retro-cue benefit) was conducted on the beta AMI using the same time periods for the alpha AMI analysis, controlling for age. This also revealed a significant interaction ($F(1.9, 101.4) = 6.3$, $p = 0.002$, $\eta^2 = 0.108$), but no main effect of Time Bin ($F(1.9, 101.4) = 1.15$, $p = 0.85$, $\eta^2 = 0.005$) or Group ($F(1,57) = 1.45$, $p = 0.23$, $\eta^2 = 0.025$). Independent sample t-tests revealed that the interaction was due to a significant difference between the high and low performers in the Late epoch ($t(58) = -3.27$, $p = 0.002$, effect size: -0.85), with a trend in the Early epoch ($t(57.2) = 2.00$, $p = 0.051$, effect size: 0.52) but not in the Middle ($t(52.6) = -0.78$, $p = 0.43$, effect size: 0.20) epoch.

In order to make sure these effects were not due to the arbitrary time periods selected for these analyses, I also conducted an analysis of variance using a cluster-based permutation approach. The analysis revealed a significant cluster distinguishing high and low performers between 800 ms and 1000 ms after cue offset, suggesting that modulation of alpha and beta power was longer lasting in the low-performance group ($p = 0.026$, one-tailed, cluster-corrected over time). There was a trend for a main effect of frequency between 400 and 680 ms ($p = 0.07$, cluster-corrected over time), suggesting that the AMI tended to be stronger for the alpha band than the beta band. There were no interactions, suggesting a similar type of modulation by performance group in the two frequency bands ($p > 0.51$, cluster-corrected over time).

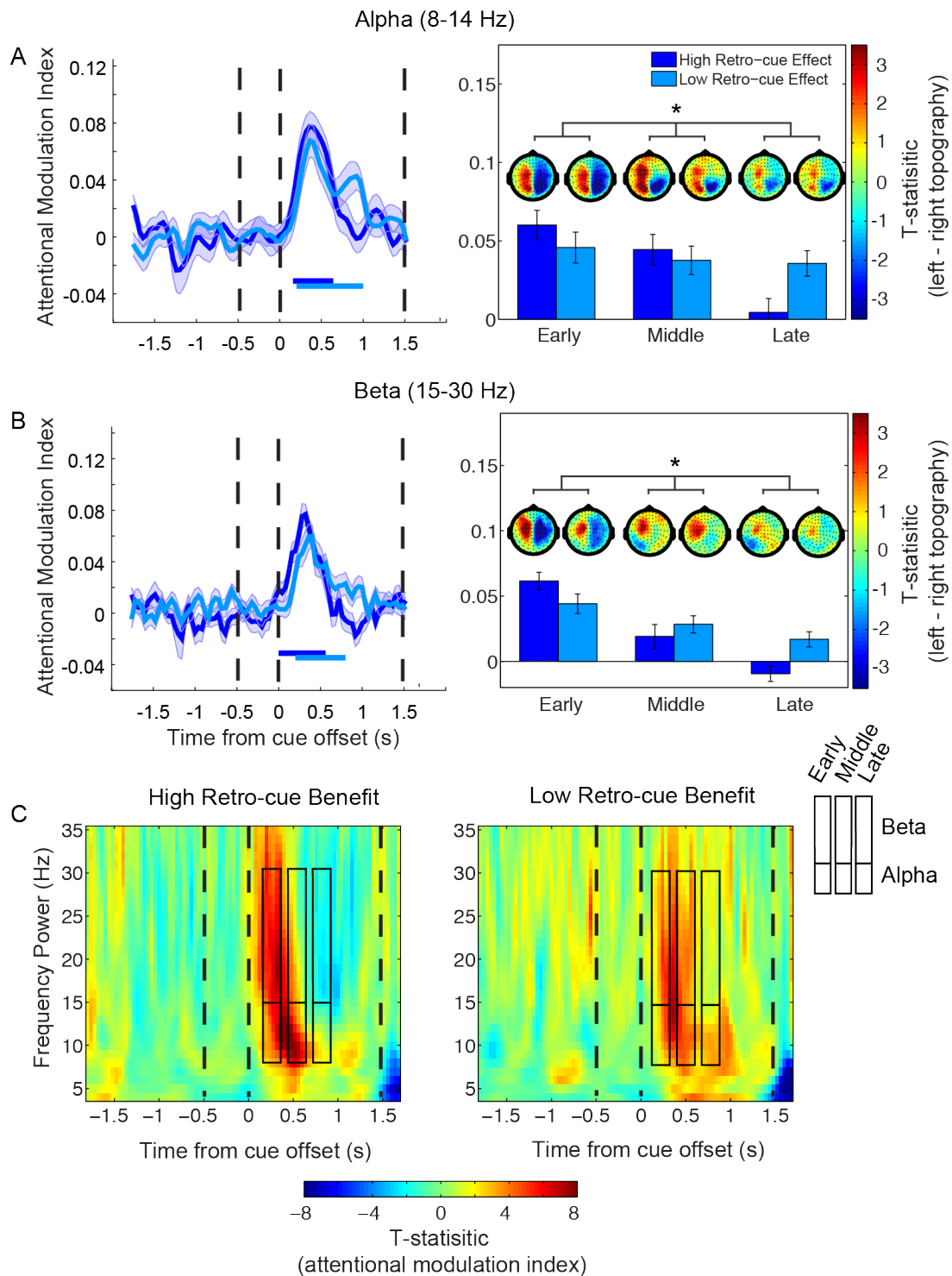


Figure 4. Temporal profile of alpha/beta lateralisation reflects magnitude of retro-cue benefit in WM accuracy. *A*) Left: Time course of the attentional modulation index (AMI) for high and low cueing benefit groups in the alpha band. The high cueing group exhibited a large increase of AMI after cue offset that shortly went back to baseline, whereas the low cueing group had a numerically smaller increase of AMI that lasted for longer. Right: Bar plots showing a significant interaction between groups for the AMI in the early, middle and late periods. Topographies display *t*-stat images of alpha power lateralisation for each group and averaged over the early, middle, and late time points above each respective bar plot. Topography colmy scale is kept constant with *t*-values of -4 to 4. The bars below the AMI denote significant lateralisation (AMI significantly different from zero) in each group. *B*) The same analysis is presented for beta. * denotes significant interaction ($p < 0.05$). *C*)

Time-frequency plots of the AMI in participants with high retro-cue benefits (left) and low retro-cue benefits (right) for visualisation. X-axis is time from cue offset; y-axis is frequency power.

Discussion

I tested a large sample of elderly participants on a WM precision task with retro-cues, and found that the ability to orient attention in WM is preserved in ageing. Despite finding a reduction in baseline WM performance with increasing age, the cueing benefit was unaffected. Posterior alpha-band power was modulated after spatial retro-cues, suggesting that the oscillatory mechanisms that accompany retrospective attention (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015) are also retained in ageing. The temporal profile of alpha-band lateralisation corresponded with behaviour: Participants with strong cueing benefits exhibited a short-lived, transient lateralisation of alpha activity, whereas those with limited benefits showed a prolonged period of alpha lateralisation. Finally, I found that these effects were also present in the beta band, which has not been reported previously in studies in young adults (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015).

In line with previous research on younger adults (e.g. Griffin & Nobre, 2003; Landman et al., 2003; Makovski, 2012; Nobre, et al., 2007; Nobre, 2004; Rerko & Oberauer, 2013; Rerko et al., 2014; Sligte, et al., 2008; Williams et al., 2013), healthy older adults were able to use retro-cues to benefit their WM performance. A model-based analysis showed that, as a group, there was a robust increase in the probability for reporting the target item and reduction in misreporting non-target items. There was also a modest increase in the precision of the reported memorandum, although this effect was not significant in the reduced data set (N = 61) used for the MEG analysis. In addition, I found that flexible orienting within WM did not decline with age, whereas baseline WM performance did. Specifically, WM accuracy in the neutral cue condition decreased as a function of increasing age, replicating the commonly reported age-related decline in WM maintenance functions (e.g. Iachini et al.,

2009; Peich et al., 2013; Reuter-Lorenz & Sylvester, 2005; Salthouse, 1992, 1994). In contrast, there was no correlation between the retro-cue benefit and age. Consistent with the current results, previous perceptual studies have shown that older adults can use spatial precues to improve performance in perceptual target detection and discrimination tasks (e.g. Madden et al., 2004; Nissen & Corkin 1985; Tales et al., 2002). However, two studies reported that older adults have an impaired ability to orient attention within WM using retro-cues (Duarte et al. 2013; Newsome et al. 2015; see below for further discussion). In addition to showing preserved orienting within WM in healthy ageing, I found that these intact orienting functions may reduce the detrimental effect of age on WM performance.

Flexible orienting of attention within WM elicited a transient pattern of lateralised alpha activity in older adults, similar to what has been observed for young participants (Myers et al. 2015; Poch et al. 2014; Wallis et al. 2015), thereby indicating relative preservation of oscillatory mechanisms in healthy ageing. This transient activity could reflect a shift of attention to the cued item in WM. For example, attentional selection could lead to a change in the item's representational state so that it can guide subsequent memory recall (Larocque, Lewis-Peacock, & Postle, 2014; Zokaei, Ning, Manohar, Feredoes, & Husain, 2014). Following completion of the selection process, alpha lateralisation may no longer be required (see Wallis et al. 2015). This brief activation may represent a state of rapid memory access to the behaviourally relevant item within WM.

High variability between subjects in the strength and timing of alpha lateralisation allowed us to investigate the neural markers of good versus poor orienting ability. I found that participants with high and low retro-cue benefit had similar overall magnitudes of alpha lateralisation in the delay after the retro-cue. However, the temporal profiles of alpha lateralisation over the delay period differed markedly between groups. Participants with a

high retro-cue benefit had a strong increase of alpha lateralisation immediately after the cue, which quickly returned to baseline. In contrast, participants with a low retro-cue benefit had a moderate increase of alpha lateralisation after the cue, which was sustained for a longer period of time before it went back to baseline. If alpha lateralisation after a retro-cue in fact corresponds to a punctate process of retrieval, or a change in accessibility, then lateralisation should last no longer than this retrieval or transition process itself. I speculate that the more sustained alpha lateralisation in the low-performing group may reflect a less efficient memory selection process.

In this group of older adults, effects of attentional modulation were also present in the beta band. I ruled out that the effects observed in the beta band resulted merely from shifts in spectral power as a function of ageing. In this cohort, alpha and beta bands had distinct peak frequencies and topographical distributions. These effects in the beta band have not been reported in similar studies testing younger participants (Myers et al. 2015; Wallis et al. 2015). These findings are in line with previous EEG studies reporting greater beta power modulation in older adults relative to younger adults in attention and WM tasks over central electrodes (Deiber et al., 2010; Karrasch, Laine, Rapinoja, & Krause, 2004), although they have not specifically reported lateralised effects related to spatial attention.

The contribution of the beta-band lateralisation during WM control in the current experiment remains unclear. I speculate that older adults may employ additional strategies and neural resources to compensate for normal declines in ageing (Cabeza, 2002; Grady, 2008; Reuter-Lorenz & Cappell, 2008), which may be reflected in beta-band modulation. For example, some studies report that older adults additionally recruit the motor network for cognitive and motor tasks (Deiber, Ibañez, Missonnier, Rodriguez, & Giannakopoulos, 2013; Kopp, Howe, & Wessel, 2011; J. B. Rowe et al., 2006). However, because the effects of alpha

and beta were not entirely separable in this study, future studies could use a longitudinal design to examine whether there are in fact separable effects and if recruitment in the beta band is a consequence of ageing.

The current study points to larger flexibility and executive control in older adults compared with other studies. In particular, my current behavioural findings stand in contrast to two previous studies showing that older adults were unable to benefit from retro-cues (Duarte et al. 2013; Newsome et al. 2015). I used a WM precision task with orientations, whereas both previous studies used a traditional colour change-detection task. The precision task may simply have been more sensitive to subtle behavioural differences between cue conditions (Zokaei et al., 2014). Furthermore, I used an accuracy measure that considered each participant's response variability (i.e. their inverse precision), whereas the previous study took standard reaction-time and accuracy measures. Another major difference between the studies was in the sample size (74 here compared with 18 and 19 in the previous studies). The absence of an effect may have been due to higher inter-subject variability in behavioural performance in older adults (Botwinick, 1978; Krauss, 1980; Welford, 1985), meaning larger samples may be required to observe reliable effects.

Prior studies have found that older adults are impaired in the ability to suppress irrelevant items from entering WM (Chadick et al., 2014; Gazzaley et al., 2005, 2008). These findings may seem at odds with the current results. One major difference is that these previous studies tested selective gating of input into WM, i.e., the ability to suppress irrelevant items at encoding. Conversely, I tested for control over WM items *after* encoding. One purpose of the current study was to investigate whether older adults have deficits in exerting control over WM. I found that older adults had preserved abilities for orienting attention within WM, which suggests no deficit in the suppression of irrelevant items in WM. It is important to

note that some studies that reported attentional deficits for the contrast between old and young groups also found differences within the old group, in which high performers show some suppression of irrelevant stimuli and low performers show no suppression (Chadick et al., 2014; Gazzaley et al., 2005).

A separate line of research investigating selective attention in ageing suggests that older adults can use pre-cues to improve target detection and discrimination performance to the same degree as young adults (Madden, 2004; Nissen & Corkin, 1985; Tales et al., 2002), contrary to studies by Gazzaley and colleagues. However, in studies that reported age-related attention deficits, distractors were often salient and foveal (such as faces and houses), whereas research using pre-cues as well as the current study used small, peripheral items. These discrepancies might be related to the greater difficulty for suppressing salient, foveal distractors compared with peripheral distractors (Zanto & Gazzaley, 2014). It is unclear whether the current results would still hold if irrelevant items were more salient or distracting. Future research should study whether control mechanisms within WM are impaired in ageing when more salient distractors are combined with retro-cues.

While the present study showed that older adults, *as a group*, are able to orient their attention flexibly within WM to optimise performance, it was also able to demonstrate high individual variability in cognitive performance. This variability was linked to differences in the temporal dynamics of neural oscillations, which may be a marker for healthy attentional mechanisms in ageing. Studying variability within elderly adults might be able to tell us about behavioural and neural signals that underlie successful cognitive ageing. Indeed, in order to examine this question, one research group has already begun to study “superagers”, which are elderly adults who have unusually high memory abilities (Gefen et al., 2014, 2015; Rogalski et al., 2013; also see Nyberg et al., 2012). The current results show that different patterns of neural activity

can distinguish between persons with different levels of flexible control in WM. This individual-differences approach may be a promising way to investigate the behavioural and neural markers of preserved cognition in ageing.

4. Emotional working memory: Task development

Chapter Abstract

Does the ability to hold any type of information in WM decline with age? WM capacity, as measured by tests that assess the short-term retention of simple visual stimuli, words, or digits, shows significant declines with age. However, different types of stimuli are processed differently in the brain and remembered differently depending on its affective and motivational value, as well as its relevance to oneself. As such, WM abilities for emotional content may not show the same pattern of decline as those observed in standard tests of WM. Only a handful of studies have tested for WM abilities for emotional content, and the task paradigms are generally not specifically tailored to test for emotional content, and often not as appropriate for testing elderly participants. In this chapter, I review the literature showing how emotional content can affect selective attention and WM in younger and older adults, and present the development and assessment of a new WM precision task to study WM abilities for emotional content through a series of experiments with young adults. I present the findings of these experiments, and illustrate the measures that can be obtained from these tasks to index WM abilities for emotional content, which will be used to test in older participants in the next chapter.

Introduction

4.1. Emotional working memory

The ability to keep information in mind over short periods of time exhibits marked decline in ageing – but is this always the case? Stimulus content affects the way sensory information is processed, and the ability to keep things in WM might depend on the stimulus features and personal relevance of the memory items. Consequently, there might be a benefit in WM abilities for objects that are more ecologically valid and motivationally salient for older adults. Affective processing, for instance, does not exhibit a simple steady decline like other cognitive functions in ageing (Grady, 2008; Hedden & Gabrieli, 2004; Mather, 2012). Elderly adults are relatively unimpaired at performing certain tasks with emotional content (e.g. Calder et al., 2003; Keightley et al., 2006; Mammarella et al., 2013; Mikels, et al., 2005; although see Ruffman et al., 2008 for some deficits in emotional recognition) and selectively attend to the emotional parts of their lives as much as, or even more than, younger adults (Carstensen et al., 2003). Could older adults have relatively preserved abilities for the short-term maintenance of emotional information? And could the individual differences in the WM ability for different affective contents depend on cognitive health (general cognitive function, non-emotional WM) or emotional health (mood) in ageing? In the following, I will review the effect of emotional content on cognition in young adults and in healthy ageing, and motivate why it is interesting to study WM for emotional content in elderly adults. I will then propose a new experimental paradigm to investigate WM for emotional content in healthy ageing, and develop the paradigm over the next few chapters. Finally, I will present a large behavioural study using the optimized version of the new paradigm to test WM abilities for emotional and non-emotional content in a large group of young and older adults.

4.2. Emotion influences attention and working memory in young and old adults

Stimuli with affective content can modulate attentional allocation and neural processing

(Compton, 2003; Vuilleumier & Driver, 2007; Vuilleumier, 2005; Yiend, 2010) and can lead to benefits or costs in behaviour (E. Fox & Damjanovic, 2006; Holmes et al., 2005; Lipp & Derakshan, 2005; Öhman, Flykt, et al., 2001; Phelps et al., 2006; Pourtois et al., 2004; Vuilleumier et al., 2001). The effects of emotional material on performance furthermore vary with anxiety (Bradley et al., 1998, 1999; E. Fox et al., 2001, 2002; Mathews & MacLeod, 2005; Yiend & Mathews, 2001) and depression (Bradley et al., 1997; Donaldson et al., 2007; Gotlib et al., 2004; Joormann & Gotlib, 2007; Leyman et al., 2007; Mogg et al., 1995). Many studies have supported the idea that young adults tend to preferentially process negative information over neutral or positive information across cognitive domains, which could be linked to innate survival mechanisms (Rozin & Royzman, 2001). Indeed, it would be evolutionarily advantageous to be alert when encountering a fear-inducing stimulus, such as a snake (Damasio & Carvalho, 2013; LeDoux, 2003; Pessoa & Adolphs, 2010; Phelps, 2006). For instance, Öhman et al. (2001) showed that participants were faster at finding a target (a discrepant image that did not belong to the category of the other items in the display) when it was a fear-related compared to a non-fear-related target (in a display of spiders, snakes, flowers or mushrooms). Spider- and snake-phobic individuals further showed a greater reaction-time benefit when the target belonged to the category of their own phobia. Lipp & Derakshan (2005) used an attentional dot-probe task and found that all participants exhibited speeded reaction times for probes that replaced pictures of spiders, but with an even greater facilitation in spider-phobic individuals. Others have similarly shown a facilitation of discriminating oriented bars or gratings following presentations of negative stimuli, in the form of reaction-time benefits (Pourtois et al., 2004) and increases in contrast sensitivity (Phelps et al., 2006). Finally, some studies have found that performance on WM tasks for negative (threatening and fear-related) stimuli is enhanced in healthy young adults (e.g. Jackson et al., 2014, 2008, 2009; Mikels et al., 2008). These studies indicate that emotional – in particular fear-related or threatening – stimuli can attract attention and facilitate perceptual

processing to prepare to act upon things identified to be behaviourally significant.

Older adults also show benefits in attention and memory tasks for emotional stimuli (D'Argembeau & van der Linden, 2004; Hartley et al., 2013; Mammarella et al., 2013; Mather & Knight, 2006; Mikels et al., 2005; Rösler et al., 2005) and exhibit a tendency to focus on positive over negative information (Carstensen & Mikels, 2005; Charles et al., 2003; Grady et al., 2007; Mather & Carstensen, 2005; Mikels et al., 2005; Reed et al., 2014). For instance, threat detection seems to be unimpaired in older adults (Mather & Knight, 2006; Rosler et al., 2005). In one study, young and old adults were asked to detect a discrepant emotional expression in a set of schematic faces (e.g. an angry face in an array of neutral faces; Mather & Knight, 2006, using the paradigm in Öhman, Lundqvist, et al., 2001). Both young and old adults were faster at detecting an angry face in an array of faces with neutral expressions compared to detecting the non-threatening (sad, happy) emotional expressions. Rosler et al. (2005) also found that both young and old participants attended to emotional stimuli more than neutral stimuli, with slightly less sustained attention (looking time) to negative stimuli in older adults. Furthermore, the amygdala – a brain structure involved in processing emotional stimuli – has been reported to show relatively little structural decline or changes in functional response to emotional information in old age (Good et al., 2001; Mather et al., 2004). A few studies that have tested for WM abilities for affective content in healthy ageing have found WM benefits for emotional stimuli. For example, Mammarella et al. (2013a) found a significant age-related deficit of WM for non-emotional words, but no such deficit occurred for WM for emotional words (positive or negative). D'Argembeau and van der Linden (2004) found that older adults were impaired at recalling the identity of a set of previously presented faces (after a five-minute delay), but showed equivalent performance to younger adults for identifying the emotional expression (angry or happy) of a recalled face. Hartley et al. (2013) found similar results using a change-detection task. They asked

participants to remember faces (one, two, or three) over a short delay period and judged whether a face presented at the end of the trial matched one of the faces in the memory array in emotional expression (experiment 1) or identity (experiment 2). Older adults performed as well as young adults in remembering the emotional expression but were significantly worse at the recalling the identity. These studies seem to suggest that WM for emotional content might be relatively preserved in healthy ageing.

Most of these studies testing for WM abilities for emotional content in both young and old used a modified version of the WM change-detection task (Luck & Vogel, 1997) containing emotional face stimuli or scenes with affective content. Behavioural measures in these types of task are often limited to accuracy and reaction time. The traditional change-detection paradigm, therefore, is not ideally suited for testing how well, or to what degree memory for emotional information is preserved (e.g. how fearful did they remember the face to be?). Furthermore, many of these tasks require participants to respond as quickly as possible, which, for reasons of fatigue and motor problems, may not be ideal for an elderly population. Here, I designed a new type of task to characterise WM accuracy and bias for emotional content in healthy ageing.

4.3. Working memory for emotional content in ageing: a new experimental paradigm

To characterise WM for emotional content in healthy ageing, an emotional analogue of the visual WM precision task (Bays & Husain, 2008) was developed. This type of WM precision task is an extension of the classic change-detection paradigm (Luck & Vogel, 1997), which enables modelling the components of WM in a way that provides more information about the WM representation in different experimental conditions. In a typical visual WM precision

task, participants encode a number of stimuli (e.g. orientations, colours) into memory over a short maintenance period and subsequently make a forced-choice judgment on the test stimulus that appears at the end of the trial. At the onset of the test stimulus, the participant has to judge how the stimulus feature (e.g. orientation, colour) changed with respect to the corresponding memorandum. For example, in orientation memory, participants judge whether the test stimulus was tilted clockwise or counter-clockwise relative to the item in memory that had appeared at that same location. The test stimulus could be tilted a small, medium, or a large amount clockwise or counter-clockwise relative to the memory item (e.g. in Bays & Husain, 2008: 5°, 20°, or 45°). Performance is generally better for large changes compared with smaller changes. The distribution of clockwise responses (plotting “proportion responded clockwise” as a function of rotation condition) can be fit and described by a cumulative Gaussian, assuming a Gaussian distribution of error in the memory representation. The precision, or quality of the WM representation can thus be characterized. A common measure is the tightness of this distribution, computed by taking the reciprocal of the standard deviation. The probability that the item was entirely dropped from memory, commonly termed the guess or lapse rate, can also be estimated by calculating the asymptote of the cumulative Gaussian function (Bays & Husain, 2008; A. M. Murray et al., 2013, 2011; W. Zhang & Luck, 2008). The bias for responding clockwise or anticlockwise can also be computed or estimated (Bays & Husain, 2008), although this is often assumed to be zero in these tasks.

To adapt the visual WM precision task to emotional WM, a set of face stimuli with happy and fearful emotional expressions were used. Photographs of faces were edited and morphed to produce facial expressions with emotional intensities ranging from 0 to 100% in order to create a set of stimuli with a continuous scale similar to orientations (see Stimuli and Apparatus section below). To test emotional WM, participants would encode and remember

the features of emotionally expressive faces for subsequent memory judgements involving emotional changes between the remembered and test stimuli.

Experiment 4A

A WM precision task with emotional face stimuli was developed to study the ability to maintain emotional content in WM. Only a few studies have attempted to characterise WM for affective content in healthy ageing (Hartley et al., 2013; Mammarella et al., 2013; Mikels et al., 2005). Most studies that have tested WM for emotional content in young adults used a modified version of the standard WM change-detection task (Luck & Vogel, 1997) using scenes with affective content or emotional faces, and mostly used measures of reaction time and proportion correct (e.g. Jackson et al., 2014, 2008, 2009; Mikels et al., 2008). Here, I designed a modified version of the visual WM precision task (Bays & Husain, 2008) in order to assess the feasibility of using a WM precision-style task to characterise WM abilities with emotional content in ageing populations.

In each trial of the experiment, participants encoded two faces into WM with an emotional expression (fearful or happy) of a certain emotional intensity (ranging from low to high). After a short delay, a test face re-appeared on the screen and the participant made a judgment as to whether the test face was more or less emotionally intense than the face in memory at the same location and with the same identity. The emotional intensity difference between the two faces was small, medium, or large (10%, 20%, and 30% difference). Participants were able to perform the task adequately, and responses produced reasonable accuracy measures. It was therefore possible to derive psychometric functions that characterised WM abilities for emotional material. This initial study also revealed parameters and procedures of the paradigm that could be further improved. These enabled further development and refinement of the task, as detailed in the next section (Chapter 4.2).

Methods

Participants

The study was reviewed and approved by the Central University Research Ethics Committee of the University of Oxford. Twenty adults (aged 18-29; mean: 24.1.1 ± 0.62) took part in this experiment. They provided written informed consent and were compensated 15 pounds for their time.

Stimuli and Apparatus

Forty-eight face stimuli (16 identities, three types of emotional expression) were selected from the NimStim stimulus set (<http://www.macbrain.org/resources.htm>). Stimuli were used and adapted with permission from Nim Tottenham (creator of the NimStim face stimulus set). Happy, fearful, and neutral face images were used to produce graded happy and fearful expressions. Stimuli were cropped (Adobe Photoshop CS5) and then morphed from neutral to fearful and from neutral to happy in 10% steps covering the whole range from 0% to 100%. The procedure yielded 336 unique stimuli in total. Ten identities were selected for the main experiment and six were selected for the practice session.

For each person (identity) in the stimulus set, one photograph was selected from each emotion type (fear, happy, neutral) in the mouth-open configuration forming a set of 3 (see figure 4.1.1 for examples). All faces had the open-mouth configuration so that morphing from the neutral face to the emotional face (which is naturally with the mouth opened) would look more natural.

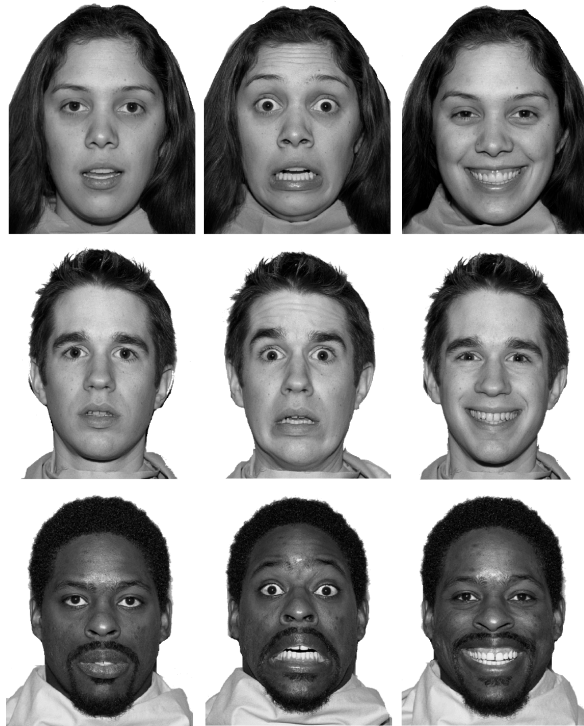


Figure 4.1.1. Example photos selected from the NimStim face stimulus set including neutral (left), fearful (middle), and happy (right) in the open-mouth configuration. See Appendix figure S4.1 for all stimuli used.

Each photo was cropped using an elliptical mask (dimensions of rectangle: 506 x 650 pixels; dimensions of ellipse: 350 x 572 pixels), so that the image mainly displayed the facial features (excluding most of the hair, neck and background). The dimensions were kept constant so that the size of all stimuli would be the same. The mask was created in Photoshop, and the size of the ellipse was determined by the size of largest face in the selected stimulus set. The colour of the mask was identical to the background screen colour during the experiment (black), so all that would be seen is an oval face stimulus. For cropping, images were loaded into Matlab and converted into greyscale. The elliptical mask was overlaid onto the photographs to create a black border and saved as images in Matlab (see figure 4.1.2).

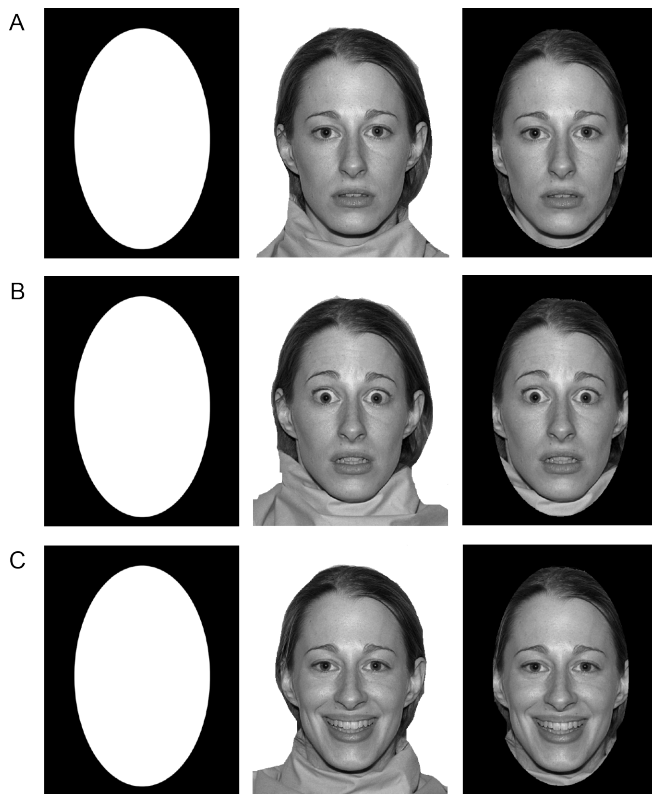


Figure 4.1.2. Cropping stimuli. An elliptical mask was laid over each photograph for A) neutral B) fearful and C) happy faces.

These images were then loaded into Morpheus Photo Morpher. For each person in the face stimulus set, a set of faces morphed from neutral-to-fear and a set of images morphed from neutral-to-happy were produced. A pair of faces (neutral-emotional) was loaded into the program, and markers were placed on the facial features that would make the morphs look the as naturalistic as possible (see figure 4.1.3 for illustration). Each marker on one photograph would correspond to a marker on the other photograph that was to be morphed to. This allowed the program to select features at the point of the marker on one photograph to morph into the features at the corresponding marker on the other photograph. In order to ensure a high quality morph, which smoothly transitioned from one face to the other in all facial features, approximately 10 markers were placed on each eye, 10 on each eyebrow, 15 on the nose, 15 on the lips, and from eight to 60 dots on the teeth. Approximately 20 dots were

applied on the outline of the face and another 10 on the hair. The morphing procedure was performed in the same way for both emotion types.



Figure 4.1.3. Morphing emotional faces using morphing software. Morphing software was used to create a set of stimuli with a gradual change from A) neutral to fearful and B) neutral to happy facial expressions. The program takes each marker on the left photograph to identify the feature and location to morph to at the corresponding marker on the middle photograph. On the right is a preview of the morphed images with A) 60% fearful and 40% neutral emotional content and B) 60% happy and 40% neutral emotional content.

The key differences between the neutral and emotional facial expressions were in the number and location of the wrinkles, mouth size and shape, and the visibility of the teeth. The most

difficult part to morph were the teeth because, in some cases, a morph had to start from a neutral face with little or no teeth visible, to an emotional face with full set of clearly visible teeth. In other cases, some teeth were shown in one photograph and different teeth were shown in the other. In these cases, care was given to morphing the photographs by adding more dots where appropriate in order to make the morph transition from one face to the other more naturalistic. Some photographs were not used because a naturalistic morph was not possible for one or both of the emotions.

This resulted in 16 facial identities with two morphed emotion stimulus sets. Ten of the highest quality stimulus sets were selected for the main experiment. See figure 4.1.4 for examples of a set of high quality morphed happy and fearful expressions. The remaining six identities were selected for practice trials (see Appendix figure S4.1 for all stimuli used).



Figure 4.1.4. Examples of the full set of morphed images from 0 to 100% in 10% steps for A) a neutral-to-happy morph and B) a neutral-to-fear morph. See all morphed face stimuli in Appendix figure S4.1.

In order to avoid retinal afterimages during the WM maintenance period, scrambled masks were produced by randomly shuffling the positions of each pixel of the face stimulus (within the elliptical mask). Each face stimulus to be encoded into WM was followed by a scrambled mask, which was a scrambled version of the same face. These scrambled masks were produced

by randomly shuffling the positions of each pixels of the face stimulus within the elliptical mask (see figure 4.1.5).

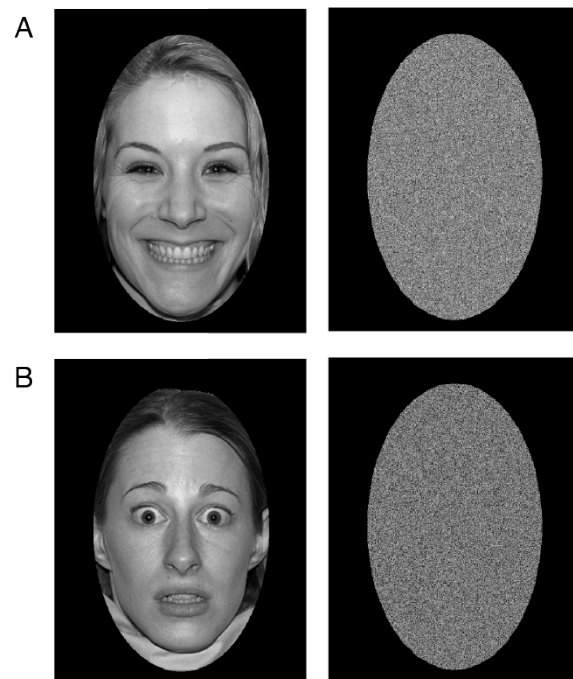


Figure 4.1.5. Examples of the scrambled face masks paired with each face stimulus. A) Right: Original happy face, Left: Scrambled happy face. B) Right: Original fearful face, Left: Scrambled fearful face.

The task was programmed and run in Matlab v.7.10 (MathWorks) using the Psychophysics Toolbox v.3.0 package (Brainard, 1997). The task was presented on an LCD screen with a spatial resolution of 1680 by 1200 pixels and a refresh rate of 60 Hz, placed ~67.5 cm from the participant.

The faces subtended $10^{\circ} \times 16.3^{\circ}$, and were presented at the left and right side of the fixation cross on the horizontal meridian (centred at $\sim 9.75^{\circ}$ in lateral visual angle from fixation). The fixation cross was a plus sign (“+”) subtending $\sim 1.5^{\circ}$ at the centre of the screen.

Task design and Procedure

A WM precision task was used to test the ability to maintain emotion-laden stimuli in WM (figure 4.1.6A). Participants were asked to hold visual fixation on a cross at the centre of the screen and encode two peripherally presented faces into memory (sample face array; 800 ms). The faces were followed by masks (scrambled versions of the same faces; 200 ms) and a blank maintenance period (1000 ms). One of the faces reappeared with the same identity and location, but with a different emotional intensity (test face; 800 ms). Participants made a response to indicate whether the current face was more or less emotionally intense than the face in memory at the same location. The fixation cross remained on the screen at all times. The sample-test emotional intensity difference was 10%, 20% or 30% in either direction (sample more emotionally intense than test, sample less emotionally intense than test). There was no time limit for responding. In order to probe participants about whether test stimuli were more or less emotionally intense than the face in memory, it was necessary to allow a margin of 30% between the sample and test stimuli (maximum emotional intensity difference). Accordingly, the emotional intensity of the sample face was constrained to vary between 30% to 70%, whereas emotional expressions of the test faces spanned from 0% to 100%. Table 4.1.1 summarises all experimental conditions.

Sample face more emotionally intense than test face (Sample : Test)					
	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5
10% difference	30 : 20	40 : 30	50 : 40	60 : 50	70 : 60
20% difference	30 : 10	40 : 20	50 : 30	60 : 40	70 : 30
30% difference	30 : 0	40 : 10	50 : 20	60 : 30	70 : 40
Sample face less emotionally intense than test face (Sample : Test)					
	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5
10% difference	30 : 40	40 : 50	50 : 60	60 : 70	70 : 80
20% difference	30 : 50	40 : 60	50 : 70	60 : 80	70 : 90
30% difference	30 : 60	40 : 70	50 : 80	60 : 90	70 : 100

Table 4.1.1. Emotional expression intensity values for the sample and test faces for each emotional intensity bin condition from low to high (columns) and sample-test emotional intensity difference (rows). Each cell displays the emotional intensity of the sample face and test face for each condition: the left number is the emotional intensity of the sample face and the right number is the emotional intensity of the test face. The conditions were identical for both fearful and happy WM.

Participants completed fear and happy conditions in separate blocks. Responses were made using the 'up' and 'down' arrow keys to judge whether the emotional expression of the test face was more intense or less intense than that of the sample. The response keys were counterbalanced across participants, so that for one participant, 'up' meant that the test face was more intense than sample, and in another participant, 'up' meant the test face was less intense than sample (or the sample face was more intense than test). Accuracy was emphasized over reaction time, and there was no time limit for the response. After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Participants were asked to keep their eyes on the fixation cross at all times. Eye position was not monitored.

Pilot experiments indicated that participants struggled to detect changes in emotional expression in the task, because the change from sample to test face was relatively subtle. Therefore, prior to the experiment, participants were shown each face stimulus once, the experimenter verbally explained the emotional change they had to detect and made sure they understood how to respond (11 emotional intensities, 16 identities). Participants were given one to two practice blocks of the emotional WM precision task (50 trials per block for each emotional condition). The practise task was exactly the same as the main experiment, except that the facial identities were selected from the practise face set, and trial-by-trial feedback was provided at the centre of the screen during the practice ("Correct" or "Incorrect").

In the main experiment, each participant completed six blocks of 50 trials for each emotion type (fearful, happy), resulting in 300 trials per emotion type. They completed six blocks of one emotion type before going onto six blocks of the other emotion type. Emotion block order was counterbalanced across participants. Identities of the faces for the whole set of trials

were randomised for each participant, so that the identities in each condition were consistently random between participants. The identity sets were randomly allocated between emotion conditions so that all identities were used in both emotion conditions. At the end of the session, participants were asked about their engagement with the task and the way they performance the task (e.g. if they used memory maintenance to perform the task, cognitive strategies employed), and the experimenter provided an explanation of the experimental task and purpose when asked.

Data Analysis

The aim of the analysis was to determine whether the task provided a sensitive measure of accuracy and reliable psychometric functions. Accuracy (proportion correct) and the proportion for reporting the test more emotionally intense than sample (for plotting psychometric functions) were computed for each participant.

To investigate the components of WM for emotional content, response distributions were binned according to sample-test emotion difference for 'proportion responded test more emotional than sample' and fit to a mixture model (Bays & Husain, 2008). In this model, the responses are assumed to come from two separate distributions: a uniform 'guess' or 'lapse' distribution in which participants had no information about the sample memory face relative to the test face, and a Gaussian distribution that represents the variability of memory representation. The guess distribution was modelled to provide an estimate of the probability the relevant aspect of the facial features were in memory, where a higher value indicates a higher probability the features were not in memory (guess rate). The probability that a participant made a correct response depends on μ , the mean of the Gaussian, σ , the width (standard deviation) of the Gaussian (precision defined as the reciprocal of the standard

deviation; $1/\sigma$), $PGUESS$, the probability that participants are guessing, and Δ , the size of the sample-test emotion difference on each trial. This is captured in equation 3:

$$(correct | \Delta) = (1 - PGUESS) * normcdf(\Delta, \mu, \sigma) + (PGUESS / 2) \quad (3)$$

where $normcdf$ is the cumulative density function of the normal distribution. The mean is a measure of bias, in which a significant shift of the mean from 0 indicates the responses were different for conditions where the sample emotion was greater than test compared with test greater than sample. $PMEM$, the probability that the relevant feature was in memory is $1 - PGUESS$. The model was fitted for each participant and each emotion type separately using maximum likelihood estimation (Myung, 2003). Paired t-tests were used to test differences between emotion types in the model parameter estimates. Cohen's d was used to determine the effect sizes.

To explore the effect of emotional intensity on WM performance, data were binned into five different emotion intensities levels, from low to high (average of the sample and test emotional intensity values; see table 1). Note that because the sample faces were restricted from 30% to 70% emotional intensity, the absolute emotion intensity values were different for the sample greater than test compared with the sample less than test emotion difference conditions. For example, when the sample-test difference was 30%, the lowest sample-test pair was sample-30 and test-0 for the sample more intense than test trials, and the lowest sample-test pair was sample-30 and test-60 for the sample less intense than test trials.

To explore the differences in WM performance for emotion type, emotional intensity, and emotional intensity difference, a repeated-measures ANOVA was conducted on WM accuracy with factors Emotion (fear, happy), Intensity (bins: 1, 2, 3, 4, 5), Sample-Test

Intensity Difference (10%, 20%, 30%), and Direction (sample more emotionally intense than test, sample less emotionally intense than test). Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity when normality assumptions were violated. Paired t-tests were used to test for the direction of the differences between conditions. To test for the direction of linear effects with more than two conditions, general linear models were applied to individual participants' data and submitted to one-sample t-tests. Cohen's *d* was used to determine the effect sizes (Cohen, 1988).

To test whether response biases contributed to participant responses, perceptual sensitivity (*d'*) and criterion (*c*) were calculated using the standard formula as in Macmillan and Creelman (1997):

$$d' = z(H) - z(F)$$

and

$$c = -[z(H) + z(F)]/2$$

where *z*(H) (or *z*(FA) stands for the *z*-transform of the hit rate (or false alarm rate). Trials were 'hits' was when participants responded test face more emotional than sample face when the test face was more emotional than sample, and 'misses' when they responded test face less emotional than sample. Trials were 'correct rejections' when participants responded test less emotional than sample when it was less emotional than sample, and 'false alarms' when participants responded test more emotional than sample. The hit rate for each participant was the total number of hits divided by the total number of trials (where the test face was more emotional than the sample face), and the false alarm rate was the number of false alarms divided by the total number of trials (where the test face was less emotional than the sample face). *d'* and criterion were computed for each Intensity condition. One-way ANOVAs were

performed on Intensity conditions for d' and criterion scores, one-sample t-tests were used to test differences from zero, and paired t-tests were used to test for the direction of the differences between conditions.

Statistical analyses were conducted in Matlab R2015a, Matlab's Statistics Toolbox and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann, Bolker, & Westfall, 2015).

Results

Working memory for emotional facial expressions

Participants performed the task with a high degree of accuracy but still far from ceiling. They were reliably better than chance – proportion correct happy: 0.8 ± 0.02 , fearful: 0.75 ± 0.02 . Psychometric functions across the group of participants (Figure 4.1.6B) were qualitatively similar to those in non-emotional visual WM tasks (e.g. Bays & Husain, 2008; A. M. Murray et al., 2013, 2011). Individual psychometric functions for each participant are shown in Appendix Figure S4.2. Participants were highly engaged in the task and reported retaining the faces in memory during the maintenance period at the debriefing session after the experiment.

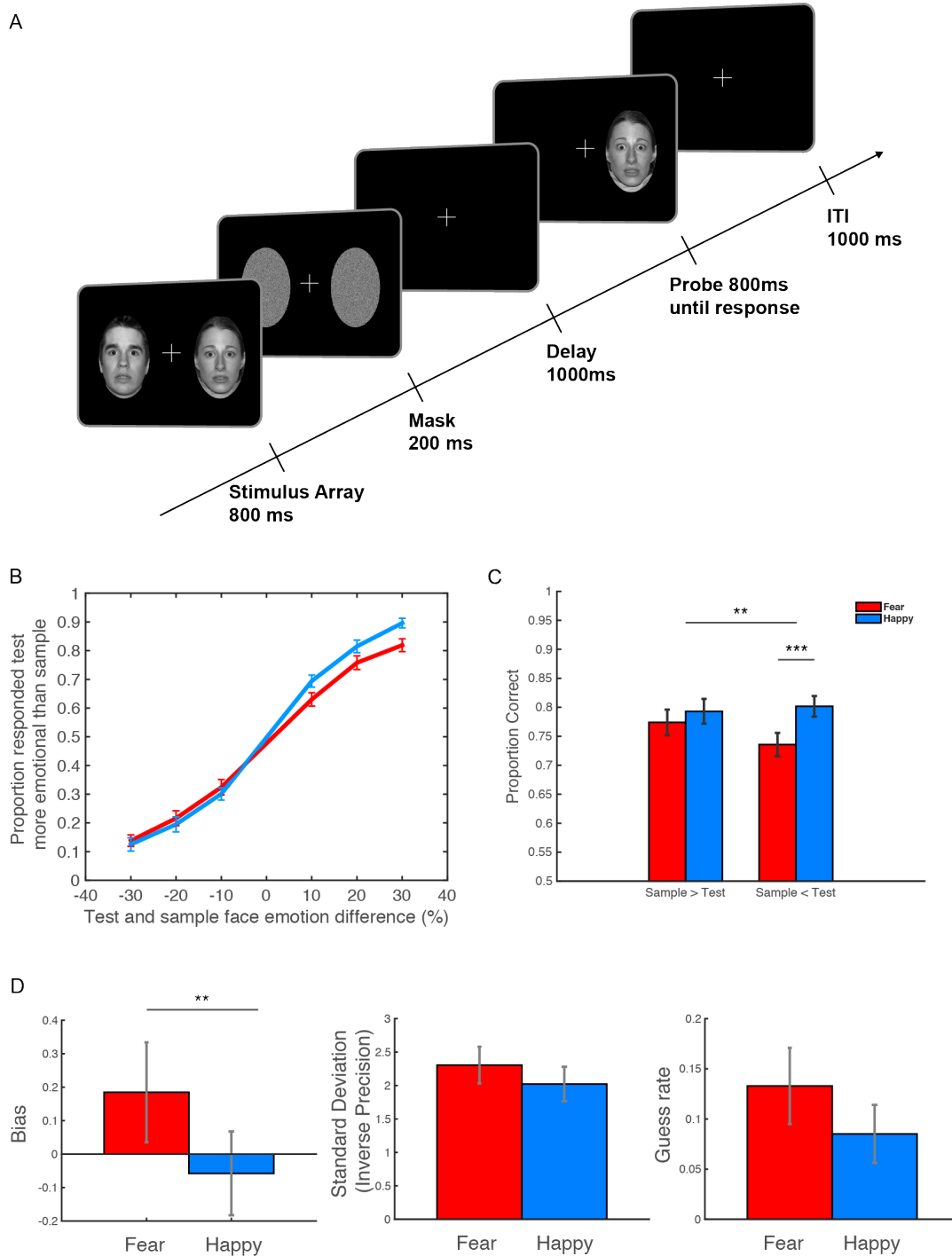


Figure 4.1.6. Task and behavioural performance for the emotional WM precision task. *A*) Emotional WM task schematic. Participants encoded two peripherally presented faces into memory. After masks and a short maintenance period, a test stimulus appeared on the left or the right of the screen. The task was to judge whether the test face was more or less emotionally intense relative to the item in memory at the same location. Fearful and happy conditions were completed in separate blocks. *B*) Group psychometric function for emotional WM. The proportion of test face stimuli judged to be more emotionally intense than the face in memory (y-axis) as a function of sample–test emotion difference for fearful face and happy face conditions (x-axis). Perfect performance would correspond to “1” for the conditions where the sample face was less emotionally intense than test (10%, 20%, 30%) and “0” for the conditions where the sample face was more emotionally intense than test (–10%, –20%, –30%). *C*) Proportion correct for fearful and happy face WM conditions for sample

*more intense than test (two left bars) and sample less intense than test (two right bars). ** Designates significant interaction, $p = 0.02$; *** designates significant effect, $p < 0.001$. D) Mixture-model parameter estimates for WM for emotional expressions. The mixture model was applied on each individual participant's psychometric function (see Appendix figure S4.2 for psychometric of individual participants). The bar graphs show the mixture model estimates of the bias (left), the standard deviation (inverse precision; middle) and the guess rate (right) for WM for fearful and happy facial expressions. * designates significant effect, $p < 0.01$.*

To examine the differences in performance for emotion type, a mixture-model analysis was performed on the psychometric curves for each individual participant to test for differences in precision (inverse of the standard deviation of the cumulative Gaussian response distribution) of the memory representation, the guess rate, and the bias. I was able to attain reasonable parameters estimates for all participants using individual psychometric curves (figure S4.2). There was some between-subject variability in the slopes and the height of the asymptote, reflected in the parameter estimates. However, not all participant curves converged to asymptote, which means the guess-rate parameter may not be as reliable with these participants. In general, it was feasible to apply this model to characterise WM performance for emotional content and compare the components generated from the model. There was a significant difference between emotion types in bias ($t(19) = 2.98$, $p = 0.008$, effect size: 0.39) but no difference in the standard deviation (inverse precision; $t(19) = 1.14$, $p = 0.26$, effect size: 0.24) or guess rate ($t(19) = 0.93$, $p = 0.36$, effect size: 0.32; figure 4.1.6D). The difference in bias can be attributed to participants' greater tendency to judge the test stimulus to be less emotionally intense in the fearful versus happy face conditions (figure 4.1.6B, three rightmost bins; also see Emotion x Intensity interaction below and figure 4.1.6C).

I also performed a standard ANOVA on accuracy (proportion correct), which produced similar results. WM accuracy was significantly different between emotion types ($F(1,19) = 24.54$, $p = 8.82 \times 10^{-5}$, $\eta p^2 = 0.56$), with more accurate responses for happy faces compared with fearful faces ($t(19) = 4.95$, $p = 8.82 \times 10^{-5}$, effect size: 0.64). There was a robust effect of Sample-Test Intensity Difference ($F(2,38) = 158.23$, $p = 1.14 \times 10^{-17}$, $\eta p^2 = 0.89$), reflecting

higher accuracy when the sample-test emotion difference is large and lower accuracy when the difference is small (mean slope: 0.09 ± 0.005 : $t(19) = 20.32$, $p = 2.39 \times 10^{-14}$, effect size = 4.54). Finally, there was an effect of Intensity ($F(3.19,60.58) = 13.76$, $p = 3.60 \times 10^{-7}$, $\eta p^2 = 0.42$), reflecting a modulation of WM accuracy with varying emotional intensity of the sample-test pairs.

There was an interaction between Emotion and Direction ($F(1,19) = 6.90$, $p = 0.02$, $\eta p^2 = 0.27$), indicating the effect of Emotion type was different when the sample was more emotional than the test face compared to when it was less than the test face for one of the emotion types (figure 4.1.6C). WM accuracy was higher for happy faces relative to fearful faces when the sample face was less emotionally intense than test ($t(19) = 7.14$, $p = 8.62 \times 10^{-7}$, effect size: 0.78; figure 4.1.6C, two right bars) but not when sample was more intense than test ($t(19) = 1.27$, $p = 0.22$, effect size: -0.2; figure 4.1.6C, two left bars), and these effects were significantly different from each other ($t(19) = 2.63$, $p = 0.02$, effect size: 0.38). This suggests that the presence of the fearful face at test could have affected performance independently of WM maintenance (see below for discussion).

There was also a significant interaction between Emotion and Intensity ($F(3.81,72.39) = 3.35$, $p = 0.017$, $\eta p^2 = 0.15$), reflecting a differential effect of intensity for emotion types.

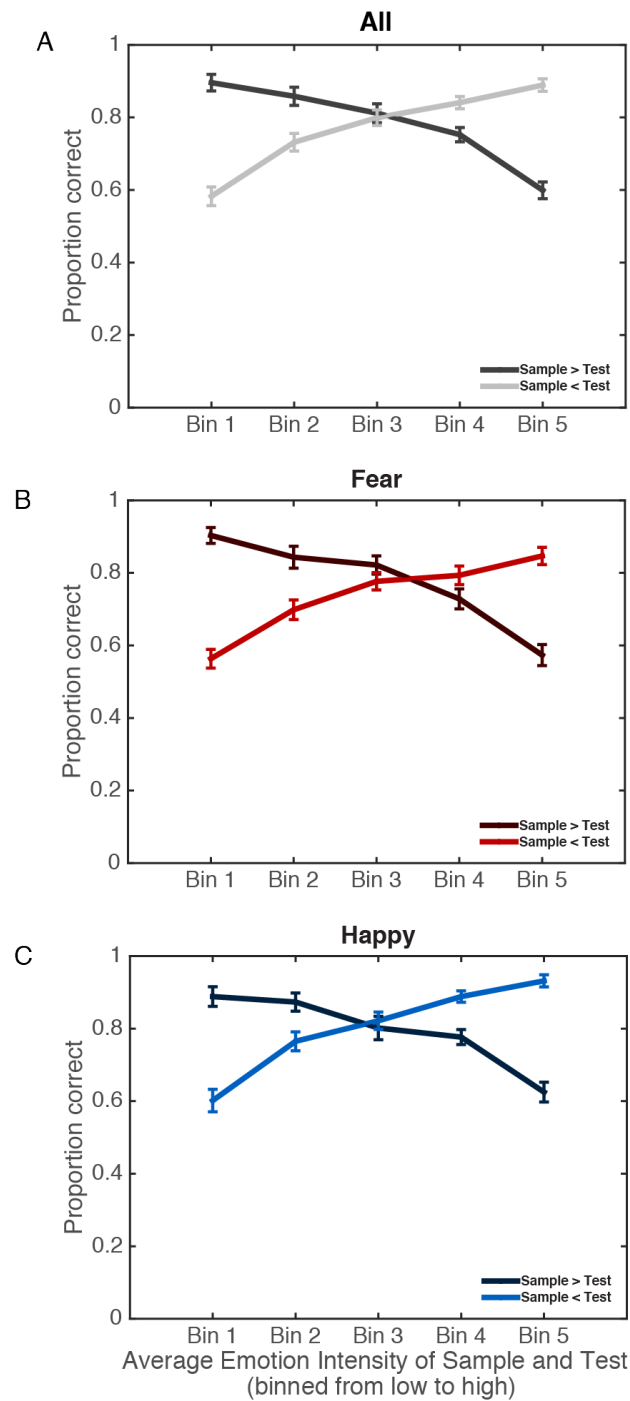


Figure 4.1.7. WM accuracy for faces with increasing/decreasing emotional intensity depended on the sample–test emotion difference direction (if the sample was more emotionally intense than the test face or less intense than the test face). A) Intensity by Direction interaction. The black line is WM accuracy for conditions when sample was more emotionally intense than test, and the grey line is WM accuracy for conditions when sample was less intense than test. B–C) Intensity by Direction interaction for B) fearful face and C) happy face conditions separately for illustrative purposes. Dark red/blue is WM accuracy for conditions when sample was more intense than test, light red/blue for conditions when sample was less intense than test. For all figures, the x-axis is the emotional intensity from low to high (see Table 1 for the emotional intensity values); y-axis is proportion correct.

There was an interaction between Intensity and Direction ($F(2.89,55) = 144.61, p = 9.19 \times 10^{-26}, \eta p^2 = 0.88$; figure 4.1.7A) related to better performance with increasing intensity in conditions where sample faces were less emotionally intense than test (mean slope: $0.07 \pm 0.006, t(19) = 12.8, p = 8.28 \times 10^{-11}$, effect size: 2.87), and a decrement in performance with increasing intensity when sample faces were more intense than test faces (mean slope: $-0.07 \pm 0.006; t(19) = -11.08, p = 9.84 \times 10^{-10}$; mean difference between slopes: $0.14 \pm 0.009; t(19) = 15.8, p = 2.09 \times 10^{-12}$, effect size: 5.32; figure 4.1.7A, see figure 4.1.7B and 4.1.7C for the same effect for fearful and happy face conditions. This effect might be due to a strategy that participants used or a response bias due to the task design.

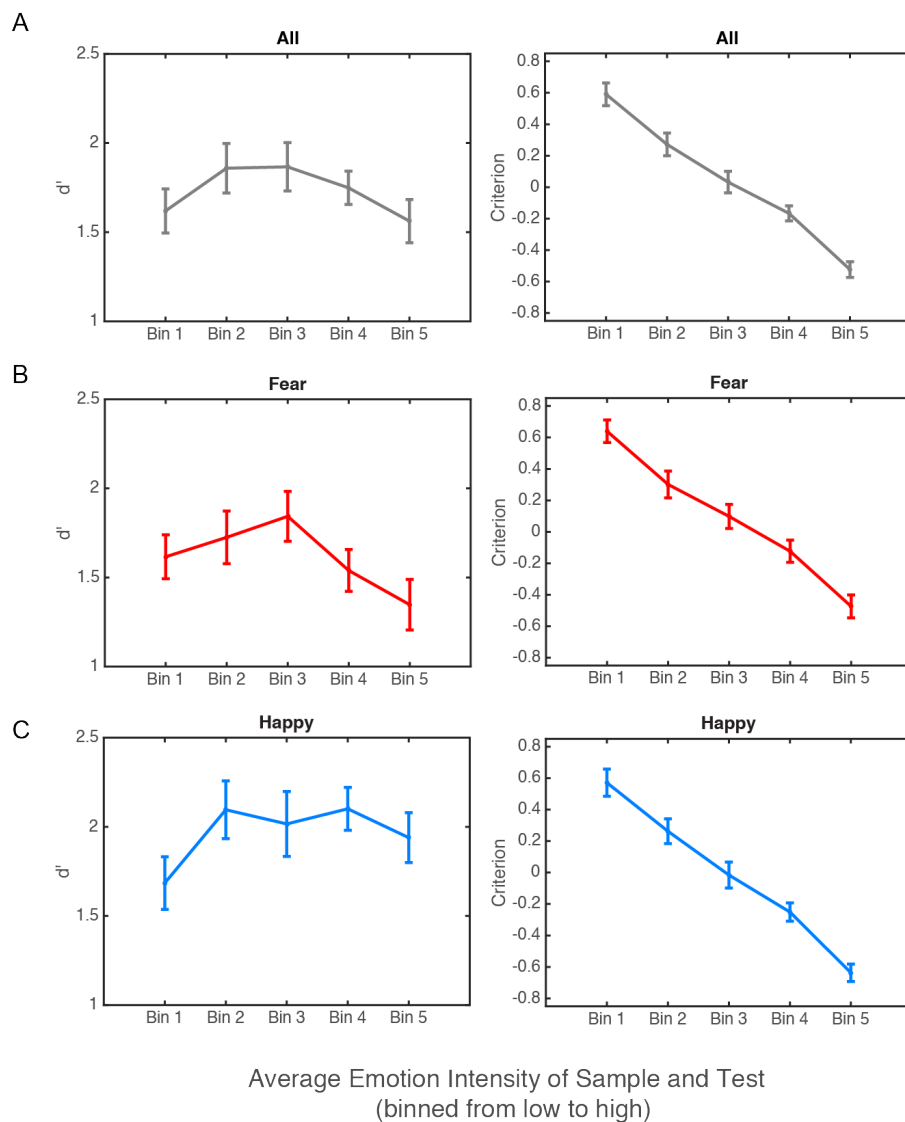


Figure 4.1.8. Sensitivity d' and criterion for faces with increasing/decreasing emotional intensity A) Main effect of Intensity for d' (left) and criterion (right). B-C) Main effect of Intensity for d' and

criterion for B) fear (red) and C) happy (blue) face conditions separately for illustrative purposes. For all figures, the x-axis is the emotional intensity from low to high (see Table 1 for the emotional intensity values); y-axis is d' or criterion.

To test whether participants were responding according to some response criterion, sensitivity d' and criterion were computed for each intensity condition (figure 4.1.8). As a group, participants performed the task properly (one-sample t-tests for d' values in all intensity bins: $t(19) > 12.87$, p 's $< 7.79 \times 10^{-11}$, effect sizes > 2.87 ; figure 4.1.8A, left; see figure 4.1.8B and 4.1.8B C for the same effects separated into the fearful and happy face conditions) with all participants' d' values numerically greater than zero in all conditions. Criterion scores revealed that participants were indeed biased to respond sample more intense than test when the test face when emotional intensities were low and sample less intense than test when intensities were high ($F(3.09,58.65) = 4.29$, $p = 0.008$, $\eta^2 = 0.18$; one-sample t-tests for intensity bins from low to high: $t(19) = 8.17$; $t(19) = 3.75$; $t(19) = 0.48$; $t(19) = -3.46$; $t(19) = -10.44$, $p = 1.22 \times 10^{-7}$; $p = 0.001$; $p = 0.64$; $p = 0.003$; $p = 2.62 \times 10^{-9}$, effect sizes: 1.83; 0.84; 0.11; -0.77; -2.33; figure 4.1.8A, right; see figure 4.1.8B and 4.1.8.C for the same effects separated into the fearful and happy face conditions).

Discussion

A new behavioural task to investigate WM abilities for emotional content was developed and implemented. Participants were able to perform the tasks with high accuracy, and reasonable psychophysical curves could be derived. A mixture model was used to characterise WM performance for emotional content, which gave sensible parameter estimates. Furthermore, performance differences were noted for different emotion types and intensities. Results using this initial task design also revealed task properties and procedures that could be further improved. These are addressed below, and will be used to refine the task further in the next chapters.

A mixture model was successfully applied to the data, which characterised WM performance into three separate sources of error. The parameters estimates from the model gave consistent results to the raw accuracy scores, but also gave an insight to the WM-performance differences between emotion types. The results suggested that the difference in WM performance was due to a shift in the mean of the psychometric functions (bias) rather than the precision of the WM representation or the probability of dropping the item from memory (guessing rate). The modelling approach enabled us to ask questions in a way that have not yet been addressed before in emotion-WM experiments. Reassuringly, the standard analysis yielded results that were consistent with the model parameters, suggesting that the modelling procedure was not crucial to understanding the data.

Participants were better at maintaining happy faces in WM compared to fearful faces, which was attributed to worse performance for the fearful conditions when the test face was more emotionally intense than the sample face. One possible explanation is that a high-intensity fearful face appearing at test – the moment at which comparison of emotional intensities is required – may have been distracting. Overall, when the test is more fearful than the sample face, it tends to have a high fear expression (ranging from 40% to 100%). This effect was not observed for happy faces. As an improvement, therefore, the next version of the task should use neutral faces at test, which are equivalent in appearance and emotional content for both happy and fearful face conditions, and therefore do not differ in their capture of attention.

Another issue was that the current task appears to encourage strong response-strategy effects, which may mask the probing of the emotional content of the WM representations. This was observed as an interaction between emotional intensity and the sample-test emotion difference direction. By design, the range of intensity values for the sample face ranged from 30% to 70%, and the values for the test face ranged from 0% to 100%. If the test face has an

emotional expression of high intensity, the participant may think that the sample is likely to be lower in emotional intensity, and if the test face had a low intensity, the sample is likely to be higher in emotional intensity. Therefore, in a given trial, if the test face was high in emotional intensity, participants may simply respond “sample less emotional than test” and if the test face was low in emotional intensity, participants may simply respond “sample more emotional than test”. The results are consistent with this idea, whereby participants judge sample faces as more intense than test faces when the test face emotional intensity is low. This results in participants being more likely to be correct when the sample face was in fact more intense than the test face (figure 4.1.7A: bins one and two, black line), but less likely to be correct when the sample was less intense than test (figure 4.1.7A: bins one and two, grey line; also see criterion scores in figure 4.1.8A, left: bins one and two). In contrast, when the emotional intensity was high, participants judged the sample faces to be less emotionally intense than test, being more likely to be correct when the sample face was less intense than the test face (figure 4.1.7A, bins four and five, grey line), but less likely to be correct when the sample was more intense than the test face (figure 4.1.7A, bins four and five, black line; also see criterion scores in figure 4.1.8A, left: bins four and five). Note that if participants applied the same strategy using the sample face emotional intensity, the results would be reversed. Therefore, although participants were performing the task properly (shown by reasonable d' values), they were also biased by the emotional content of the test stimulus. Since discrimination judgements on relative emotional intensity differences can induce these response strategies, they are not ideal for characterising emotional WM. In designing the next experiment, I will modify the task to encourage genuine memory maintenance rather than the use of response strategies.

Overall, the first version of the emotional WM paradigm showed some success – participants were highly engaged in the task, and were able to maintain faces with emotional expressions

in WM and discriminate emotional intensity differences between the morphed emotional expressions. Despite this, two major issues may have compromised the ability to measure *maintenance* of emotional stimuli in WM with the best sensitivity. Even if participants were maintaining emotional expressions of faces in mind, the design might have encouraged biases or strategies that reduce the memory demands of the task. Based on these issues, I propose to use a new WM task using the same emotional face stimuli, but to ask participants to recall the emotional expressions from memory, rather than compare the relative emotional intensity differences from the sample to the test face.

4.2. Working memory for emotional content II: free recall

To characterise WM for emotional content whilst avoiding the problems in the previous version of the task, an emotional analogue of a visual WM precision task with a free-recall response method (e.g. Bays & Husain, 2008) was developed. Recently, researchers developed a free-recall version of the visual WM precision task, in which participants recall the orientation or colour of the item in memory (Bays et al., 2009; Wilken & Ma, 2004; W. Zhang & Luck, 2008), rather than discriminate differences between the sample and test stimulus (e.g. Bays & Husain, 2008). In a typical free-recall visual WM precision task (e.g. Bays et al., 2009; Bays, Wu, & Husain, 2011; Wilken & Ma, 2004; W. Zhang & Luck, 2008), participants encode a number of stimuli (e.g. orientations, colours) into memory over a short maintenance period until a test stimulus appears at the end of the trial. There are several response methods that have been used to test WM recall. For orientation memory, the same oriented stimulus could be presented at a random orientation, and participants adjust the stimulus to match the orientation stored in memory using a mouse or keyboard (e.g. Bays et al., 2011). For colour memory, a coloured square may be presented to the participant, and they would use the mouse or keyboard to scroll through the colours in that square and respond when the colour matches (e.g. van den Berg, Shin, Chou, George, & Ma, 2012).

They could also recall the colour of a memory item by clicking on a colour wheel (e.g. Bays et al., 2009; Wilken & Ma, 2004; W. Zhang & Luck, 2008). To compute a measure of WM accuracy, the reported orientation angle or colour (1° - 180° or 1° - 360° in orientation space, or 1° - 360° in colour space on a colour wheel) is subtracted from the angle of the tested memory item, giving the angular deviation of the response from the actual stimulus. The mean value of the unsigned error (i.e. angular deviation irrespective of the sign of the deviation) from the target is commonly termed “WM error” or “mean absolute deviation”, a measure of (inverse) WM accuracy. The bias for responding more clockwise or anticlockwise in orientation or colour can also be computed or estimated by finding the mean of the signed error (e.g. Bays & Husain, 2008; Fougne, Suchow, & Alvarez, 2012), although this is assumed to be zero in most tasks. These responses generate continuous data and provide a rich dataset for assessing WM performance.

To adapt this paradigm to test WM with emotion-laden stimuli, a set of emotional face stimuli were used. As before, I used the same faces with fearful and happy facial expressions but increased the number of morphed face stimuli to range from 0% to 100% emotional intensity in 1% steps. Instead of comparing the test face to the sample face emotional intensity, participants recalled emotional expressions by adjusting the facial expression of an emotionally neutral test face to the expression in memory. This response mode avoids the two main issues identified in the previous task. Since the test face is always neutral (0% emotional intensity), this design avoids the distracting effect a fearful test face might have on WM performance. In addition, the test stimulus provides no useful information regarding the correct response. Instead, participants must rely on the emotional content of the sample faces in memory in order to perform the task, and will not be able use the expression of the test face to guide their responses as they did in the previous version of the task. Finally, the free-recall

response generates fine-grained behavioural data and should provide a better characterisation of WM for emotion-laden stimuli over the previous design.

Experiment 4B

To avoid the issues that arose in the previous version of the task and to improve the sensitivity of the task, a WM precision task with a free-recall response method was developed to study the ability to maintain emotional content in WM. In each trial of the experiment, participants encoded one or two sequentially presented faces into WM with an emotional expression (fearful or happy) of a certain intensity (ranging from low to high). After a short delay, an emotionally neutral face re-appeared at the centre of the screen matching the identity of one of the presented faces. Participants recalled the emotional expression and intensity of the corresponding facial identity from memory and used a trackball mouse to adjust the emotional expression of the face on the screen to match the emotion type and intensity of the remembered face as precisely as possible. All participants were able to perform the task adequately, and their errors for the short-term retention of emotional facial expressions followed Gaussian distributions. The task, therefore, was judged to be suitable for characterising WM for emotional material. In the next few sections, further refinements will be made to the paradigm, in order to optimise parameters such as timing and load, and to include a perceptual control task with emotional stimuli.

Methods

Participants

The study was reviewed and approved by the Central University Research Ethics Committee of the University of Oxford. Twenty adults (aged 18-31; mean: 22.75 ± 0.82) took part in this experiment. They provided written informed consent and were compensated 15 pounds for their time. None of the volunteers had participated in the previous experiment.

Stimuli and Apparatus

The same original set of face stimuli were used as in Experiment 4A (48 stimuli: 16 identities, each with emotional expressions of fear, happy and neutral in the open-mouth configuration), and the same procedures were followed for generating additional emotional expressions through morphing. The set of face stimuli was extended to include morphs from emotional expressions with intensities from 0% to 100% in 1% steps, resulting in 3,216 unique stimuli in total. In contrast to experiment 1, all possible emotional intensities were used. As before, the same ten identities were selected for the main experiment, and the remaining six identities were used for the practice session. Scrambled masks were produced for each face stimulus as in experiment 1.

The task was programmed and run in Matlab v.7.10 (MathWorks) using the Psychophysics Toolbox v.3.0 package (Brainard, 1997). The task was presented on an LCD screen with a spatial resolution of 1680 by 1200 pixels and a refresh rate of 60 Hz, placed ~67.5 cm from the participant. The faces were presented at the centre of the screen and subtended 10° x 16.3°. The fixation cross was a plus sign (“+”) placed at the centre of the screen and subtended ~1.5°.

All participants were asked to complete eight self-report questionnaires measuring state and trait anxiety (State-Trait Anxiety Inventory, STAI; Spielberger, 1983) and positive and negative affective states and traits (Positive and Negative Affect Scale: PANAS negative trait and state, positive trait and state, positive trait 21 and state 21; Watson, Clark, & Tellegen, 1988). Qualtrics online survey software (Qualtrics, Provo, UT) was used to deliver the questionnaire surveys and generate the summary statistics.

Task Design and Procedure

The experiment tested the ability to remember faces with emotional expressions in WM. A modified WM precision task (Bays et al., 2011; Wilken & Ma, 2004; W. Zhang & Luck, 2008) with emotional face stimuli was used to study WM performance for emotional content (figure 4.2.1A).

In the main experiment, participants encoded one or two faces into memory and were tested on one of the faces at the end of the trial. Stimuli were happy or fearful faces with pseudo-randomly selected levels of emotions from intensity values of 0 to 100% in 1% steps. Emotion type conditions were intermixed within each block, whereas load conditions (one, two) were completed in separate blocks. In the load-1 condition, each trial began with a fixation cross at the centre of the screen (100 ms), after which a face stimulus (350 ms) appeared immediately followed by a scrambled mask (80 ms). In load-2 blocks, the initial face-mask pair was followed by a second face-mask pair with the same presentation parameters after a 1000 ms inter-pair interval. The second face had a distinct identity. After the final face-mask pair, a maintenance period of 1000 ms followed, after which a test face with a neutral expression was presented. Participants adjusted the emotional expression of the test face to match the emotion type and intensity of the face in memory with the corresponding identity. The test face was always presented at 0% emotional intensity (neutral), and participants adjusted the face using a trackball mouse, scrolling left for one emotion and right for the other (counterbalanced across participants). The interval between trials, commencing after response termination, was 800 ms. After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Participants were asked to keep their eyes on the fixation cross at all times. Eye gaze was not monitored.

This type of response generated continuous data. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of probe presentation in the interest of time and to reduce memory degradation.

Participants first completed questionnaires reporting anxiety and mood on a desktop computer, and then proceeded to the main experimental task. Participants were given one or two practice blocks of the emotional WM precision task for each of the load-1 and load-2 conditions (25 trials per block). Most participants only required one practise block. The practise tasks were exactly the same as the main experiment, except that the facial identities were selected from the practise face set.

In the main experiment, each participant completed sixteen blocks of 50/51 trials, resulting in a total of 808 trials. Load-condition block order was counterbalanced across participants. For each emotion type (fear, happy), an image from each emotion intensity level (0 to 100% in 1% steps) was presented four times for each load condition (load 1, load 2). There were 404 trials for the load-1 condition, with 202 trials per emotion type. For the load-2 condition, there were 101 trials for each possible combination of face-pair presentations, giving four sub-conditions: a) fear-fear, b) happy-happy, c) fear-happy, and d) happy-fear. In each sub-condition, participants were tested on the first face on half the trials and the second face on the other half of the trials. Unfortunately, due to a technical error, the target and non-target emotional intensities in the load-2 conditions were not properly randomised, and were positively correlated. Therefore, the effects of intensity of the target versus the non-target intensity on WM performance could not be tested. The facial identities were randomly allocated between emotion conditions and all identities were used in both emotion types. At the end of the session, participants were asked about their engagement with the task and the way they performed the task (e.g. cognitive strategies employed), and the

experimenter provided an explanation of the experimental task and purpose when asked. The whole testing session lasted approximately 105 minutes.

Data Analysis

The aim of this analysis was to characterise the ability to retain stimuli with emotional content in WM and test whether performance on these tasks are correlated with individual differences in mood and anxiety.

To characterise WM for emotional facial expressions, I computed the WM error, corresponding to inverse behavioural accuracy, and the WM bias, corresponding to the degree to which participants overestimated or underestimated the emotional content in the facial expressions in their response. To compute these measures, participants' responses were subtracted from the target face emotional intensity values on each trial, giving a distribution of the deviation of the responses from the target face emotional values (signed error in percent emotional intensity). The mean of the absolute (positive) values represents the response error (hereon simply referred to as "error"), and the mean of the signed values represents the bias. The magnitude of error indicates how far each response was from the target stimulus emotional value in percent emotional intensity irrespective of the sign of deviation. Lower error means higher accuracy and higher error means lower accuracy. The bias gives a measure of a systematic bias to report emotions as consistently more or less emotionally intense relative to the target. If participants made responses that were on average higher intensity (more emotional) than the target face, they would have a positive bias; if they mostly made responses that were lower in intensity (less emotional) than the target, they would have a negative bias. When a response was incorrectly adjusted to the opposite emotion, the error would be negative because it was on the other side of the response spectrum to neutral (0%). Both measures were computed within participant to derive a mean error and mean bias per participant. Note that measures of WM error and bias are positively correlated if all errors

were positively signed errors (responses more emotional than the target face), or negatively correlated if all errors were negatively signed errors (responses less emotional than the target face). The data are usually a mix of positively and negatively signed errors, but when responses are consistently positively or negatively biased, mean bias and error will reflect an equivalent measure of behavioural performance.

To characterise the bias and error in WM for emotional content, the range of target emotional intensities was restricted to 21 – 80% in emotional intensity for the analyses for error and bias. This was motivated by the range of emotional expressions used not forming a circular distribution, which in turn introduces response ceiling and floor effects when reporting expressions at the high and low end of the emotional range respectively. In the high-intensity conditions, it is always possible to report a face that was less emotionally intense than the target face (responses to the left of zero on the error distributions), whereas there are a smaller number of possible responses when reporting the face as more emotionally intense than the target face (responses to the right of zero on the error distributions). For the low-intensity conditions, there is a much smaller range of possible responses when giving responses that are less emotionally than target face, unless they report the other emotion type. In trials with high or low emotional intensity, responses would show a negative or positive skewed distribution of errors, respectively. Therefore the range of emotional intensities of the target faces were restricted to 21 – 80% in intensity in order to allow all intensity conditions to show symmetric distributions of error and enable a better measure of behavioural performance.

Responses to the correct emotion type reflect accurate WM representations of the target emotion type and intensity (with some error), whereas responses to the incorrect emotion type (e.g. reporting a 20% fearful face when the target was a 20% happy face) do not.

Responses to the incorrect emotion type (e.g., like incorrect responses in other psychophysical tasks) do not belong to the same distribution as the correct responses. Accordingly, analyses were performed after excluding responses to the incorrect emotion type.

To inspect the effect of emotional intensity of the faces on WM performance, intensities were binned into five equal bins (1 – 20, 21 – 40, 41 – 60, 61 – 80, 81 – 100) of emotional intensity conditions (a total of 160 trials per bin – 40 trials for each emotion type and load condition). Bin 1 and bin 5 conditions were excluded in the analyses for WM error and bias.

After excluding trials with neutral (0% intensity) targets, there were 800 trials (400 per emotion type), within which there were 160 trials per emotional intensity bin (80 per emotion type). After removing misreported emotion trials, there were 370.1 ± 0.88 trials for the fearful face conditions and 349.9 ± 0.95 trials for the happy face conditions (out of 400 trials). Split into number of trials per emotional intensity bin, the mean (\pm S.E.M.) number of trials per bin were as follows: bin 1: 114.7 ± 0.71 , bin 2: 140.3 ± 0.28 , bin 3: 152.7 ± 0.39 , bin 4: 155.1 ± 0.24 , bin 5: 157.4 ± 0.15 .

To explore the differences in WM performance for emotion type, emotional intensity, and the effect of load, a repeated-measures ANOVA was conducted on WM error for Emotion (fear, happy), Intensity of the target face (bins: low, medium, high), and load (one, two). A repeated-measures ANOVA was also performed for the WM bias with the same factors. Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity when normality assumptions were violated.

To explore whether emotion type or intensity had an effect on misreporting the wrong emotion type (e.g. recalled a 25% fearful but it was in fact a 25% happy face), a

repeated-measures ANOVA was conducted on the proportion of misreported responses with factors Emotion (fear, happy), Intensity (bins: 1, 2, 3, 4, 5), and load (one, two).

Paired t-tests were used to test for the direction of the condition differences and one-sample t-tests were used to test for differences from zero. In order to test for the direction of linear effects with more than two conditions, I fit a line to each participant's data across conditions, and tested whether the slope of the line was larger or smaller than zero (one-sample t-test at the group level). This reveals whether the performance measure increased or decreased across conditions. Cohen's d was used to determine the effect sizes (Cohen, 1988).

Spearman's rank correlations were used to explore possible relationships between WM performance (error and bias scores separately, averaged over load conditions and intensities) individual differences in mood and anxiety. To reduce the number of comparisons, three composite measures were computed for each participant: negative affect (mean of PANAS negative state and trait), positive affect (mean of PANAS positive state, positive state 21, positive trait, and positive trait 21), and anxiety (mean of STAI state and trait). Given the exploratory nature of the analysis and the limited small sample size, non-significant correlations will be considered when there is a hint of an association, either statistically or because there are consistent patterns of trend correlations between measures.

Statistical analyses were conducted in Matlab R2015a, Matlab's Statistics Toolbox and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann et al., 2015).

Results

Working memory for fearful and happy facial expressions

Participants were able to complete the task with high accuracy (mean error: $17.5\% \pm 0.97$) in both emotion types and load conditions (fearful load one: $15.7\% \pm 0.74$; fearful load two: $19.5\% \pm 1.2$; happy load one: $15.8\% \pm 0.69$; happy load two: $18.8\% \pm 0.94$). The error distributions for single participants followed a Gaussian distribution of error, but with a negative skew – likely due to the trials where participants mistakenly reported the wrong emotion type and because it was not possible to respond much more emotionally intense for the trials with high emotional intensity faces. Therefore, the main analyses were performed on the faces with 21% – 80% emotional intensities (excluding extreme emotions) and after excluding trials where participants mistakenly reported the wrong emotion type.

Figure 4.2.1 summarises the task and displays the main behavioural results at the group level. Participants were able to complete the task with high accuracy (mean error: $14.1\% \pm 0.75$) in both emotion types and load conditions (fear load one: $14.1\% \pm 0.73$; fear load two: $15.3\% \pm 0.83$; happy load one: $12.6\% \pm 0.64$; happy load two: $14.2\% \pm 0.72$). Error distributions for single participants followed a Gaussian distribution, and were qualitatively similar to what has been shown in visual WM tasks (4.2.1B for group histograms; see Appendix figure S4.3 for individual participant response error histograms).

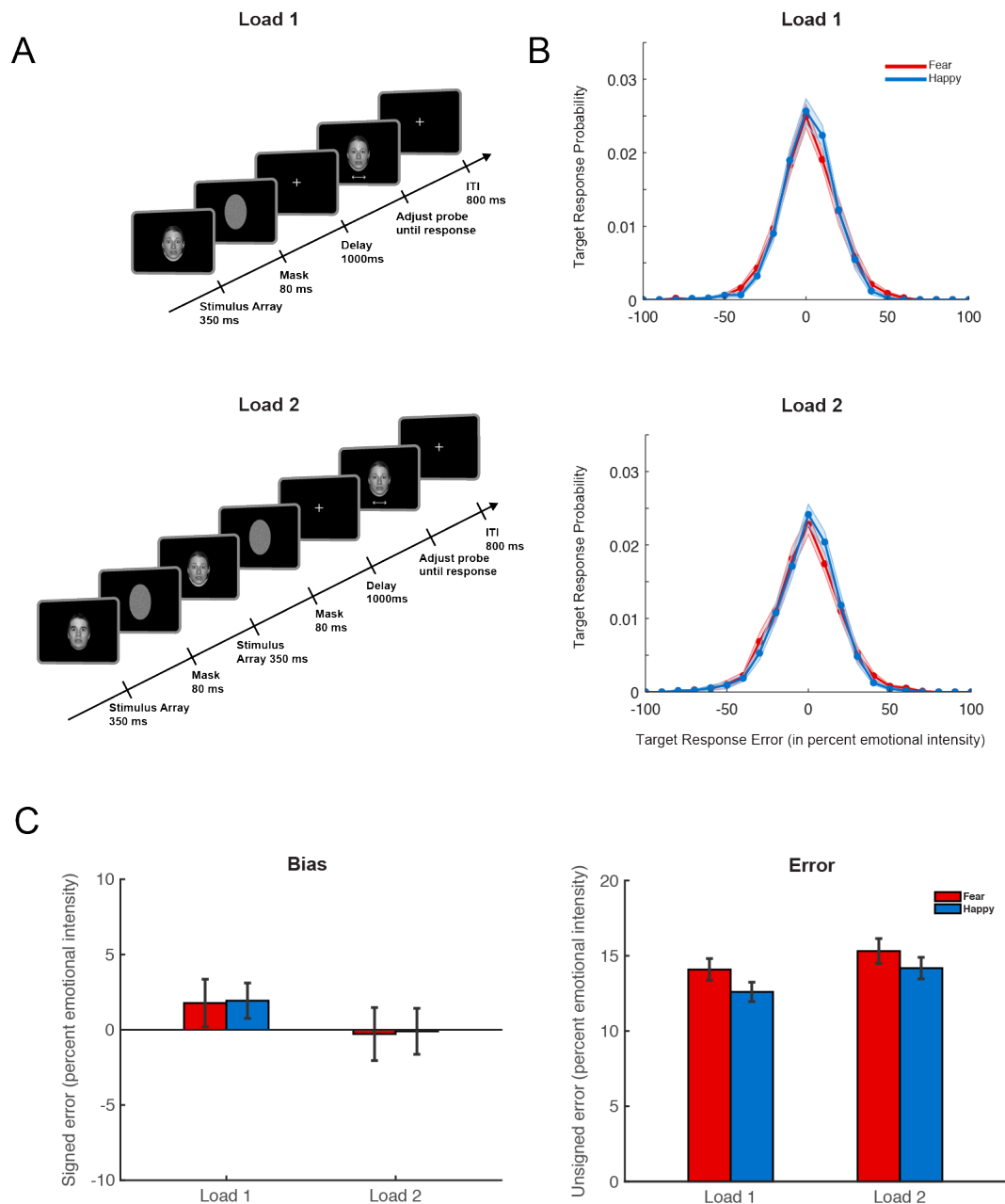


Figure 4.2.1. Task schematic and behavioural performance for WM. *A*) Task schematic for emotional WM. *Top*: In load-1 blocks, participants encoded a facial expression into WM. After a fixed delay of 1000 ms, a test face appeared with the same facial identity but a neutral facial expression (0% emotional intensity). Participants made their response by changing the face to match the emotional expression in memory using a trackball mouse. *Bottom*: In load-2 blocks, participants encoded two sequentially presented faces into WM. After a fixed delay of 1000 ms, a test face appeared with the one of the two facial identities and a neutral facial expression. Participants made their response by changing the face to match the emotional expression of the tested facial identity in memory using a trackball mouse. The faces that were encoded into memory ranged from 0% to 100% fearful or 0% to 100% happy in 1% steps. Load conditions were performed in separate blocks, whereas emotion type was intermixed within blocks. *B*) Error distributions for emotional WM centred on the target face emotional intensity for load one (*top*) and load two (*bottom*) conditions. The error probability is plot at each bin and connected by the lines for fear (red) and happy (blue) WM conditions. The shaded areas show the standard error of the mean. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, y-axis

is the response error probability. C) Bias (mean of the error distributions in B; left) and error (unsigned error of the distributions in B; right) for fear (red) and happy (blue) for both load conditions. Bias and Error were calculated using trials with emotional expressions between 21 and 80% and for which participants reported the correct emotion type.

In a sizable proportion of trials, participants mistakenly reported the wrong emotion type (mean proportion of happy faces reported fearful: 0.13 ± 0.01 , mean proportion of fearful faces reported happy: 0.07 ± 0.01). Furthermore, participants were more likely to report a happy face as fearful than reporting a fearful face as happy ($F(1,19) = 9.89$, $p = 0.005$, $\eta p^2 = 0.34$; $t(19) = 3.14$, $p = 0.005$, effect size: 1.10; figure 4.2.2A). There were more misreported emotion trials with greater WM load (proportion misreported in load one: 0.08 ± 0.01 , load two: 0.12 ± 0.01 ; $F(1,19) = 23.99$, $p = 9.98 \times 10^{-5}$, $\eta p^2 = 0.56$; $t(19) = -4.90$, $p = 9.98 \times 10^{-5}$, effect size: -0.97). Furthermore, the lower the emotional intensity, the more likely an emotion type was misreported ($F(1.37,26.02) = 129.19$, $p = 8.61 \times 10^{-13}$; $\eta p^2 = 0.87$; mean slope: -0.06 ± 0.004 ; $t(19) = -14.19$, $p = 1.45 \times 10^{-11}$, effect size: -3.17), and the effect was stronger for happy compared with fear (Intensity by Emotion interaction: $F(1.41,26.87) = 20.38$, $p = 2.40 \times 10^{-5}$, $\eta p^2 = 0.52$; mean difference in slope: -0.05 ± 0.01 , $t(19) = 4.84$, $p = 1.15 \times 10^{-4}$, effect size: 1.58). Plotting target face intensities as a function of participant responses (figure 4.2.2B) showed that most responses were centred on the target (grey identity line on the right of each scatter plot) but a proportion of the trials were responses to the incorrect emotion type (responses to the left of zero on each plot). The pattern of responses was generally consistent across participants, with some between-subject variability in the accuracy of responses and number of misreported emotion trials (see figure S4.4 for scatterplots of each participant).

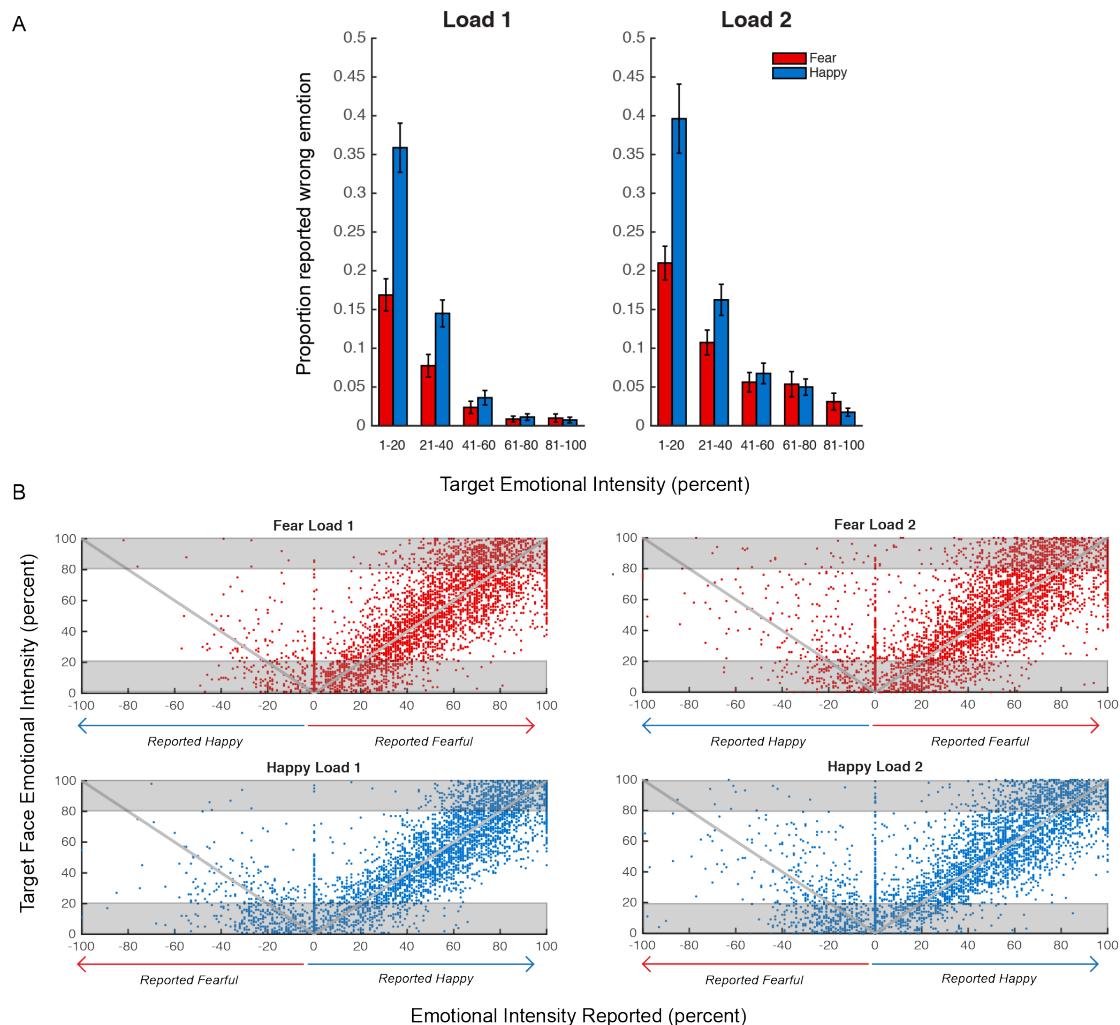


Figure 4.2.2 Proportion of trials where participants misreported the emotion type for each Emotion and Intensity value condition. A) Bar plots showing the proportion of misreported-emotion trials for each emotional intensity bin from 10% to 90% in 20% steps for fearful (red) and happy (blue) faces for load one (left) and two (right) conditions. B) Scatterplots of target face emotional intensities plotted as a function of participant responses. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. A 'mirrored' version of the identity line ($y = -x$) is plot on the left side for reference. Each point is an individual trial, and each scatter plot includes all the trials in the specified condition for all participants. The areas in grey are trials from 0% – 19% and 81% – 100% emotional intensity, which were removed from the main analyses.

To explore how the task characterises WM abilities for emotional content, I tested for the effect of Emotion-Type, WM-Load and Emotion-Intensity on WM error and bias in the trials of interest. As expected, there was a significant effect of WM-Load on error ($F(1,19) = 8.20$, $p = 0.01$, $\eta p^2 = 0.30$; figure 4.2.1C, right) reflecting better performance for trials with one memory item relative to two memory items ($t(19) = -2.91$, $p = 0.01$, effect size: -0.44).

There was also a significant effect of Emotion-Type ($F(1,19) = 18.24, p = 0.0004, \eta p^2 = 0.49$) reflecting lower WM error for happy faces relative to fearful faces ($t(19) = -4.15, p = 0.0005$, effect size: -0.44 ; figure 4.2.1C, right). Finally, there was a main effect of Intensity ($F(1.70,32.30) = 8.37, p = 0.002, \eta p^2 = 0.31$), reflecting higher error with greater intensity (mean slope: $0.90 \pm 0.26, t(19) = 3.55, p = 0.002$, effect size = 0.79 ; figure 4.2.3A).

Bias showed an effect of WM-Load ($F(1,19) = 5.25, p = 0.03, \eta p^2 = 0.22$), with greater positive bias in load-1 relative to load-2 conditions ($t(19) = 2.29, p = 0.03$, effect size: 0.34 ; but neither were different from zero: load-1: $t(19) = 1.46, p = 0.16$, effect size: 0.33 , load 2: $t(19) = -0.16, p = 0.88$, effect size: -0.03 ; figure 4.2.1C, left). There was an effect of Emotion-Intensity ($F(1.85,35.11) = 26.20, p = 1.96 \times 10^{-7}, \eta p^2 = 0.58$), reflecting a difference between low and high intensities ($t(19) = 5.17, p = 5.42 \times 10^{-5}$, effect size: 0.89) and medium and high intensities ($t(19) = 13.60, p = 3.06 \times 10^{-11}$, effect size: 0.87), but not between low and medium intensities ($t(19) = -0.74, p = 0.47$, effect size: -0.11 ; figure 4.2.3B). Low intensities were recalled as more emotionally intense than presented at sample ($t(19) = 2.25, p = 0.036$, effect size: 0.50), with a similar trend for the medium intensities ($t(19) = 1.99, p = 0.06$, effect size: -1.97) and a trend in the opposite direction for the high intensities ($t(19) = -1.87, p = 0.076$, effect size: -0.42). There was no effect of Emotion-Type ($F(1,19) = 2.69, p = 0.12, \eta p^2 = 0.12$).

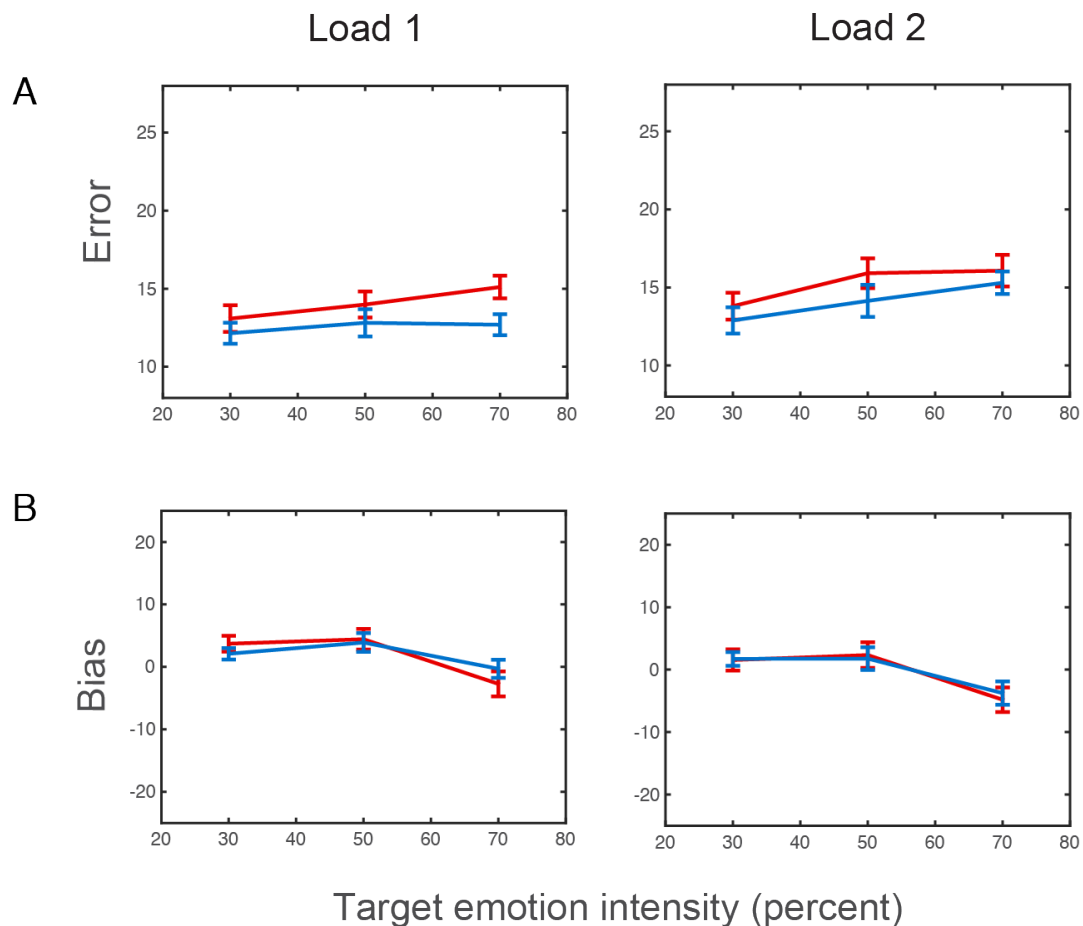


Figure 4.2.3. Effect of emotion type and emotional intensity on WM performance. A) WM error (unsigned) plotted as a function of emotional intensity for load one (left) and load two (right) conditions. B) WM bias (signed error) plotted as a function of emotional intensity for load one (left) and load two (right) of each panel. In all plots, the x-axis is the target face emotional intensity binned from 30% to 70% in 20% steps, the y-axis is the behavioural measure.

Correlations between emotional WM performance and mood

In order to assess the feasibility of linking individual differences in mood with emotional WM abilities, I tested for correlations between behavioural measures and mood/anxiety scores (see Figure 4.2.4 for distributions of mood scores). There was a relatively good distribution of mood scores for positive affect (mean: 48.25 ± 1.84 ; range: 38.75 – 63.25) and anxiety (mean: 32.63 ± 1.81 ; range: 20.5 – 55.5), but less so for negative affect (mean: 15.85 ± 1.46 ; range: 10.5 – 34), which also showed a skewed distribution with a large proportion of the participants around the lower limit.

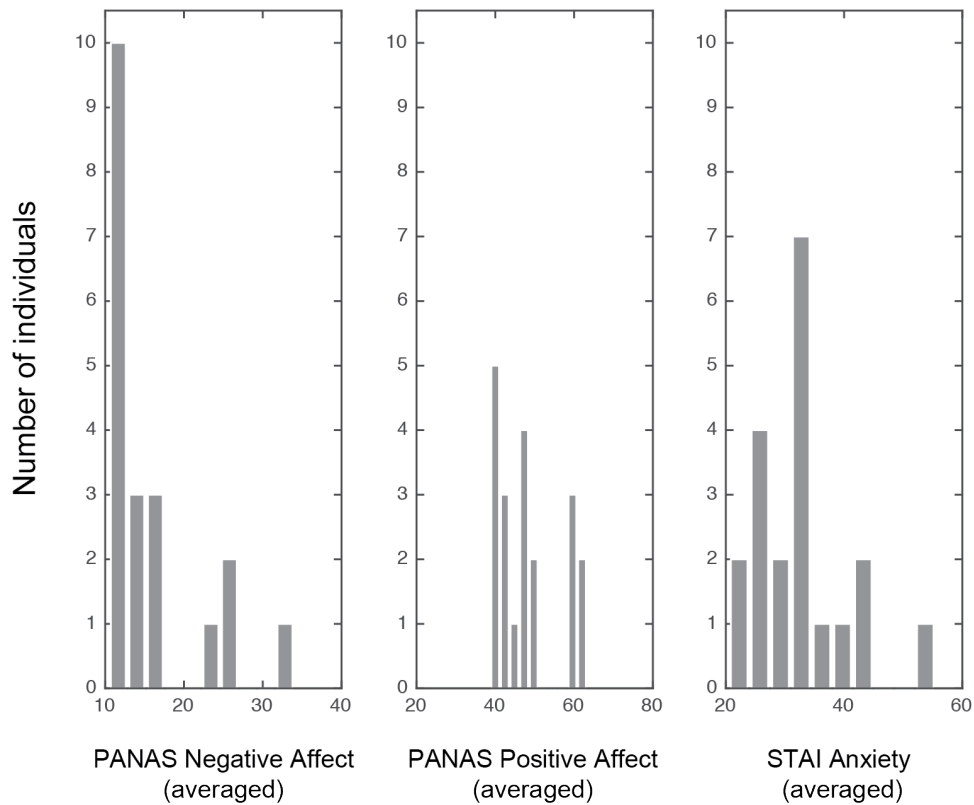


Figure 4.2.4. Distributions of mood and anxiety scores over participants. Histograms showing the distribution of mood scores for negative affect (left), positive affect (middle) and anxiety (right). X-axis is the mood/anxiety measure and y-axis is the number of individuals.

In general, high negative mood or anxiety was positively correlated with WM error, and positive mood was associated with lower error (figure 4.2.5). Negative affect and anxiety showed a trend to correlate positively with WM error for fearful faces (negative affect: $r = 0.40$, $p = 0.078$; anxiety: $r = 0.40$, $p = 0.078$), with a similar trend for anxiety with WM error for happy faces ($r = 0.32$, $p = 0.16$). Positive affect was negatively correlated with WM error for happy faces ($r = -0.45$, $p = 0.045$). Although not significant, all correlational analyses with negative affect or anxiety showed positive correlation coefficients, and analyses with positive affect produced negative correlation coefficients. There were no reliable effects for the bias.

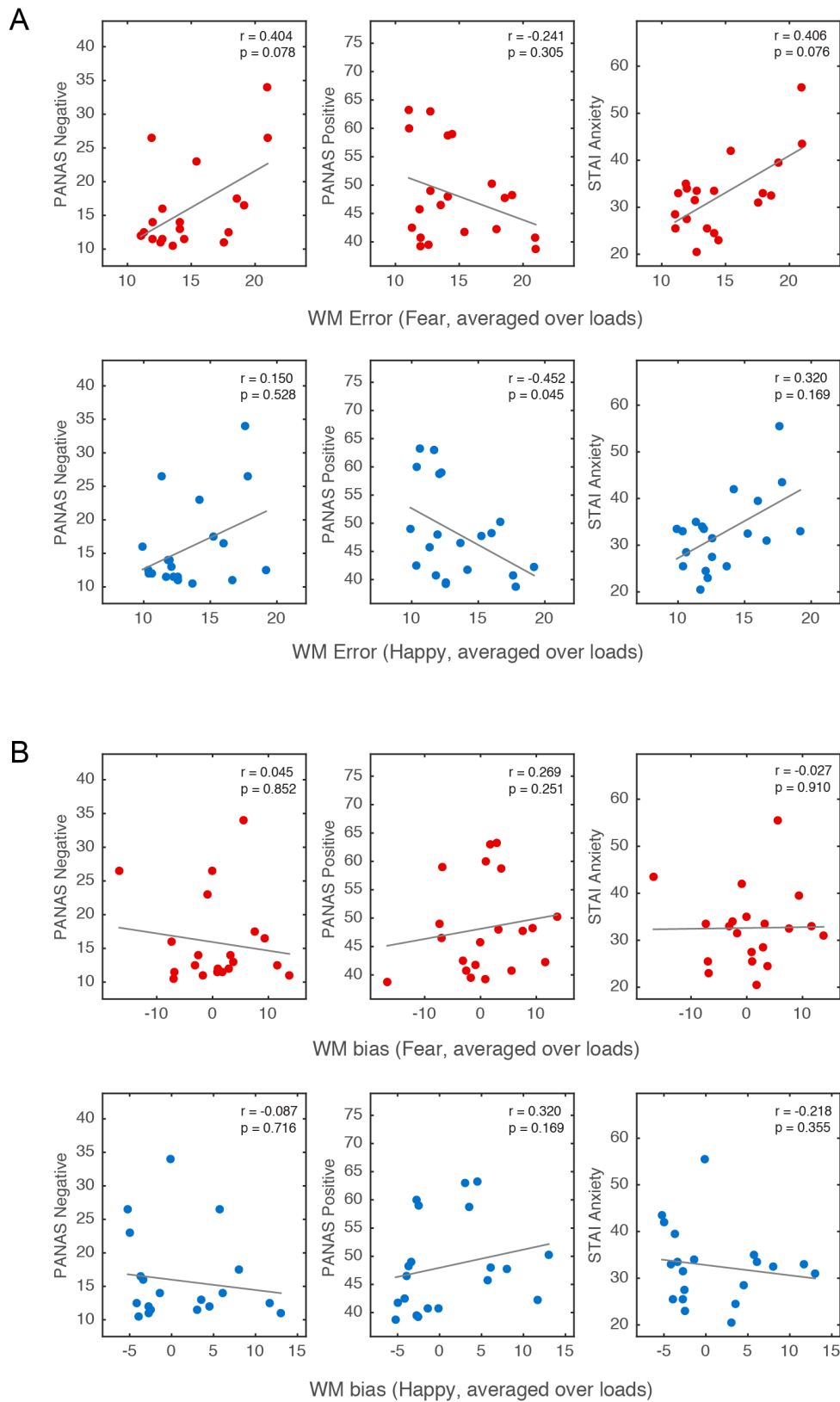


Figure 4.2.5. Correlations between mood/anxiety and WM performance. A) Scatter plots of composite mood measures as a function of WM error for fearful faces (top, red) and happy faces

(bottom, blue), averaged over load conditions and emotional intensities. X-axis is WM error averaged over load conditions, y-axis is the composite mood measure. B) Scatter plots of composite mood measures as a function of WM bias for fearful faces (top, red) and happy faces (bottom, blue), averaged over load conditions and emotional intensities. X-axis is WM bias averaged over load conditions, y-axis is the composite mood measure. In all plots, each point is an individual participant, and correlation values are Spearman's rank correlation coefficients.

Discussion

A new version of the emotional WM precision task using a free-recall response was successfully implemented. Participants were able to perform the task with high accuracy, showed reasonable distributions of WM error, and exhibited differences in performance for different emotion types and load conditions. It was possible to obtain two measures of performance to characterise WM for emotional content: error – memory recall accuracy – and bias – the emotional intensity to which the target faces were recalled from memory. The bias might be useful for investigating individual differences in representing emotional intensity in WM that are not be simply attributable to memory performance. Unexpectedly, participants reported the incorrect emotion type to that which was presented on a sizable number of trials. Finally, there was a hint of a relationship between WM performance for emotional content and mood and anxiety measures taken prior to the experimental session. Good performance tended to be positively correlated with self-reported positive mood and negatively correlated with negative mood and anxiety.

The new emotional WM precision task revealed several interesting findings in participant behaviour. Similar to Experiment 4A, WM accuracy for happy facial expressions was significantly higher than for fearful expressions. Unlike in the previous experiment, this benefit cannot be attributed to the distractibility of the test face. Response accuracy was higher in trials with one face compared to two faces, consistent with studies of visual WM using non-emotional stimuli. Participants also had a tendency to report emotional intensities as more emotionally intense in load-1 compared to load-2 trials. This raises the possibility

that the faces were actually recalled as more emotionally intense than they were initially perceived to be in the load-1 trials. Although the faces were not recalled as more intense than the objective value of the target face intensity (i.e. the bias was not significantly different from zero) in either of the conditions, the emotional intensity that the participants perceived at sample presentation was not examined. To determine whether participants recalled the faces as more emotionally intense than they perceived them to be, WM bias for emotional content could be compared with the bias in a perceptual version of the experiment.

Mood questionnaires were administered to assess the feasibility of linking individual differences in mood or anxiety with emotional WM performance. Based on previous research, I hypothesised that WM for emotional content might be modulated by mood states and traits (Mathews & MacLeod, 2005; Yiend, 2010). Since the sample size was too small for correlational analyses, the results are interpreted with great caution, and are only used to motivate the measures to be used and validated in subsequent experiments. There were several notable trends between the emotional WM precision task and measures of self-reported mood, which predominantly reflected worse performance with greater negative mood and better performance with greater positive mood. Overall, the behavioural measures in the current emotional WM task seems to pick up some aspects of general emotional processing abilities, reflected in the correspondence to various mood trait and state measures. However, the results also reflect worse cognitive performance with more negative mood. Further experiments should explore whether these effects are specific to emotional processing, baseline WM ability, perceptual abilities, or a combination of these factors. Finally, the sample size should be increased in future experiments to test for reliable relationships between individual-difference measures and WM performance for emotional content.

There were a surprising number of trials in which participants reported the incorrect emotion type – that is, reported seeing a happy face when the face was actually a fearful expression, and reporting a fearful face when it was actually a happy face. This type of response was possible because participants had to recall both the emotion type and intensity of the face at test. Participants may in fact be misinterpreting the valence of the emotion expression, especially for the more ambiguous, low intensity emotional expressions. They also were more likely to report happy faces as fearful than report fearful faces as happy. This is consistent with studies that have shown that neutral faces are interpreted negatively (Phillips et al., 1998), and so low intensity happy faces were more often judged to be negatively valenced. Although unexpected, this might be a useful measure for comparing between groups. For example, individuals who exhibit more positive mood might interpret happy faces with low emotional intensity as more positive than people who experience more negative mood traits. Older adults may also interpret faces as more positive relative to younger adults, which may affect their WM performance for emotional stimuli in general. Therefore, this measure will be used as an additional measure of WM for emotional content in addition to WM error and bias.

Overall, the modified emotional WM precision task was a success, with reasonable measures of WM accuracy (error), affective bias (bias), and emotion type misinterpretation. No major problematic issues surfaced, and the task therefore was judged to be suitable to be used to test WM for emotional content in healthy ageing. In the next section, I will present a perceptual version of the task, which can be used as a control task or as a separate measure of emotional processing.

Experiment 4C

In the previous section, I developed a task that provided good performance measures of WM for emotional content. Since all conditions in the experiment required memory maintenance,

it was not possible to determine if the effects of emotion type and intensity were specific to WM or related to emotional processing in general. Therefore, a perceptual matching task was also designed to test the ability to match emotional expressions without memory demands. In this experiment, two faces were simultaneously presented on the screen, and the participant adjusted one of the faces to match the emotional expression of the other face. The task provides a measure of perceptual processing of emotional expressions, so that it becomes possible to separate effects of perception versus WM for emotional information. The perceptual task can also be used to ensure, in future experiments, that individual differences in WM performance are not limited to differences in visual acuity – which is especially important when testing older adults.

Methods

Participants

The study was reviewed and approved by the Central University Research Ethics Committee of the University of Oxford. Ten adults (aged 19-41; mean: 26 ± 2.11) took part in this experiment. They provided written informed consent and were compensated 10 pounds for their time. None of the participants had been involved in the previous experiments.

Stimuli and Apparatus

The same set of face stimuli and computer apparatus were used as in Experiment 4B. The faces subtended $10^\circ \times 16.3^\circ$, and were presented at the left and right side of the fixation cross on the horizontal meridian (centred at $\sim 9.75^\circ$ in lateral visual angle from fixation). The fixation cross was a plus sign (“+”) subtending $\sim 1.5^\circ$ and placed at the centre of the screen.

Task Design and Procedure

The task tested the ability to perceptually judge and match emotional facial expressions (figure 4.3.1A).

In the main experiment, participants were presented with a target face on the left of the screen and adjusted the face on the right of the screen to match the emotion type and intensity of the target face. The right face was always presented with a neutral (0%) emotional intensity, and participants adjusted the expression of the face using a trackball mouse, scrolling left for one emotion and right for the other (counterbalanced across participants). As in the WM experiment, the target stimuli were happy or fearful faces with pseudo-randomly selected levels of emotions from intensity values of 0 to 100% in 1% steps. Emotion type conditions were intermixed within each block. Each trial began with a fixation cross at the centre of the screen (100 ms) after which two faces with the same identity appear on the left and right side of the screen. Participants adjusted the emotional expression of the right, neutral face to match the emotion type and intensity of the face on the left. The interval between trials, commencing after response termination, was 800 ms. After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of probe presentation. Participants could move their eyes freely during the whole trial.

Participants were given one or two practice blocks of the task (25 trials per block). Most participants only required one practise block. The practise task was exactly the same as the main experiment, except that the facial identities were selected from the practise face set.

In the experiment, each participant completed eight blocks of 50 or 51 trials, resulting in a total of 404 trials. For each emotion type (fearful, happy), an image from each emotion intensity level (0 to 100% in 1% steps) was presented four times. The facial identities were randomly allocated between emotion conditions and all identities were used in both emotion types. At the end of the session, participants were asked about their engagement with the task

and any strategies they used to perform the task. If asked, the experimenter provided an explanation of the experimental task and purpose. The testing session lasted approximately 40 minutes.

Data Analysis

The aim of this analysis was to characterise the ability to match emotional expressions without memory demands and to test if performance on these tasks is correlated with individual differences in mood or anxiety.

To characterise perceptual matching performance for emotional facial expressions, I computed performance error and bias in the same way as in the WM version of the task. As in the WM task, responses to the incorrect emotion type were excluded, the range of target emotional intensities was restricted from 21 – 80% in the analyses for error and bias, and emotional intensities were binned into five equal bins where bin 1 and bin 5 were excluded in the analyses for error and bias.

After excluding trials with neutral (0% intensity) targets, there were 400 trials (200 per emotion type), with 80 trials per emotional intensity bin (40 per emotion type). After removing misreported emotion trials, there were 192.1 ± 1.50 trials for the fearful face conditions and 189.1 ± 1.70 trials for the happy face conditions (out of 200 trials). Split into number of trials per emotional intensity bin, the mean (\pm S.E.M.) number of trials per bin were as follows: bin 1: 65.1 ± 1.59 , bin 2: 76.5 ± 0.78 , bin 3: 79.7 ± 0.21 , 79.9 ± 0.10 , bin 5, 80 ± 0.00).

To explore the differences in performance for emotion type and emotional intensity, a repeated-measures ANOVA was conducted on performance error for Emotion (fear, happy)

and Intensity of the target face (bins: low, medium, high). A repeated-measures ANOVA was also performed for the bias with the same factors. Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity when normality assumptions were violated.

To explore whether emotion type or intensity had an effect on misreporting the wrong emotion type, a repeated-measures ANOVA was conducted on the proportion of misreported responses with factors Emotion (fear, happy), Intensity (bins: 1, 2, 3, 4, 5).

Paired t-tests were used to test for the direction of the condition differences and one-sample t-tests were used to test for differences from zero. In order to test for the direction of linear effects with more than two conditions, I fit a line to each participant's data across conditions, and tested whether the slope of the line was larger or smaller than zero (one-sample t-test at the group level). Cohen's d was used to determine the effect sizes (Cohen, 1988).

Statistical analyses were conducted in Matlab R2015a, Matlab's Statistics Toolbox and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann et al., 2015).

Results

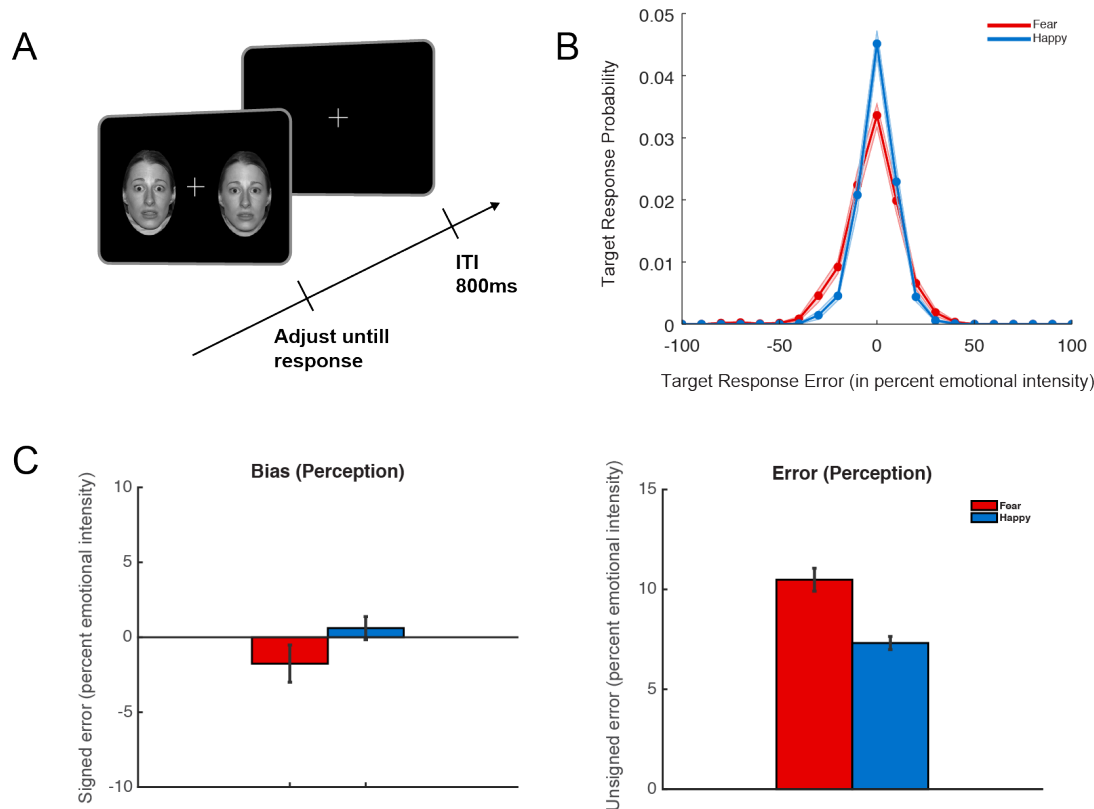


Figure 4.3.1. Task schematic and behavioural performance for perceptual matching of emotional expressions. A) Task schematic for emotional-expression matching. In each trial, participants were simultaneously presented with an emotional face on the left of the screen and a neutral face on the right. They adjusted the emotional expression of the neutral, right face to match the emotion type and intensity of the face on the left. There was no time limit. The inter-trial-interval was 800 ms. Participants made their response using a trackball mouse. Emotion type was intermixed within blocks. B) Error distributions for emotional-expression matching centred on the target face emotional intensity. The error probability is plotted at each bin and connected by the lines for fear (red) and happy (blue) WM conditions. The shaded areas show the standard error of the mean. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, y-axis is the response error probability. C) Bias (mean of the error distributions in B; left) and error (unsigned error of the distributions in B; right) for fear (red) and happy (blue).

Perceptual matching performance for fearful and happy facial expressions

Figure 4.3.1 summarises the perceptual task and the behavioural results at the group level. Participants were able to complete the task with high accuracy (mean error: 9.43% \pm 0.42) for both emotion types (fear: 11.18% \pm 0.60; happy: 7.69% \pm 0.36). Error distributions for single participants followed a Gaussian distribution (4.3.1B for group histograms; see Appendix figure S4.5 for individual participant response error histograms).

Participants mistakenly reported the wrong emotion type on only a minority of trials (proportion of happy faces reported fearful: 0.05 ± 0.01 , proportion of fearful faces reported happy: 0.04 ± 0.01). Similar to what was observed in the WM Experiment 4B, the likelihood of misreporting the emotion type was higher for target faces of low emotional intensity ($F(1.17,10.57) = 74.37$, $p = 2.61 \times 10^{-6}$; $\eta p^2 = 0.89$; mean slope: -0.04 ± 0.005 ; $t(19) = -8.61$, $p = 1.22 \times 10^{-5}$, effect size: -2.72). Unlike the previous Experiment 4B, there was no effect of Emotion-Type ($F(1,9) = 1.68$, $p = 0.23$, $\eta p^2 = 0.16$; figure 4.3.2A). Plotting emotional intensities of target faces as a function of participant responses (figure 4.3.2B) showed that most responses were centred on the target (grey identity line on the right of each scatter plot) but a small proportion of the trials were responses to the incorrect emotion type (responses to the left of zero on each plot) (see figure S4.6 for scatterplots of each participant).

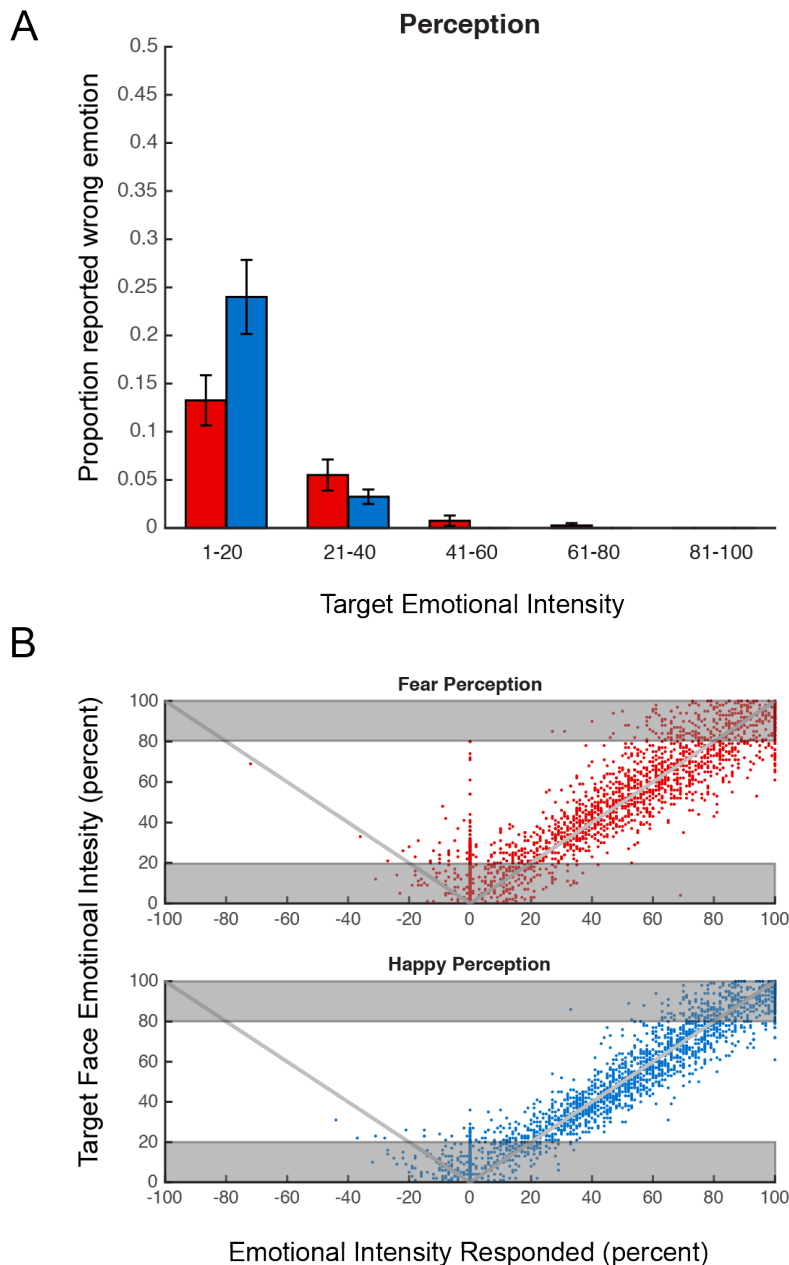


Figure 4.3.2. Proportion of trials in which participants misreported the emotion type for each Emotion and Intensity condition. A) Bar plot showing the proportion of misreported-emotion trials for each emotional intensity bin from 10% to 90% in 20% steps for fearful (red) and happy (blue) faces conditions. B) Scatterplots of target face emotional intensities plotted as a function of participant responses. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. Incorrect responses that reflect a 'mirrored' response (e.g. reported 50% fearful when it was a 50% happy face) would lie on a 'mirrored' version of the identity line ($y = -x$). Each point is an individual trial, and each scatter plot includes all the trials in the specified condition for all participants. The areas in grey are trials from 0% – 19% and 81% – 100% emotional intensity, which were removed from the main analyses.

To characterise the ability to match emotional expressions, I tested for the effect of Emotion-Type and Emotion-Intensity on the behavioural measures of error and bias. Similar to the WM Experiment 4B, there was a significant effect of Emotion-Type ($F(1,9) = 32.69$, $p = 0.0003$, $\eta p^2 = 0.78$) reflecting lower WM error for happy faces relative to fearful faces ($t(9) = -6.60$, $p = 0.0001$, effect size: -2.23; figure 4.3.1C, right). There was also a main effect of Intensity ($F(1.40,12.60) = 5.56$, $p = 0.03$, $\eta p^2 = 0.36$), reflecting higher error for low compared to medium intensities ($t(9) = 4.96$, $p = 0.0008$, effect size = 1.59) and high compared to medium intensities ($t(9) = -5.74$, $p = 0.0003$, effect size = -1.50), but no difference between low and high intensities ($t(9) = 1.47$, $p = 0.18$, effect size = 0.47; figure 4.3.3A).

Bias showed an effect of Emotion-Intensity ($F(1.68,15.15) = 12.48$, $p = 0.0009$, $\eta p^2 = 0.58$) reflecting more of a negative bias for low compared to medium intensities ($t(9) = -4.33$, $p = 0.002$, effect size: -1.36) and low compared to high intensities ($t(9) = -3.24$, $p = 0.01$, effect size: -0.88), but no difference between medium and high intensities ($t(9) = 1.73$, $p = 0.12$, effect size: 0.42). In contrast to the WM results, faces were reported as less emotionally intense than target face when they had low emotional intensity (one-sample t-test: $t(9) = -2.54$, $p = 0.03$, effect size: -0.80) but not in medium ($t(9) = 1.70$, $p = 0.12$, effect size: 0.54) or high intensities ($t(9) = 0.02$, $p = 0.98$, effect size: 0.01; figure 4.3.3B). As in the WM experiment, there was no effect involving Emotion-Type on bias ($F(1,9) = 3.55$, $p = 0.09$, $\eta p^2 = 0.28$).

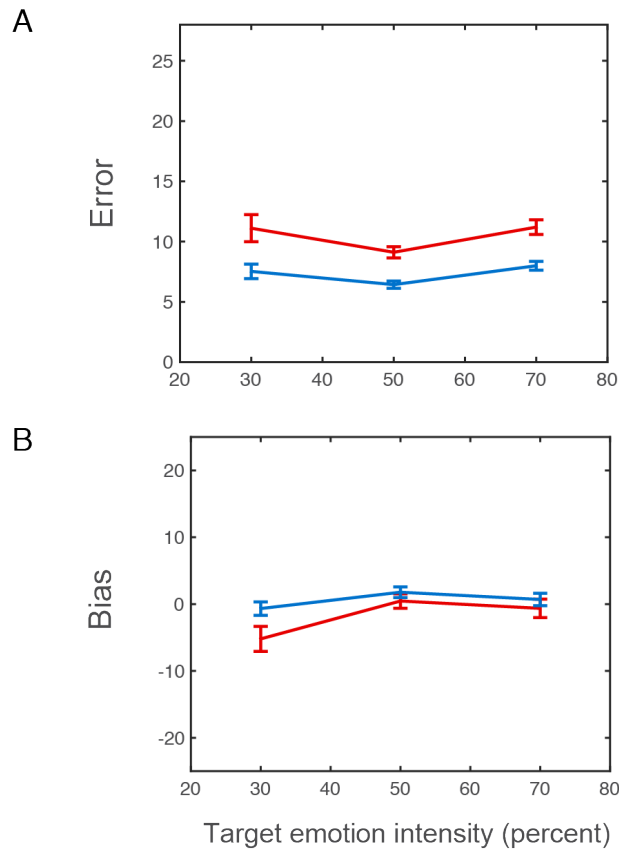


Figure 4.3.3. Effect of emotion type and emotional intensity on emotional-expression matching performance. A) Performance error (unsigned) plotted as a function of emotional intensity. B) Bias (signed error) plotted as a function of emotional intensity. In all plots, the x-axis is the target face emotional intensity binned from 30% to 70% in 20% steps, the y-axis is the behavioural measure.

Discussion

An emotional expression-matching task was designed and implemented as a perceptual counterpart to the emotional WM precision task. Participants were able to perform the task with high accuracy, showed reasonable distribution of error, and exhibited differences in performance for emotion type and intensities that were qualitatively similar to the WM task. Participants misreported the emotion type of the face, but only on a small fraction of trials.

Overall, the emotional expression-matching task produced reasonable measures of performance error and bias, and showed high performance in both emotion conditions. Similar to the WM task, participants performed better for happy faces compared with fearful faces. The present task was easier than the WM version of the task and therefore accuracy

was comparatively higher. In sum, the emotional expression-matching paradigm provided good measures of performance on participants' perceptual abilities to match emotional expressions, and will be a useful task to test and control for perceptual differences between conditions and individuals. In the next section, I will manipulate the WM maintenance interval duration to test for the optimal maintenance period for assessing emotional WM, and to increase between-participant variability with a view to increase the tasks' sensitivity to detect inter-individual differences in WM for emotional content.

Experiment 4D

The last two experiments showed that it is possible to measure WM and perceptual abilities for emotional material using free-recall response paradigms. This lays the foundation for testing the extent to which effects in emotional WM tasks reflect differences in perceptual functions during encoding of the stimuli. Participants could be asked to partake in both precision WM tasks and in perceptual matching involving emotional expressions, so that perceptual performance variables can be regressed out of WM effects. This approach will be followed in Chapter 5.

Another way to isolate emotional WM effects that specifically rely on mnemonic functions is to manipulate the duration of the maintenance period. In theory, the shorter the maintenance period, the more similar performance should be to perceptual matching, and the longer the maintenance period, the greater the reliance on memory. In the current experiment, I tested WM performance for emotional content over different WM maintenance periods.

To investigate how WM for emotional content changes over the maintenance period, participants performed the emotional WM precision task with array-test intervals of 500, 1500, and 3000 ms. I reduced the number of emotional intensity conditions to gain statistical

power. Similar results despite minor changes in the stimulus set would also provide reassurance about the robustness of the experimental approach, and enable flexible modifications to the task for testing different aspects of WM abilities for emotional content.

Methods

Participants

Twenty adults (aged 18-34; mean 22 ± 0.83) took part in this experiment. The study was approved by the Central University Research Ethics Committee of the University of Oxford. All participants provided written informed consent and were compensated for their time and travel expenses. They provided written informed consent and were compensated 20 pounds for their time. None of the volunteers had participated in the previous experiment.

Stimuli

The same apparatus and set of face stimuli were used as in Experiment 4B. To reduce the number of intensity value conditions, half the intensities conditions were used and the 50% condition was taken out. Specifically, the set of face stimuli included emotional expressions with intensities from 0% to 48% in 2% steps, and 52% to 100% in 2% steps, resulting in 1,584 unique stimuli in total.

All participants were asked to complete eight self-report questionnaires measuring state and trait anxiety (State-Trait Anxiety Inventory, STAI; Spielberger, 1983) and positive and negative affective states and traits (Positive and Negative Affect Scale: PANAS negative trait and state, positive trait and state, positive trait 21 and state 21; Watson et al., 1988). Qualtrics (Qualtrics, Provo, UT) was used to deliver the surveys and summarise results.

Task Design

The experiment tested the ability to remember faces with emotional expressions in WM over different memory maintenance periods (figure 4.4.1A).

On each trial, participants encoded a face into memory and were subsequently prompted to retrieve its emotional expression at the end of the trial. Stimuli were happy or fearful faces with pseudo-randomly selected levels of emotions from intensity values of 0% to 49% and 52% to 100% in 2% steps. The WM maintenance duration was blocked, lasting 500 ms, 1500 ms, or 3000 ms.

Each trial began with a fixation cross at the centre of the screen (100 ms) after which a face stimulus (350 ms) and its scrambled mask (80 ms) were presented. After a delay of 500 ms, 1500 ms, or 3000 ms, a probe face with the same identity was presented with a neutral (0%) expression. Participants adjusted the expression of the test face to match the remembered emotion type and intensity using a trackball mouse, scrolling left for one emotion and right for the other emotion (happy and fear; counterbalanced across participants).

In the main experiment, each participant completed 12 blocks of 50 trials, resulting in a total of 600 trials. The order of the delay-duration blocks was randomised across participants. For each emotion type (fear, happy), an image from each emotion intensity level (was presented two times for each delay condition (short, medium, long). There were 200 trials for each delay condition, with 100 trials per emotion type. The facial identities were randomly allocated between emotion conditions and all identities were used in both emotion types. At the end of the session, participants were asked about their engagement with the task and about their

performance strategies. The experimenter explained the task and its purpose when asked. The testing session lasted approximately 75 minutes.

Data Analysis

The aim of this analysis was to characterise the ability to retain stimuli with emotional content over different WM maintenance periods.

To characterise WM performance for emotional facial expressions, I computed performance error and bias in the same way as for Experiment 4B. As before, responses to the incorrect emotion type were excluded, the range of target emotional intensities was restricted from 20 – 80% in the analyses for error and bias, and emotional intensities were binned into five equal bins where bin 1 and bin 5 were excluded in the analyses for error and bias.

After excluding trial with neutral target faces (0% intensity), there were 196 trials per delay condition (98 per emotion type), within which there were 40 trials (36 for intensity bin 1, which included 0% intensity) per emotional intensity bin (20 per emotion type, 18 for intensity bin 1). After removing misreported emotion trials, there were 279.8 ± 1.60 trials for the fearful face conditions and 260.5 ± 3.42 trials for the happy face conditions (out of 294 trials). Split into number of trials per emotional intensity bin, the mean (\pm S.E.M.) number of trials per bin were as follows: bin 1: 35.85 ± 1.84 , bin 2: 47.55 ± 1.58 , bin 3: 57.50 ± 0.63 , bin 4, 58.20 ± 0.47 , bin 5: 59.15 ± 0.27 (note that bin 1 has a total of 54 trials and others have a total of 60 trials).

To explore the differences in performance for emotion type, emotional intensity, and the effect of maintenance delay, a repeated-measures ANOVA was conducted on performance error for Emotion (fear, happy), Intensity of the target face (bins: low, medium, high), and

Delay (short, medium, long). A repeated-measures ANOVA was also performed for the bias with the same factors. Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity when normality assumptions were violated.

To explore whether emotion type, intensity and delay had an effect on misreporting the wrong emotion type (e.g. recalled a 25% fearful but it was in fact a 25% happy face), a repeated-measures ANOVA was conducted on the proportion of misreported responses with factors Emotion (fear, happy), Intensity (bins: 1, 2, 3, 4, 5), and delay (short, medium, long).

Paired t-tests were used to test for the direction of the condition differences and one-sample t-tests were used to test for differences from zero. In order to test for the direction of linear effects with more than two conditions, I fit a line to each participant's data across conditions, and tested whether the slope of the line was larger or smaller than zero (one-sample t-test at the group level). Independent samples t-tests were used to test for performance and mood differences between experiments. Cohen's d was used to determine the effect sizes (Cohen, 1988).

Spearman's rank correlations were used to test the relationship between performance (error and bias scores separately, averaged over delay conditions and intensities) and self-reported mood measures. As before, three composite measures were computed for each participant: negative affect (mean of PANAS negative state and trait), positive affect (mean of PANAS positive state, positive state 21, positive trait, and positive trait 21) and anxiety (mean of STAI state and trait).

Statistical analyses were conducted in Matlab R2015a, Matlab's Statistics Toolbox and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann et al., 2015).

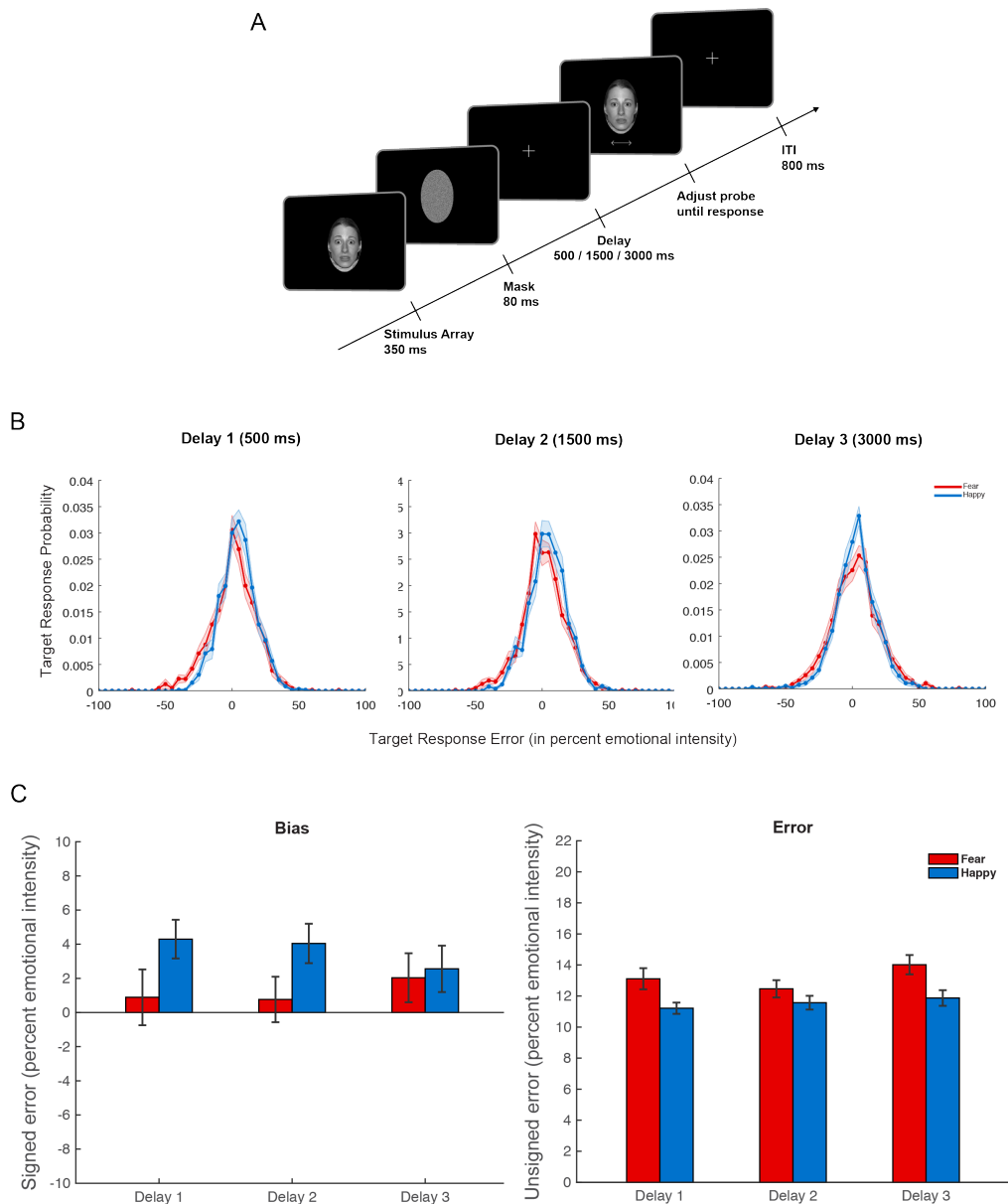


Figure 4.4.1. Task schematic and behavioural performance for emotional WM for different memory maintenance durations. *A*) Task schematic for emotional WM. In each trial, participants encoded a facial expression into WM. After a short (500 ms) medium (1500 ms) or long (3000 ms) memory maintenance period, a test face appeared with the same facial identity but a neutral facial expression (0% emotional intensity). Participants made their response by changing the face to match the emotional expression in memory using a trackball mouse. Delay conditions were performed in separate blocks, whereas emotion type was intermixed within blocks. *B*) Error distributions for emotional WM centred on the target face emotional intensity for each of the memory delay conditions. The error probability is plot at each bin and connected by the lines for fear (red) and happy (blue) WM conditions. The shaded areas show the standard error of the mean. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, y-axis is the response error probability. *C*) Bias (mean of the error distributions in *B*; left) and error (unsigned error of the distributions in *B*; right) for fear (red) and happy (blue) for each memory maintenance duration condition.

Results

Figure 4.4.1 summarises the task and the behavioural results at the group level. Participants were able to complete the task with high accuracy (mean error: 12.40% \pm 0.35) in both emotion types (fear: 13.21% \pm 0.55; happy: 11.55% \pm 0.35) and delay conditions (short: 12.17% \pm 0.42, medium: 12.03% \pm 0.38, long: 12.99% \pm 0.43). Error distributions for single participants were Gaussian in nature (4.4.1B for group histograms).

Just like in the previous free-recall WM experiment, participants mistakenly reported the wrong emotion type on a sizable proportion of trials (proportion of happy faces reported fearful: 0.11 \pm 0.01, proportion of fearful faces reported happy: 0.05 \pm 0.01). The effect was accentuated at lower emotional intensities ($F(1.84,34.96) = 195.13$, $p = 3.11 \times 10^{-19}$; $\eta p^2 = 0.91$; mean slope: -0.06 ± 0.004 ; $t(19) = -16.15$, $p = 1.49 \times 10^{-12}$, effect size: -3.61). There was an effect of Emotion-Type ($F(1,19) = 30.89$, $p = 2.32 \times 10^{-5}$, $\eta p^2 = 0.16$; happy versus fear: $t(19) = 5.47$, $p = 2.83 \times 10^{-5}$, effect size: 1.62) and an interaction between Emotion-Type and Emotion-Intensity ($F(1.23,23.40) = 36.33$, $p = 1.13 \times 10^{-6}$, $\eta p^2 = 0.66$), reflecting a stronger effect of intensity in the happy compared to fearful conditions (mean difference in slope: -0.06 ± 0.01 ; $t(19) = -6.18$, $p = 6.15 \times 10^{-6}$, effect size: -2.12 ; see figure 4.4.2A). The probability for the emotion type being misreported was not modulated by the delay ($F(1.73,32.95) = 0.17$, $p = 0.82$, $\eta p^2 = 0.01$). Plotting target face intensities as a function of participant responses (figure 4.4.2B) showed that most responses were centred on the target (grey identity line on the right of each scatter plot), but a small proportion of the trials were responses to the incorrect emotion type (responses to the left of zero on each plot). All participants misreported the incorrect emotion type on a small proportion of trials.

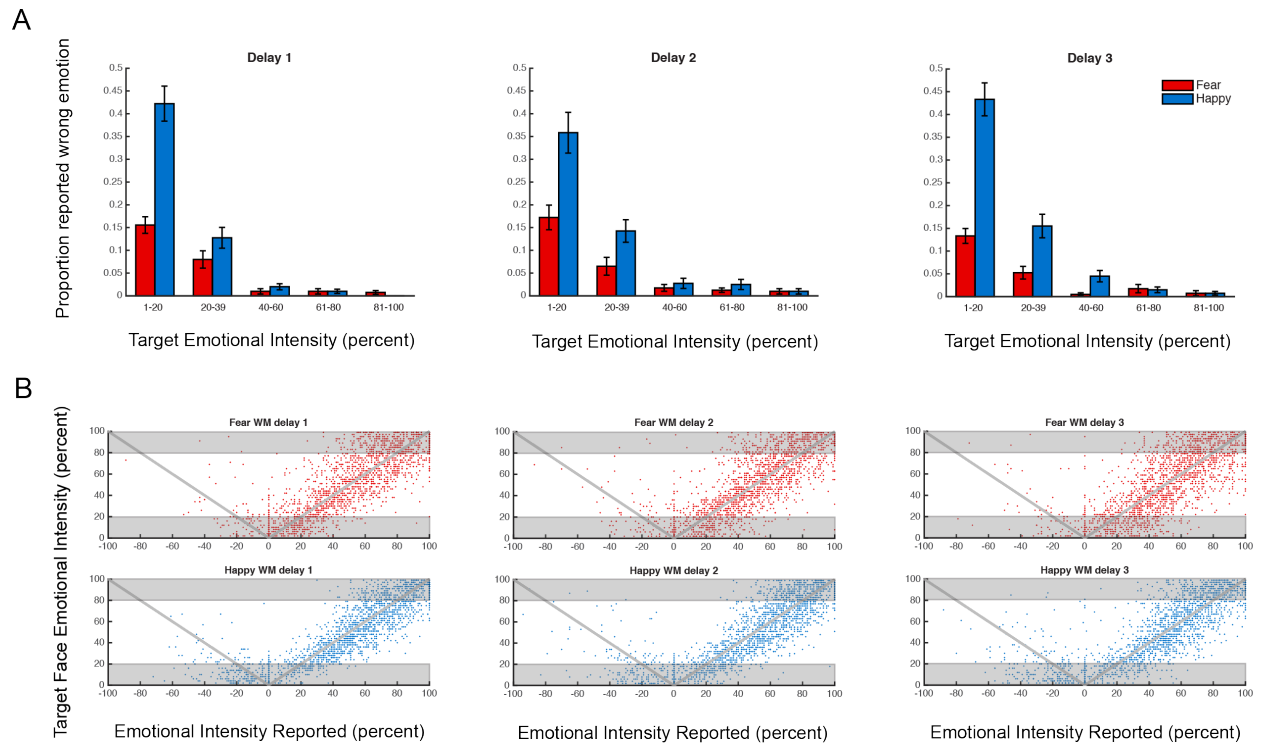


Figure 4.4.2 Proportion of trials where participants misreported the emotion type for each Emotion and Intensity value condition. A) Bar plots showing the proportion of misreported-emotion trials for each emotional intensity bin from 10% to 90% in 20% steps for fearful (red) and happy (blue) faces for the short (left; 500 ms), medium (middle; 1500 ms) and long (right; 3000 ms) delay conditions. B) Scatterplots of target face emotional intensities plotted as a function of participant responses. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. A 'mirrored' version of the identity line ($y = -x$) is plot on the left side for reference. Each point is an individual trial, and each scatter plot includes all the trials in the specified condition for all participants. The areas in grey are trials from 0% – 19% and 81% – 100% emotional intensity, which were removed from the main analyses.

To explore WM abilities for emotional content over different WM maintenance durations, I tested for the effect of Emotion-Type, Emotion-Intensity and Delay on WM error and bias. There was a significant effect of Delay duration on WM error ($F(1.93,36.76) = 3.93$, $p = 0.03$, $\eta^2 = 0.17$; figure 4.4.1C, right) reflecting a detriment in performance for the longest WM maintenance duration (short versus long: $t(19) = -2.37$, $p = 0.028$, effect size: -0.43; medium versus long: $t(19) = -2.48$, $p = 0.023$, effect size: -0.53; short versus medium: $t(19) = 0.41$, $p = 0.68$, effect size: 0.08). There was also a significant effect of Emotion-Type ($F(1,19) = 7.23$, $p = 0.01$, $\eta^2 = 0.28$) reflecting lower WM error for happy faces relative to fearful faces

($t(19) = -2.80$, $p = 0.01$, effect size: -0.81 ; figure 4.4.1C, right). In contrast to the previous WM task, there was no effect of Intensity ($F(1.33,25.20) = 0.61$, $p = 0.48$, $\eta p^2 = 0.03$). There was a significant interaction between Emotion-Type and Emotion-Intensity ($F(1.66,31.58) = 7.26$, $p = 0.004$, $\eta p^2 = 0.28$), reflecting a differential modulation of error by intensity in the fear compared to happy conditions (mean slope difference: 1.36 ± 0.43 , $t(19) = 3.16$, $p = 0.005$, effect size: 0.65), with a trend for worse performance with greater intensity in the fearful faces conditions (mean slope: 0.93 ± 0.53 ; $t(19) = 1.77$, $p = 0.09$, effect size: 0.40) but not in happy conditions (mean slope: -0.43 ± 0.40 ; $t(19) = -1.07$, $p = 0.30$, effect size: -0.24 ; figure 4.4.3A).

Bias was affected by Emotion-Intensity ($F(1.23,23.39) = 70.49$, $p = 3.87 \times 10^{-9}$, $\eta p^2 = 0.79$), with a greater positive bias for low versus high intensities ($t(19) = 8.32$, $p = 9.38 \times 10^{-8}$, effect size: 1.51), medium versus high intensities ($t(19) = 15.15$, $p = 4.63 \times 10^{-12}$, effect size: 1.24), but not low versus medium intensities ($t(19) = 1.65$, $p = 0.12$, effect size: 0.22 ; figure 4.4.3B) – consistent with the previous WM Experiment 4B. There was an effect of Emotion-Type ($F(1,19) = 7.07$, $p = 0.02$, $\eta p^2 = 0.27$), reflecting a larger positive bias in happy ($t(19) = 3.32$, $p = 0.004$, effect size: 0.74) compared to fearful conditions ($t(19) = 0.90$, $p = 0.38$, effect size: 0.2 ; difference between conditions: $t(19) = 2.50$, $p = 0.02$, effect size: 0.43). There was no effect of Delay ($F(1.83,34.83) = 0.04$, $p = 0.96$, $\eta p^2 = 0.002$), but there was a significant interaction between Emotion-Type and Delay ($F(1.72,32.63) = 5.87$, $p = 0.009$, $\eta p^2 = 0.24$) due to a positive bias in happy conditions for the short and medium delays but not in the long delay conditions (short, medium, and long delays: $t(19) = 3.80$; $t(19) = 3.50$; $t(19) = 1.88$], $p = 0.001$; $p = 0.002$; $p = 0.075$, effect sizes: 0.85 ; 0.78 ; 0.42) but no bias in the fearful conditions ($t(19) = 0.55$; $t(19) = 0.58$; $t(19) = 1.42$], $p = 0.59$; $p = 0.57$; $p = 0.17$], effect sizes: 0.12 ; 0.13 ; 0.32 ; difference between emotion-type conditions: $t(19) = 3.10$; $t(19) = 3.12$; $t(19) = 0.47$, $p = 0.006$; $p = 0.006$; $p = 0.64$], effect sizes: 0.54 ; 0.60 ; 0.08). There was an interaction between

Emotion-Intensity and Delay $F(2.82, 53.53) = 8.81$, $p = 0.001$, $\eta p^2 = 0.32$), which reflected several differences between emotion types in the three delay conditions. First, there was a positive bias in the low and medium intensities but not in the high intensities in the short delay (low, medium, high intensities: $t(19) = 3.87$; $t(19) = 2.74$; $t(19) = -0.61$, $p = 0.001$; $p = 0.013$; $p = 0.55$], effect size: 0.87; 0.61; -0.14) and medium delay conditions ($t(19) = 4.52$; $t(19) = 3.83$; $t(19) = -1.28$], $p = 0.0002$; $p = 0.001$; $p = 0.22$], effect size: 1.01; 0.86; -0.29; difference between conditions: p 's > 0.39), but there was also a negative bias for the high intensities for the long delay condition ($t(19) = 5.16$; $t(19) = 3.85$; $t(19) = -3.28$], $p = 0.0001$; $p = 0.001$; $p = 0.004$], effect size: 1.15; 0.86; -0.73). Furthermore, the low intensities were more positively biased in the long versus the medium delay conditions ($t(19) = 2.48$, $p = 0.023$, effect size: 0.40) with a similar trend when compared to the short delays ($t(19) = 2.05$, $p = 0.055$, effect size: 0.37), whereas the high intensities were more negatively biased compared to the medium ($t(19) = -2.60$, $p = 0.017$, effect size: -0.43) and the short ($t(19) = -2.80$, $p = 0.01$, effect size: -0.58) delay conditions (comparisons between medium intensity conditions p 's > 0.38).

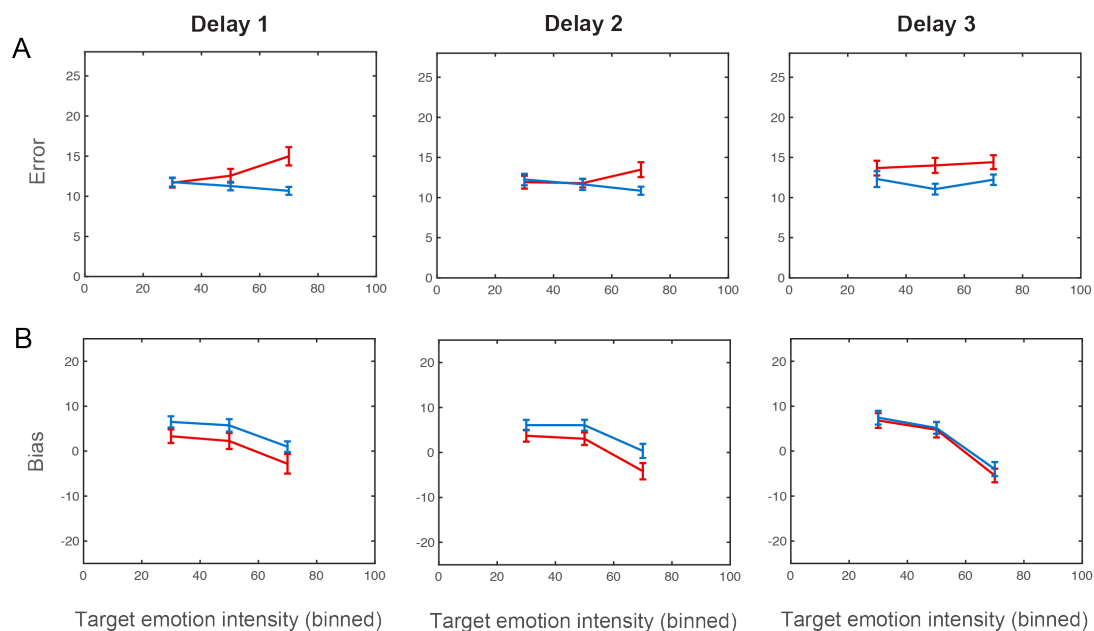


Figure 4.4.3. Effect of emotion type and emotional intensity on emotional WM performance for the short (500 ms, left), medium (1500 ms, middle), and long (3000 ms, right) memory maintenance durations. A) WM error (unsigned) plotted as a function of emotional intensity. B) WM bias (signed)

error) plotted as a function of emotional intensity. In all plots, the x-axis is the target face emotional intensity binned from 30% to 70% in 20% steps, the y-axis is the behavioural measure.

Correlations between emotional WM performance and mood

I tested for correlations between behavioural and mood/anxiety measures (see figure 4.4.4. for distributions of mood scores). There was a relatively good distribution of mood scores for positive affect (mean: 44.63 ± 2.15 ; range: 25.50 – 58.25) and anxiety (mean: 34.38 ± 1.78 ; range: 20.5 – 52.0) but less of a range for negative affect (mean: 15.07 ± 0.64 ; range: 11 – 21).

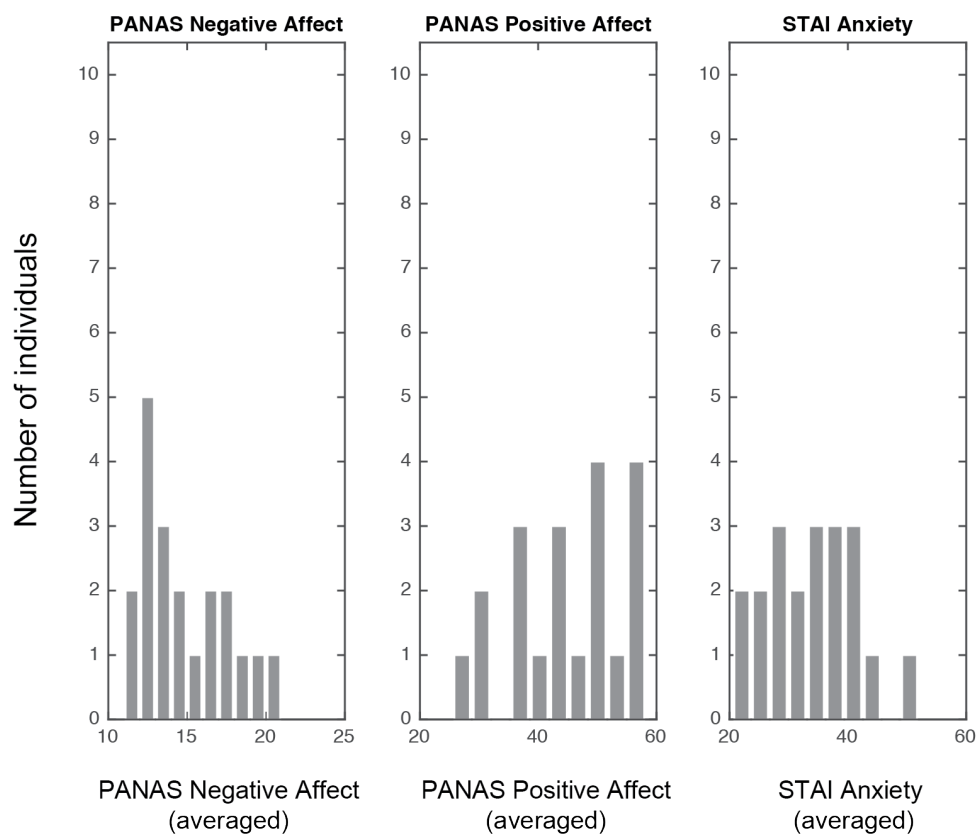


Figure 4.4.4. Distributions of mood and anxiety scores over participants. Histograms showing the distribution of mood scores for negative affect (left), positive affect (middle) and anxiety (right). X-axis is the mood measure, y-axis is the number of individuals.

The results from the correlational analyses between WM error and mood were consistent with the experiment 4B, where high negative mood or anxiety was positively correlated with

WM error, and positive mood was associated with lower error (figure 4.4.5). Notably, negative affect and anxiety showed a trend to correlate positively with WM error for happy faces ($r = 0.44$, $p = 0.053$; $r = 0.40$, $p = 0.077$), and positive affect was negatively correlated with WM error for happy faces ($r = -0.52$, $p = 0.019$).

In contrast to experiment 4B, there were some notable correlations of WM bias with mood and anxiety measures, where greater negative affect and anxiety was positively correlated with WM bias, and greater positive affect was negatively correlated with bias. There was a trend for a negative correlation between WM bias for fearful faces and positive affect ($r = -0.43$, $p = 0.057$) and a positive correlation with anxiety ($r = 0.54$, $p = 0.014$). There was a hint of an association between WM bias for happy faces with negative affect ($r = 0.43$, $p = 0.051$) and anxiety ($r = 0.50$, $p = 0.025$), with a weak trend for a negative correlation with positive affect ($r = -0.36$, $p = 0.12$). This suggests that individuals with more negative affect or anxiety show an exaggerated representation of emotional intensity in WM, regardless of valence.

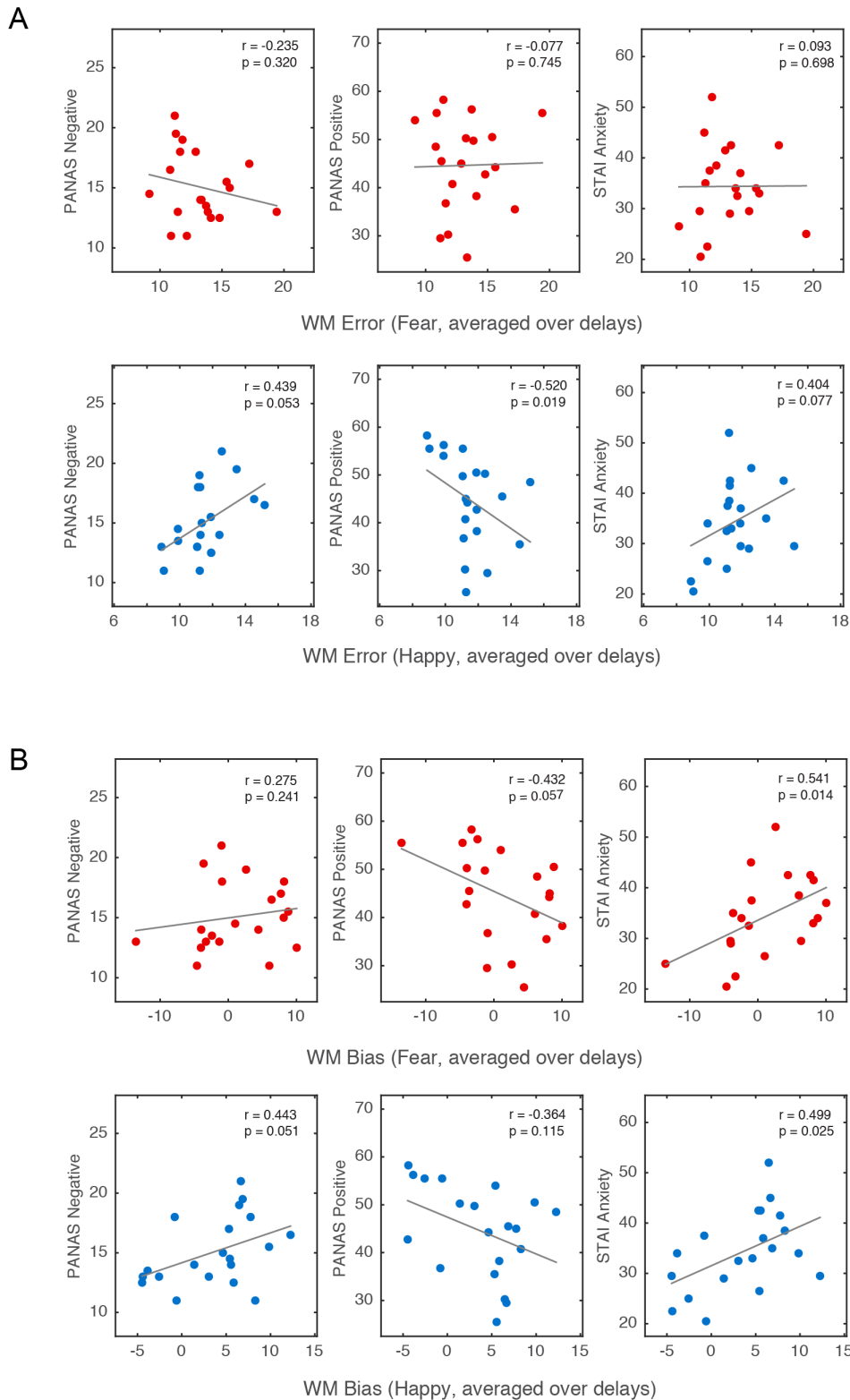


Figure 4.4.5. Correlations between mood/anxiety WM performance. *A*) Scatter plots of composite mood measures as a function of WM error for fearful faces (top, red) and happy faces (bottom, blue), averaged over delay conditions and emotional intensities. X-axis is WM error averaged over delay conditions, y-axis is the composite mood measure. *B*) Scatter plots of composite mood measures as a function of WM bias for fearful faces (top, red) and happy faces (bottom, blue), averaged over delay conditions and emotional intensities. X-axis is WM bias averaged over delay conditions, y-axis is

the composite mood measure. In all plots, each point is an individual participant, and correlation values are Spearman's rank correlation coefficients.

Discussion

I characterised WM performance for emotional content over different WM maintenance durations. Participants were able to perform the task with high accuracy on all delay duration conditions, showed reasonable distributions of WM error, and exhibited differences in performance for the different delay conditions. There were a considerable number of trials where participants reported the incorrect emotion type to that which was tested, but this was not modulated by the memory maintenance duration. Similar to the last WM experiment, performance error was positively correlated with positive mood and negatively correlated with negative mood. This experiment revealed that individuals with more negative affect and anxiety tended to report both happy and fearful faces to be more emotionally intense.

There was a decrement in WM performance with the longest WM maintenance duration compared with the short and the medium maintenance durations, similar to what has been observed in visual WM experiments with non-emotional content (e.g. Cornelissen & Greenlee, 2000; B. Lee & Harris, 1996; W. Zhang & Luck, 2009).

WM bias was more positive for low and medium intensities compared to high intensities, and with relatively similar patterns across delays – consistent with the results in experiment 4B. There were, however, some differences in the bias for different emotional intensities over delay conditions. The bias in the long delay condition was more positive in the low emotional intensities compared with the short and medium delays, whereas it was more negative for the high emotional intensities. This suggests that the emotional intensity of a facial expression is modulated by the amount of time it is stored in WM. This raises the intriguing possibility that this effect is how emotional content changes and is maintained in higher-level memory

stores. This representation, having kept in mind for longer, may be more likely to interact with the individual's emotional state and personality, leading to a slightly different representation of the emotional content in memory compared to that in veridical perception. In the next Chapter, I will test a larger group of participants in order to test whether there is a genuine difference between emotion types for WM bias.

The probability that participants mistakenly reported the emotion type was not modulated by the delay duration. In Experiment 4B, the participants were more likely to misreport the incorrect emotion in load-2 relative to load-1 trials, which indicated that, with greater cognitive load, participants were more likely to misreport the emotion type. However, extending the duration of the memory maintenance period did not increase this type of response, which suggests that the increase in misreporting the incorrect emotion type in load-2 trials might be due to retrieval-related confusion when participants had more than one face in mind. Since misreporting the incorrect emotion type did not increase or interact with delay, the main effects of Emotion-Type and Intensity might be related to perceptual aspects of the stimuli, which increases with memory load (since the effects are less pronounced in the perceptual matching task in 4.3), but does not scale with the duration that one has to hold the item in mind.

WM error was correlated with mood measures in a qualitatively similar way to the previous tasks – better performance was associated with more positive mood or lower anxiety scores. However, the correlations with mood were stronger with the happy face WM conditions and weaker with the fearful face conditions, whereas it was the opposite in the previous two experiments. Visually comparing the two sets of correlation plots suggests that it is likely to be an issue of statistical power where the correlations exist and are the same for both facial

expression conditions, since there were a small number of participants in all three studies. In contrast to the previous experiments, there was a significant association between mood and bias – the extent to which participants recalled emotional intensities as more or less emotionally intense than they were presented. Specifically, the more negative affect or anxiety participants reported to experience, the more emotionally intense they reported the faces to be, and the more positive affect they reported to experience, the less emotionally intense they reported the faces to be (irrespective of emotion type). This effect cannot be attributed to motivational factors, where individuals with more negative affect are less motivated in performing the task, since they report intensities as *greater* than participants with more positive affect, which requires the participant to scroll the trackball further along to intensity scale (more effort) to reach their response. The effect is also unlikely due to general performance (error), since the participants who experience more negative affect or anxiety report faces to be more emotionally intense than the face presented (greater than zero) whereas the more positive participants seemed to underreport the emotional intensity (less than zero; see figure 4.4.5B). If it was just related to performance (error), I would expect individuals with greater positive affect to lie around zero, and individuals with more negative affect to be negatively or positively biased. This suggests that participants actually remembered the faces as more or less emotional content than the encoded stimulus depending on their affective traits.

Overall, I obtained reliable measures of WM performance for emotional content over different memory maintenance durations. Similar to WM for neutral objects, WM for emotional content is impaired with longer maintenance durations. Performance on the short and medium delay durations were similar, whereas the long delay duration condition was significantly worse, suggesting that the longest delay duration placed greater demands on memory. I found correlations between mood/anxiety and WM error similar to the previous

experiments, but also found that the more negative affect or anxious traits participants had, the more emotionally intense they recalled the emotional faces to be. In conclusion, the current results confirm that the task can effectively characterise WM abilities for emotional content, and with the aim of characterising genuine WM maintenance abilities in future experiments, I will use the longer memory maintenance periods that will be most sensitive to mnemonic functions.

Chapter Discussion

In this chapter, I developed an emotional WM precision task in order to characterise WM abilities for emotional content. I shall use this task to investigate emotional WM in healthy ageing, but the task should also prove highly informative for comparing emotional WM in groups that differ in mood. The first emotional WM paradigm (4.1) produced a reasonable characterisation of behavioural performance in a WM task, but also encouraged response biases and cognitive strategies that may have interfered with measuring effects specifically linked to WM abilities for emotional content. Based on the lessons of Experiment 4A, I developed a modified emotional WM paradigm (4.2) in which participants use a continuous response mode to reproduce the type and intensity of the remembered facial emotional expression. The free-recall task (Experiments 4B and 4D) consistently revealed sensitive measures of the quality of emotional WM in young healthy participants, and provided a means to investigate how different task demands such as memory load (Experiment 4B) and memory delay (Experiment 4D) influence emotional WM. Although there were only a modest number of participants per experiment, preliminary exploratory correlation analyses suggested that inter-individual differences in emotional WM performance were, to an extent, associated with self-reported mood and anxiety measures.

My aim in developing this experimental task was to be able to characterise WM abilities for emotional content in young and older adults and to test how these abilities change with age. There were some minor differences in the performance bias between experiments, which could reflect genuine differences related to task manipulations across the experiments. In general, the task was relatively impervious to minor changes in the task parameters, suggesting it should not matter too much which task I use to assess emotional WM in healthy ageing. Therefore, I selected the simple load-1 version of the task to avoid any complicating issues related to interactions between memorised stimuli or confusion about which stimulus to report, and combined this with the longest practical delay period (3000 ms), in order to emphasise reliance on mnemonic functions. In order to control for individual differences in visual acuity, I will include the perceptual emotional expression-matching task (Experiment 4) as well as a non-emotional perceptual matching task (using the oriented stimuli from Chapter 2) in separate tasks. To control for individual differences in non-emotional visual WM maintenance abilities, I will also include a separate non-emotional visual WM task (using the oriented stimuli from Chapter 2).

The emotional WM precision task has shown reliable results across several experiments, and can start revealing consequences of different memory parameters such as WM load and maintenance duration. Now I will use this paradigm to investigate age-related differences and individual differences in emotional processing in a large cohort. In the next Chapter, I will test the emotional WM task with one face (load-1) and a memory maintenance period of 3000 ms in a large group of healthy young and older adults. In addition to this, I will test them on the emotional expression-matching task, a visual WM task and a visual matching task. In the visual WM task, there will be one memory stimulus and a memory maintenance period of 3000 ms, and in the visual matching task, participants will match the orientation of the stimulus on the screen to a target stimulus' orientation.

5. Emotional working memory: Individual differences in emotional and non-emotional working memory in younger and older adults

Chapter abstract

Using a new emotional WM task developed in the previous chapter, I tested for age-related changes in performance in WM and perception for emotional faces in a large sample of younger and older adults (N = 101). Older adults exhibited a general deficit in both emotional WM and perceptual matching performance. WM accuracy was no worse than perceptual abilities for emotional content in older adults. Older adults showed a slight tendency to report fearful faces as less fearful than younger adults (reduced negative bias), and were more likely to mistakenly report fearful faces as happy faces (positive interpretation bias), especially for faces with low emotional intensities. This suggests that older adults exhibit a reduced negative bias for processing negative stimuli compared to younger adults, and show a positive interpretation bias for ambiguous stimuli, interpreting slightly negative or ambiguous affective stimuli as positively valenced. There was a slight correlation between WM accuracy for happy faces and a measure of depression (Beck's Depression Inventory), where the higher the depression scores, the worse individuals were at maintaining happy faces in WM. Overall, these findings suggest that emotional processing experience significant changes in healthy ageing, and provides support to the theory that older adults show a general positive bias in cognitive processing (Mather & Carstensen, 2005). The findings also highlight the importance of the different types of biases that can be observed depending on the task and response measure. In this respect, future studies should more clearly define the affective biases that are hypothesised and observed in order to chart the changes in emotional processing in ageing more precisely.

Introduction

Emotional stimuli carry important signals about potentially dangerous or rewarding events and are often prioritised in perception (LeDoux, 2003; Vuilleumier & Driver, 2007). Emotional material has priority over other stimuli for both young (e.g. Lipp & Derakshan, 2005; Öhman, Flykt, et al., 2001; Phelps et al., 2006; Pourtois et al., 2004) and older adults (e.g. Mather & Knight, 2006; Rösler et al., 2005), but only a handful of studies have looked at whether there is a similar prioritisation of emotional content for WM.

Some studies have found a WM benefit for negative (threatening) stimuli in young adults (Jackson et al., 2014, 2008, 2009; Mikels et al., 2008), consistent with previous work showing attention effects for threat- and fear-related stimuli in young adults (e.g. Öhman, Flykt, et al., 2001; Phelps et al., 2006). More recently, researchers have found an apparently specific benefit of WM for emotional information in older adults (D'Argembeau & van der Linden, 2004; Hartley et al., 2013; Mammarella et al., 2013; Mikels et al., 2005), in which they were unimpaired for the short-term retention of emotional stimuli relative to young adults, but significantly impaired for non-emotional visual or verbal stimuli (as would be expected in normal healthy older adults; see Introduction in Chapter 4.1 for discussion of these studies).

Some researchers have proposed that older adults exhibit a 'positivity' bias (e.g. Carstensen & Mikels, 2005; Charles et al., 2003; Mather & Carstensen, 2005), in contrast to the 'negativity bias' in young (Rozin & Royzman, 2001; also see Baumeister et al., 2001; Cacioppo & Berntson, 1994; Cacioppo et al., 1997, 1999). Although this theory has enjoyed some success, studies have produced mixed results (see Murphy & Isaacowitz, 2008 for a meta-analysis on the positivity effect in ageing). For example, Charles et al. (2003) found that older adults showed a reduction in the number of negative images that were recalled in a memory task, suggesting a reduced negative bias but not a positive bias for memory. In a dot-probe task,

older adults exhibited a bias away from negative faces, whereas there was no significant attentional bias in the young adults (Mather & Carstensen, 2003). They also asked participants to perform a recognition memory task, in which the older adults showed better memory for happy faces relative to negative faces, suggesting a reduced negative bias in attention but a positive bias for memory in older adults. Finally, one study found that older adults showed better WM performance compared to young adults for positive images, and worse for negative images (Mikels et al., 2005), suggesting that older adults have both a positive bias and a reduced negative bias in WM. However, older adults show preserved threat-detection, shown by comparable reaction-time benefits to threat-related information in younger and older adults (Mather & Knight, 2006; Rosler et al., 2005). Several studies showed that older adults have a benefit for emotional content in WM, regardless of valence (D'Argembeau & van der Linden, 2004; Hartley et al., 2012; Mammarella et al., 2013), suggesting no valence-specific bias. Notably, studies that claim to support to the 'positivity bias' hypothesis often show different patterns of results, such as a reduced negative bias but not a positive bias, a positive bias but no reduced negative bias, or a greater positive bias than a negative bias.

To investigate i) whether older adults show a WM benefit for emotional information, ii) if the benefit is specific to positive or negative stimuli, and; iii) if there is a negative bias in young and a positive bias in old, I tested younger and older adults with a novel emotional WM task (developed in Chapter 4). Control tasks were included in order to assess whether the emotion effects were specific to emotional WM (emotional perception), and to control for differences in non-emotional WM abilities (visual WM) and visual acuity between age groups. Since emotional processing can be modulated by mood, depression, and anxiety levels (e.g. Bradley et al., 1998, 1997, 1999; Donaldson et al., 2007; E. Fox et al., 2001, 2002; Gotlib et al., 2004; Joormann & Gotlib, 2007; Leyman et al., 2007; Mathews & MacLeod,

2005; Mogg et al., 1995; Yiend & Mathews, 2001), I also tested for the relationship of WM performance with measures of affective traits. I was mainly interested in clinically relevant measures of depression and trait anxiety (Beck's Depression Inventory and State-Trait Anxiety Inventory, trait measure), which are associated with mood and emotional stability in daily life, and the vulnerability to mood disorders (Mathews & MacLeod, 2005).

In the previous chapter, I developed an emotional WM precision task which provides a sensitive, continuous measure of performance error for emotional material, and has a measure of bias built into the performance measure (how much more or less emotionally intense the emotional stimulus was perceived or remembered to be). Here, I will use an optimised version of this task to test for differences in emotional WM performance between age groups. Given the stronger correlations between behaviour and anxiety in previous chapters and the clinical significance of the STAI trait and BDI measures, I will test how individuals' levels of depression and trait anxiety correlate with emotional processing and whether this interacts with age.

Experiment 5.1

To characterise WM for emotional content in healthy ageing, an emotional analogue of a visual WM precision task with a free-recall response method (e.g. Bays et al., 2009; 2011; Wilken & Ma, 2004; W. Zhang & Luck, 2008) was used.

In each trial of the emotional WM experiment, the participant encoded a centrally presented face into WM with an emotional expression (fearful or happy) with a certain emotional intensity (ranging from low to high). After a short delay, a neutral face with the same identity re-appeared at the centre of the screen. Participants recalled the emotional expression and intensity of the corresponding facial identity from memory and used a trackball mouse to

adjust the emotional expression of the face on the screen to match the emotion type and intensity of the remembered face as precisely as possible. To control for differences in the perceptual acuity of the emotional stimuli, and address the possibility that the effects are not specific to WM, participants completed an emotional expression-matching experiment. In this experiment, two faces are simultaneously presented on the screen, and the participant adjusted one of the faces to match the emotional expression of the target face. To control for individual differences in visual WM maintenance abilities, a non-emotional visual WM task was administered to all participants. Mirroring the emotional WM tasks, participants encoded one centrally presented stimulus (an oriented stimulus as in Chapter 2) over a WM maintenance period of 3000 ms. To assess visual acuity, performance in a perceptual matching task using non-emotional stimuli (oriented stimuli as in Chapter 2) was also administered. In the visual matching task, participants matched the orientation of the stimulus on the screen to a target stimulus' orientation, mirroring the emotional expression-matching task. All participants were able to perform all four tasks adequately well, and their errors for the short-term retention of emotional facial expressions and orientation stimuli followed normal (Gaussian, von Mises) distributions.

I found that older adults showed a general impairment in emotional expression task performance (both WM and matching), had a tendency to underestimate the intensity of fearful expressions and interpret low intensity fearful faces as happy, and WM performance for happy faces was negatively correlated with measures of depression in young adults.

Methods

Participants

The study was approved by the Central University Research Ethics Committee of the University of Oxford. All participants provided written informed consent and received compensation of £10 per hour and travel expenses where required.

Fifty-four young adults and 54 older adults were invited to participate in the experiment. Young adults were recruited from the Oxford Psychology Research Participant Recruitment Scheme and via an online advertisement on the Psychiatry departmental website. Older adults were recruited from the Oxford Dementia and Ageing Research database (Friends of OxDARE: <http://www.oxdare.ox.ac.uk/become-a-friend>) and via an online advertisement on the Psychiatry departmental website. Before taking part in the study, individuals were sent a screening questionnaire via email, which included a trait anxiety questionnaire (State-Trait Anxiety Inventory, trait version) and a series of questions about their current and past medication, history of mental illness, and participation in recent studies. People who reported current use of psychoactive medication, history of recreational drug use, history of neurological illness, or took part in any studies involving working memory training or emotional face stimuli in the past six months were not invited to participate in the study. Data from one elderly participant was excluded because of a low score on the Montreal Cognitive Assessment (less than 26 on the MoCA; Nasreddine et al., 2005), and data from two other elderly participants were not saved because of a technical error. The remaining 54 young participants (39 female) were 18-35 years old (mean: 23.42 ± 0.60) and 51 older participants (29 female) were 61-82 years old (mean 69.25 ± 0.78). All participants were fluent in English, had normal or corrected-to-normal vision and hearing, and all older participants scored >26 on the MoCA (mean: 28.16 ± 0.16 ; younger adults did not complete the MoCA).

Stimuli and Apparatus

For the emotional WM task and the emotional expression-matching task, the same set of face stimuli were used as in Chapter 4. To reduce the number trials, a reduced number the intensities conditions were used and the 50% condition was taken out. Specifically, the set of face stimuli included emotional expressions with intensities from 0% to 45 % in 5% steps, and 55 % to 100% in 5% steps, resulting in 624 unique stimuli in total. In the emotional WM task, the faces were presented at the centre of the screen and subtended $10^\circ \times 16.3^\circ$. In the emotional expression-matching task, the faces were presented at the left and right side of the fixation cross on the horizontal meridian (centred at $\sim 9.75^\circ$ in lateral visual angle from fixation).

In the non-emotional visual WM task, the stimuli were presented at the centre of the screen and consisted of an oriented bar (2.32° in length, 0.16° in width), with a disc (0.72° diameter) at its centre. For the visual matching task, the same orientated bars were presented at the left and right side of the fixation cross on the horizontal meridian (centred at $\sim 9.75^\circ$ in lateral visual angle from fixation).

In all tasks, the fixation cross was a plus sign (“+”) subtending $\sim 1.5^\circ$ and placed at the centre of the screen.

The task was programmed and run in Matlab v.7.10 (MathWorks) using the Psychophysics Toolbox v.3.0 package (Brainard, 1997). The task was presented on an LCD screen with a spatial resolution of 1680 by 1200 pixels and a refresh rate of 60 Hz, placed ~ 67.5 cm from the participant.

Eye movements were monitored on-line with an eye-tracker (EyeLink 1000, SR Research, Ontario, Canada) recording at 500 Hz. If participants broke fixation during trials, I reminded them to refrain from moving their eyes in the next break.

All participants were asked to complete four self-report questionnaires measuring state and trait anxiety (State-Trait Anxiety Inventory, STAI; Spielberger, 1983) and positive and negative affective states and traits (short version of the Positive and Negative Affect Scale; Watson et al., 1988). Qualtrics online survey software (Qualtrics, Provo, UT) was used to deliver the surveys and was used to generate the summary statistics.

Task Design and Procedure

Emotional WM task

The experiment tested the ability to remember faces with emotional expressions in WM over short periods of time (figure 5.1). On each trial, participants encoded a face into memory and were tested on one of the faces at the end of the trial. Stimuli were happy or fearful faces with pseudo-randomly selected levels of emotions from intensity values of 0% to 45% and 55% to 100% in 5% steps (missing out the 50% emotional intensity). Emotion type conditions were intermixed within each block.

Trials were self-initiated. A “GO” screen signalled that participants could initiate the trial by a left mouse click. A fixation cross was presented at the centre of the screen (800 ms in duration), after which a face stimulus (500 ms) and a scrambled mask (100 ms) were presented. After a delay of 3000 ms with a central fixation cross, a probe face was presented and participants had to adjust the face’s emotion to match the emotion type and intensity of the face in memory. The probe face was presented at 0% emotion (neutral), and participants adjusted the emotional content of the face using a trackball mouse, scrolling left for one

emotion and right for the other emotion and clicked to confirm their response (happy and fear; counterbalanced across participants). After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Participants were asked to keep their eyes at the centre of the screen during the task. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of probe presentation in the interest of time and to reduce memory degradation.

Each participant completed eight blocks of 20 trials, resulting in a total of 160 trials. For each emotion type (fear, happy), an image from each emotion intensity level was presented four times, with 80 trials per emotion type. The facial identities were randomly allocated between emotion conditions and all identities were used in both emotion types. Each condition (emotion-type, emotion-intensity) was associated with a facial identity (fixed over all participants) in order for the behavioural measures to reflect error for the same set of visual stimuli. This is important for the correlational analyses between performance and questionnaire measures across subjects, so that the stimuli presented remain constant and the only thing that varies are the individuals.

Emotional expression-matching task

The emotional expression-matching task tested the ability to perceive and match emotional facial expressions (figure 5.2A). Participants were presented with a target face on the left of the screen and adjusted the face on the right of the screen to match the emotion type and intensity on the target face. As in the WM experiment, stimuli were happy or fearful faces with pseudo-randomly selected levels of emotions from intensity values of 0% to 45% and 55% to 100% in 5% steps (missing out the 50% emotional intensity). Emotion type conditions were intermixed within each block.

Each trial began with a “GO” screen signalled that participants could initiate the trial by a left mouse click. A fixation cross was presented at the centre of the screen (800 ms in duration), after which two faces with the same identity appear on the left and right side of the screen. Participants adjusted the right face’s emotional expression to match the emotion type and intensity of the face on the left. The right face was always presented with a neutral (0%) emotional intensity, and participants adjusted the expression of the face using a trackball mouse, scrolling left for one emotion and right for the other (counterbalanced across participants). The interval between trials, commencing after response termination, was 800 ms. After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of stimulus presentation for the interest of time. Participants could move their eyes freely during the trial.

Each participant completed two blocks of 20 trials, resulting in a total of 40 trials. For each emotion type (fear, happy), an image from each emotion intensity level was presented two times, with 20 trials per emotion type. The facial identities were randomly allocated between emotion conditions and all identities were used in both emotion types. Each condition (emotion-type, emotion-intensity) was associated with a facial identity (fixed over all participants) in order for the behavioural measures to reflect error for the same set of visual stimuli.

Visual WM task

The visual WM task tested the ability to remember orientations in WM over short periods of time (figure 5.1A). Each trial began with a “GO” screen signalled that participants could

initiate the trial by a left mouse click. A fixation cross was presented at the centre of the screen (800 ms in duration), after which an orientation stimulus appeared (500 ms) followed by a coloured mask (100 ms). After a delay of 3000 ms with a central fixation cross, a probe orientation was presented at a random orientation and participants had to adjust the stimulus' orientation to match the orientation of the stimulus in memory. Participants adjusted the probe orientation using a trackball mouse, scrolling left counter-clockwise and right for clockwise, and clicked to confirm their response.

The interval between trials, commencing after response termination, was 800 ms. After each block, feedback was given (percent correct: mean unsigned angular error divided by possible angular error) to motivate good performance and to ensure that participants understood the task. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of stimulus presentation for the interest of time and memory degradation. Each participant completed two blocks of 20 trials, resulting in a total of 40 trials.

Visual matching task

The visual matching task tested the ability to perceptually judge and match visual orientations (figure 5.9A). Each trial began with a "GO" screen signalled that participants could initiate the trial by a left mouse click. A fixation cross was presented at the centre of the screen (800 ms in duration), after which two oriented stimuli appeared on the left and right side of the screen. Participants adjusted the right stimulus' orientation to match the orientation of the stimulus on the left. The right orientation was presented at a random orientation, and participants adjusted the orientation using a trackball mouse, scrolling left counter-clockwise and right for clockwise, clicking to confirm their response. The interval between trials,

commencing after response termination, was 800 ms. After each block, feedback was given (percent correct) to motivate good performance and to ensure that participants understood the task. Accuracy was stressed over reaction time. There was no maximum response time, but participants were encouraged to respond within six seconds of stimulus presentation for the interest of time. Participants could move their eyes freely during the whole trial. Each participant completed two blocks of 10 trials, resulting in a total of 20 trials.

Participants first completed self-reported affective questionnaires on an iPad, and then proceeded to the main experimental task. The experimenter verbally explained each experimental task with a PowerPoint slide presentation, each of which was followed by practice trials. Participants were given one to two practice blocks of each task (10 trials per block) in the following order: emotional WM, emotional expression-matching, visual WM, visual matching. Most participants only required one block of practice for each task. The practise tasks were exactly the same as the main experiment, except that for the emotion tasks, the facial identities were selected from the practice set. In the main experiment, each participant completed all tasks in the same order: emotional WM, emotional expression-matching, visual WM, visual matching, with breaks in between.

At the end of the session, participants were asked about their engagement with the all four tasks, the way they performed the tasks (e.g. cognitive strategies employed), and the experimenter provided an explanation of the experimental task and purpose when asked. The whole testing session took approximately two to three hours to complete.

Data Analysis

The aim of these analyses was to characterise the ability to retain stimuli with emotional content in WM in healthy ageing, and test whether behavioural measures acquired from these tasks are correlated with individual differences trait anxiety and depression scores.

To characterise WM performance for emotional facial expressions, I computed performance error and bias in the same way as in Chapter 4.2. As before, responses to the incorrect emotion type were excluded, the range of target emotional intensities was restricted from 21 – 80% in the analyses for error and bias, and emotional intensities were binned into five equal bins where bin 1 and bin 5 were excluded in the analyses for error and bias.

After excluding trials with neutral (0% intensity) targets, there were 152 trials (76 per emotion condition) for the WM task, within which there were 16 trials per emotional intensity bin (12 trials for intensity bin 1, which did not include 0% emotional intensity). After removing misreported emotion trials, there were 72.8 ± 0.32 / 70.33 ± 0.60 (young / old) trials for the fearful face conditions and 67.1 ± 0.67 / 67.6 ± 0.67 (young / old) trials for the happy face conditions (out of 76 trials). Split into number of trials per emotional intensity bin, the mean (\pm S.E.M.) number of trials per bin (young / old) were as follows: bin 1: 17.33 ± 0.37 / 17.45 ± 0.44 , bin 2: 27.83 ± 0.34 / 26.37 ± 0.37 , bin 3: 31.15 ± 0.15 / 30.67 ± 0.20 , bin 4: 31.70 ± 0.09 / 31.57 ± 0.14 , bin 5: 31.87 ± 0.05 / 31.86 ± 0.05 (note that bin 1 has a total of 24 trials and others have a total of 36 trials).

For the emotional expression-matching task, there were 38 trials (19 per emotion condition) after excluding trials with neutral (0% intensity) targets, within which there were 4 trials per emotional intensity bin (3 trials for intensity bin 1, which did not include 0% emotional intensity). After removing misreported emotion trials, there were 18.30 ± 0.11 / 17.76 ± 0.21 (young / old) trials for the fearful face conditions and 18.48 ± 0.09 / 18.27 ± 0.12 (young /

old) trials for the happy face conditions (out of 19 trials). Split into number of trials per emotional intensity bin, the mean (\pm S.E.M.) number of trials per bin (young / old) were as follows: bin 1: 2.09 ± 0.14 / 1.86 ± 0.13 , bin 2: 3.72 ± 0.07 / 3.20 ± 0.15 , bin 3: 3.96 ± 0.03 / 4.00 ± 0.00 , bin 4: 4.00 ± 0.00 / 4.00 ± 0.00 , bin 5: 4.00 ± 0.00 / 3.98 ± 0.02 (note that bin 1 has a total of 3 trials and the others have a total of 4 trials).

To explore the differences in performance for emotion type, emotional intensity, task, and age, a repeated-measures mixed ANCOVA was conducted on performance error. Within-subject factors were Emotion-Type (fear, happy), Emotion-Intensity (bins: low, medium, high), and Task (emotional WM, emotional expression-matching); Age was a between-subject factor (young, old); covariates were visual WM (unsigned) error, visual perceptual matching (unsigned) error, and gender. A mixed repeated-measures ANCOVA was also performed for the bias with the same factors. Degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity when normality assumptions were violated. After removing trials where participants misreported the emotion-type, two older adults were removed from the analysis since they did not have any trials in the perceptual matching task in intensity bin 2. An ANCOVA on the emotional WM task (with and without emotion expression-matching average unsigned performance error for fearful and happy faces as additional covariates) and emotion-expression matching task were performed separately (which included the two previously excluded participants), which produced similar results consistent with the main findings.

To explore whether emotion type, intensity, task and age had an effect on misreporting the wrong emotion type (e.g. recalled a 25% fearful but it was in fact a happy face), a repeated-measures mixed ANCOVA was conducted on the proportion of misreported responses with factors Emotion-Type (fear, happy), Emotion-Intensity (bins: 1, 2, 3, 4, 5),

Task (emotional WM, emotional expression-matching), and Age (young, old); with visual WM (unsigned) error, visual perceptual matching (unsigned) error, and gender as covariates.

To test for differences in performance on the non-emotional visual WM and perceptual matching tasks, a repeated-measures mixed ANCOVA was performed on the averaged unsigned performance error with Task (visual WM, visual matching) and Age (young, old) as factors, and gender as a covariate.

Paired t-tests were used to test for the direction of the condition differences and one-sample t-tests were used to test for differences from zero. In order to test for the direction of linear effects with more than two conditions, I fit a line to each participant's data across conditions, and tested whether the slope of the line was larger or smaller than zero (one-sample t-test at the group level). This tells us whether the performance measure increased or decreased across conditions. Cohen's d was used to determine the effect sizes (Cohen, 1988).

Spearman's rank partial correlations were used to test the relationship between emotional WM performance (error and bias scores separately) and self-reported affective measures (STAI and BDI), with emotional expression-matching performance, visual WM, visual matching performance, and gender as covariates. To ensure that any effects were specific to emotional WM, Spearman's correlations were also performed for emotional expression matching (with visual matching and gender as covariates), visual WM (with visual matching and gender as covariates) and visual matching (with gender as a covariate) with STAI and BDI scores separately. Correlation coefficients were transformed into z-scores using Fisher's r-to-z transformation and compared with test for significant differences (Cohen & Cohen, 1983).

Statistical analyses were conducted in Matlab R2015a, Matlab's Statistics Toolbox and R version 3.2.1 (R Core Team, 2015) using the afex package (Singmann et al., 2015).

Results

Emotional WM and emotional expression matching

Figure 5.1 summarises the emotional WM task and the behavioural results for the younger and older adults. Participants were able to complete the task with high accuracy in both emotion types (error: fear (young / old): $16.16\% \pm 0.58$ / $17.65\% \pm 0.47$; happy (young / old): $11.66\% \pm 0.37$ / $13.59\% \pm 0.43$, and the error distributions for single participants followed a Gaussian distribution of error (5.1B for group histograms; see Appendix figure S.5.1 for individual participant response error histograms).

Figure 5.2 summarises the emotional expression-matching task and the behavioural results for the young and older adults. Participants performed well in both emotion types (error: fear (young / old): $9.94\% \pm 0.52$ / $11.87\% \pm 0.50$; happy (young / old): $6.40\% \pm 0.30$ / $7.52\% \pm 0.34$), and the error distributions for single participants followed a Gaussian distribution of error (5.2B for group histograms; see Appendix figure S.5.2 for individual participant response error histograms).

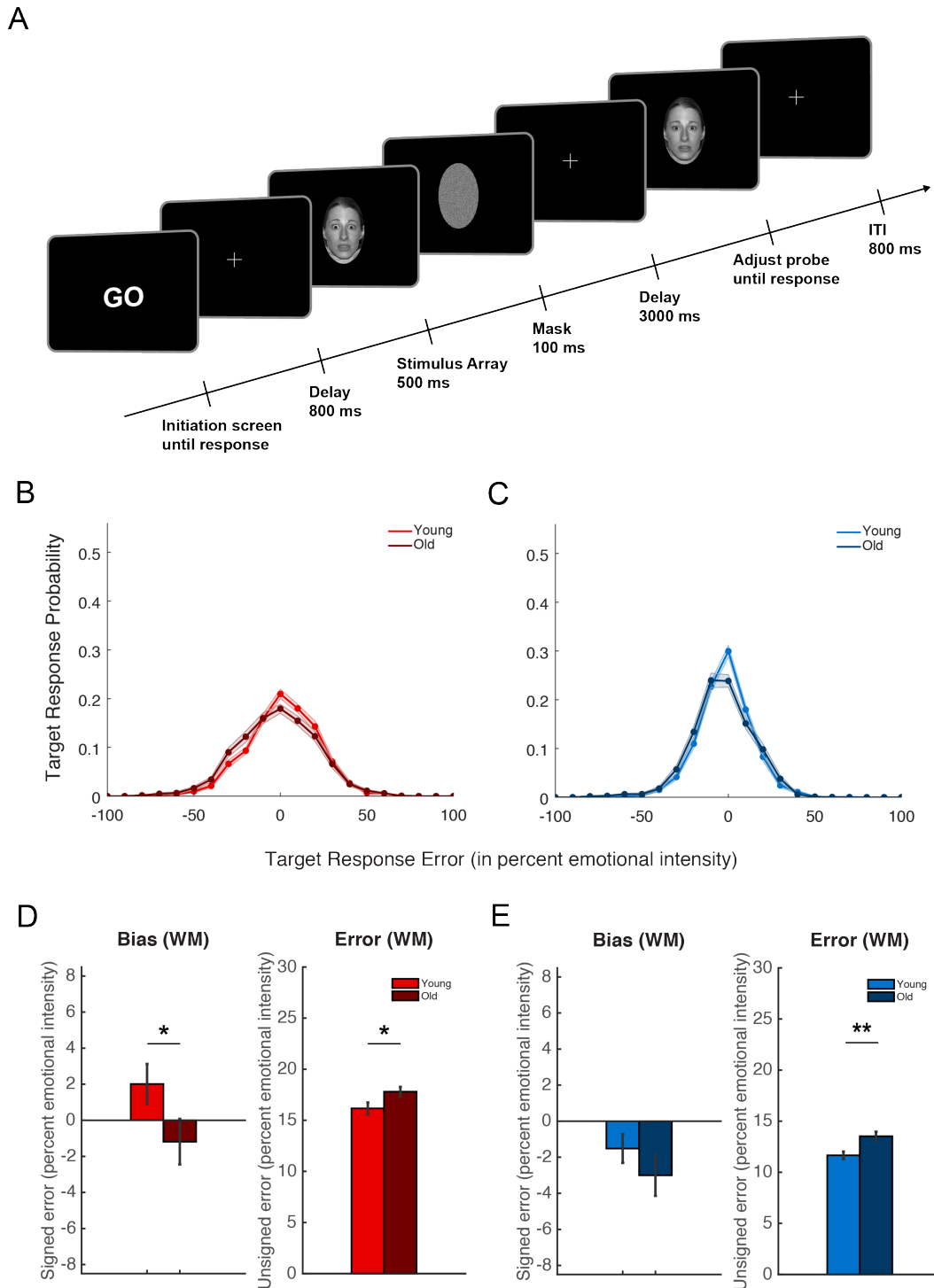


Figure 5.1. Task schematic and behavioural performance for emotional WM. *A)* Task schematic for emotional WM. After initiating the trial with a mouse click, participants encoded a facial expression into WM. After a fixed delay of 3000 ms, a test face appeared with the same facial identity but a neutral facial expression (0% emotional intensity). Participants made their response by changing the face to match the emotional expression in memory using a trackball mouse. The faces that were encoded into memory ranged from 0% to 100% fearful or 0% to 100% happy in 5% steps, missing out the 50% intensity. Emotion type was intermixed within blocks. The inter-trial-interval was 800 ms. *B-E)* Emotional WM performance. *B)* Error distributions centred on the target face emotional intensity during WM for fearful faces, plot in light red for young adults and dark red for older adults. *C)* Error distributions centred on the target face intensity during WM for happy faces, plot in light

blue for young adults and dark blue for older adults. In both of the plots, the error probability is plot at each bin and connected by the lines. The shaded areas show the standard error of the mean. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, y-axis is the response error probability. D) Bias (mean of the error distributions in B) and error (unsigned error of the distributions in B) for fear WM in the young (light red) and old (dark red) participant groups. E) Bias (mean of the error distributions in C) and error (unsigned error of the distributions in C) for happy WM in the young (light blue) and old (dark blue) participant groups. Bias and Error were calculated using trials with emotional expressions between 21 and 80% and for which participants reported the correct emotion type. * denotes $p < 0.05$; ** denotes $p < 0.01$.

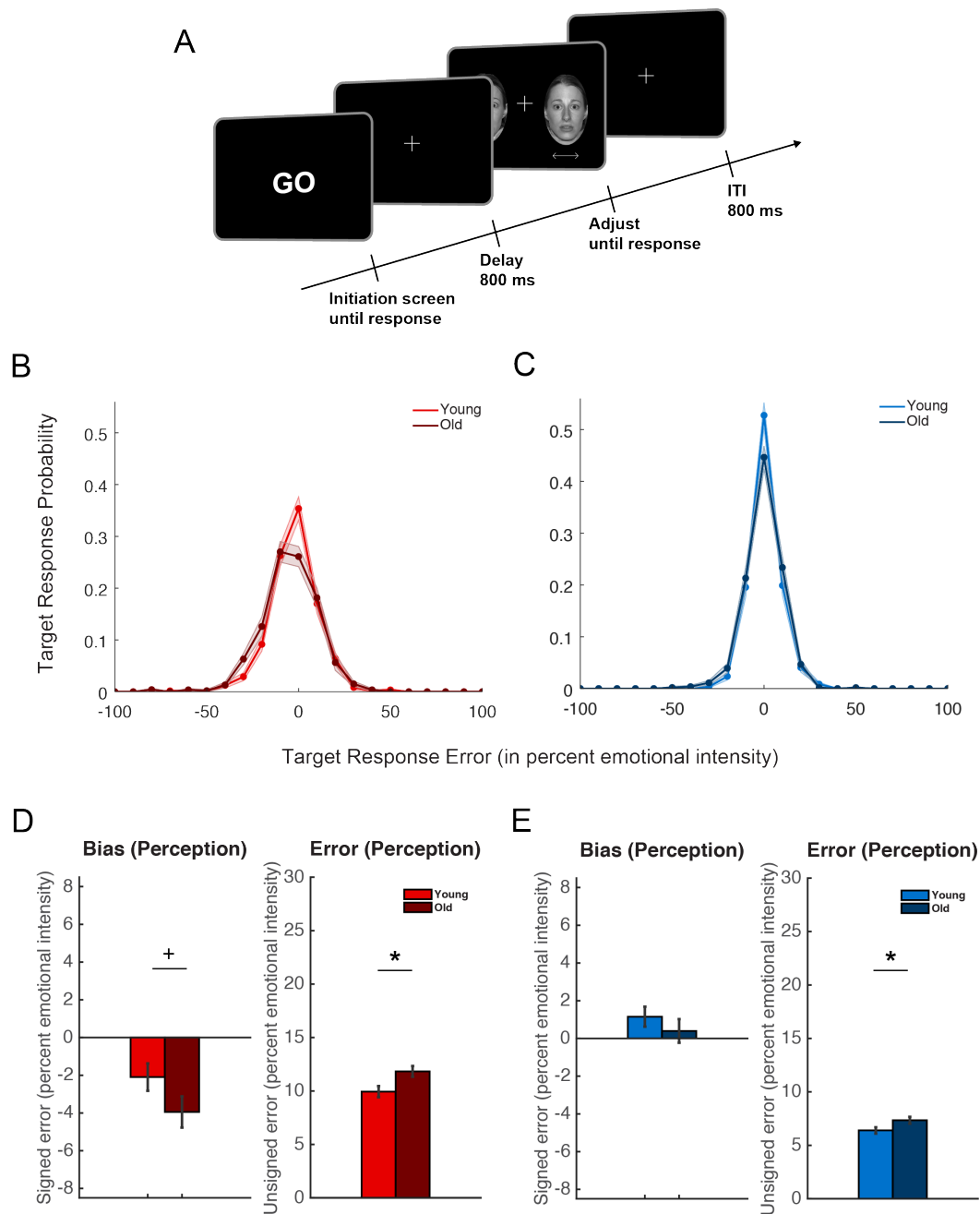


Figure 5.2. Task schematic and behavioural performance for perceptual matching of emotional expressions. A) Task schematic for emotional-expression matching. After initiating the trial with a mouse click, participants are simultaneously presented with an emotional face on the left of the screen and a neutral face on the right, and adjusted the right face's emotional expression to match the emotion type and intensity of the face on the left. The inter-trial-interval was 800 ms. Participants made their response by changing the face on the right to match the emotional expression on the left using a trackball mouse. Emotion type was intermixed within blocks. B) Error distributions centred on the target face emotional intensity during perceptual matching for fearful faces, plot in light red for young adults and dark red for older adults. C) Error distributions centred on the target face intensity during perceptual matching for happy faces, plot in light blue for young adults and dark blue for older adults. In both of the plots, the error probability is plot at each bin and connected by the lines. The shaded areas show the standard error of the mean. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, y-axis is the response error probability. D) Bias (mean of the error distributions in B) and error (unsigned error of the distributions in B) for perceptual matching of fearful faces in the young (light red) and old (dark red) participant groups. E) Bias (mean of the error distributions in C) and error (unsigned error of the distributions in C) for perceptual matching of happy faces in the young (light blue) and old (dark blue) participant groups. Bias and Error were calculated using trials with emotional expressions between 21 and 80% and for which participants reported the correct emotion type. * denotes $p < 0.05$; ** denotes $p < 0.01$; + denotes $p < 0.07$.

General deficit in matching emotional expressions in older adults

Older adults showed a deficit in performance over both tasks ($F(1,98) = 7.09, p = 0.009, np^2 = 0.07$; young versus old: $t(99.80) = -3.63, p = 0.0004$, effect size: -0.71) but there was no difference in this impairment between the type of task (Age by Task interaction: $F(1,98) = 0.12, p = 0.73, np^2 = 0.001$), indicating an age deficit in matching emotional expressions that was not specific to WM.

To confirm that the age deficit was not specific to emotional WM, I conducted two separate ANCOVAs on emotional WM error with and without emotional expression-matching performance error for fearful faces and happy faces as additional covariates. There was an effect of age on emotional WM performance ($F(1,100) = 4.50, p = 0.04, np^2 = 0.04$; young versus old: $t(191.6) = -3.01, p = 0.003$, effect size: -0.59), but this effect was no longer significant when emotion matching performance conditions were included as covariates ($F(1, 98) = 0.61, p = 0.44, np^2 = 0.006$), confirming that the deficit in performance was not specific to WM.

More generally, participants were better at happy compared to fearful faces ($F(1,98) = 243.60$, $p = 2.54 \times 10^{-28}$; $np^2 = 0.71$; $t(102) = 15.29$, $p = 3.83 \times 10^{-28}$, effect size: 1.53) and better at the perceptual matching task compared to the WM task ($F(1,98) = 410.70$, $p = 8.02 \times 10^{-37}$, $np^2 = 0.81$, $t(102) = 19.90$, $p = 6.65 \times 10^{-37}$, effect size: = 2.10; see figures 5.1C and 5.2C, right). There was an effect of Intensity ($F(1.89, 185.27) = 9.37$, $p = 0.0002$, $np^2 = 0.09$), reflecting an increase in error with greater emotional intensity (mean slope: 0.62 ± 0.17 ; $t(102) = 3.73$, $p = 0.0003$, effect size: 0.37). There was an interaction between Emotion-Type and Intensity ($F(2,195.92) = 3.74$, $p = 0.03$, $np^2 = 0.04$), reflecting an increase in error with emotional intensity in happy (mean slope: 0.50 ± 0.09 , $t(102) = 5.74$, $p = 9.94 \times 10^{-8}$, effect size: 0.57) but not in fearful face conditions (mean slope: 0.12 ± 0.13 , $t(102) = 0.90$, $p = 0.37$, effect size: 0.09; difference in slope: 0.39 ± 0.15 , $t(102) = 2.64$, $p = 0.01$, effect size: 0.35). There was also an interaction between Intensity and Task ($F(1.88,184.04) = 4.42$, $p = 0.006$, $np^2 = 0.05$), reflecting an effect of intensity in the WM (mean slope: 0.56 ± 0.13 , $t(102) = 4.51$, $p = 1.74 \times 10^{-5}$, effect size: 0.44) but not the in expression-matching task (mean slope: 0.06 ± 0.11 , $t(102) = 0.51$, $p = 0.61$, effect size: 0.05; difference in slope: 0.51 ± 0.17 , $t(102) = 2.92$, $p = 0.004$, effect size: 0.42; see figures 5.3A and 5.4A).

Older adults under-report the emotional intensity of fearful faces

In light of the proposal that older adults exhibit a 'positivity bias' in attention and memory (Mather & Carstensen, 2005), I hypothesised that young adults would tend to report fearful emotional expressions as more emotionally intense than old adults (negative bias) and old adults would report happy emotional expressions as more emotionally intense than young adults (positive bias). To test this, I conducted several hypothesis-driven comparisons.

First, there was a trend effect for age on bias ($F(1,98) = 3.25, p = 0.07, \eta^2 = 0.03$), where older adults were underreporting the emotional intensity ($t(96.6) = 2.09, p = 0.039$, effect size: 0.41; see figures 5.1C and 5.2C, left). Over both tasks, young adults reported fearful faces as more emotionally intense than the older adults (young: -0.04 ± 0.76 ; old: -2.74 ± 0.80 ; $t(102.4) = 2.45, p = 0.01$, effect size: 0.48). Moreover, old adults reported fearful faces as less intense relative to the actual intensity of targets faces ($t(50) = -3.43, p = 0.001$, effect size: -0.48) whereas young adults did not show such a bias ($t(53) = -0.05, p = 0.96$, effect size: -0.007). There were no differences in bias for happy faces (young / old: $-0.18 \pm 0.56 / -1.53 \pm 0.73$; $t(95.67) = 1.47, p = 0.15$, effect size: 0.29).

Comparing between tasks, there was a difference between young and old groups in WM bias for fearful faces (young / old: $2.02 \pm 1.11 / -1.37 \pm 1.23$; $t(101.3) = 2.05, p = 0.04$, effect size: 0.40) but only a trend occurred in the matching task (young / old: $-2.10 \pm 0.72 / -4.13 \pm 0.83$; $t(100.2) = 1.84, p = 0.07$, effect size: 0.36). However, these were not significantly different ($t(97.3) = 0.78, p = 0.44$, effect size: 0.15). There were no significant differences on bias between age groups in the happy face conditions in the WM task, expression-matching task, or between tasks (p 's > 0.22).

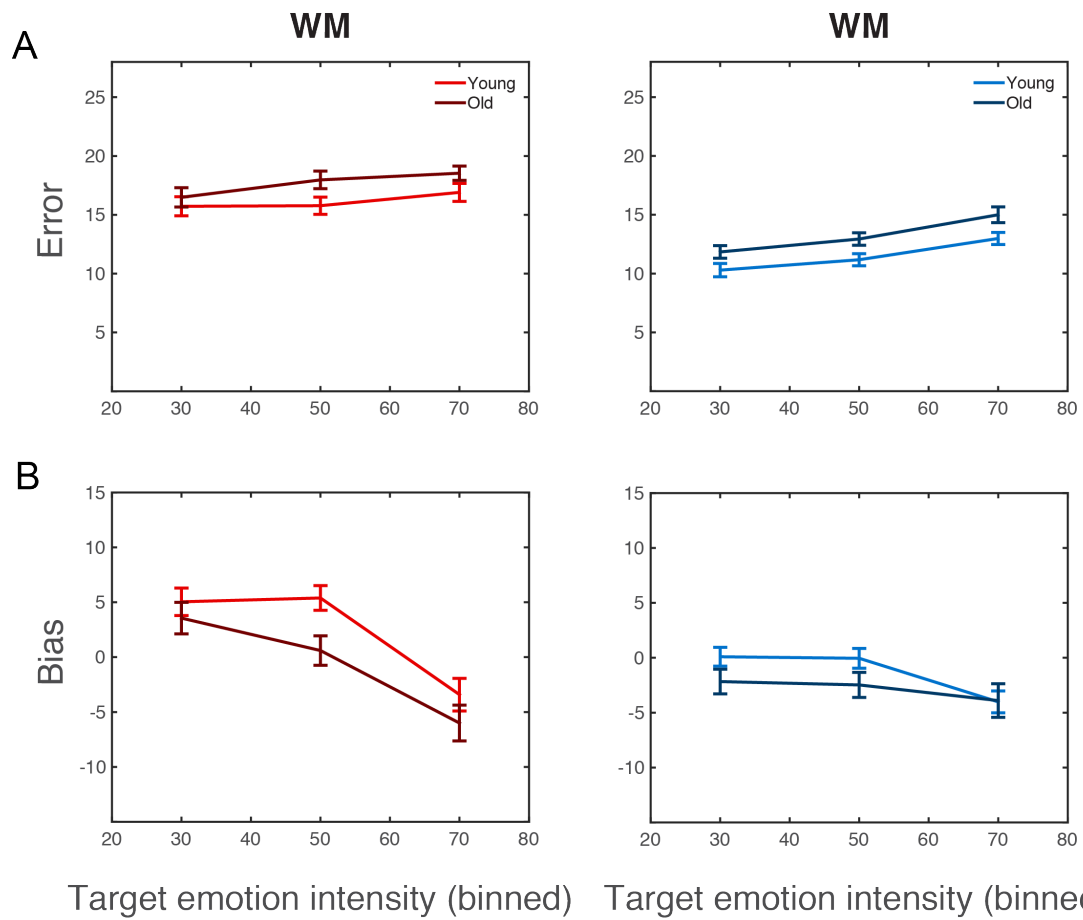


Figure 5.3. Effect of emotion type and emotional intensity on WM performance in younger and older adults. A) WM error (unsigned) plotted as a function of emotional intensity for fearful faces (left) and happy faces (right) in younger (light red/blue) and older (dark red/blue) participants. B) WM bias (signed error) plotted as a function of emotional intensity for fearful faces (left) and happy faces (right) in younger (light red/blue) and older (dark red/blue) participants. In all plots, the x-axis is the target face emotional intensity binned from 30% to 70% in 20% steps, the y-axis is the behavioural measure.

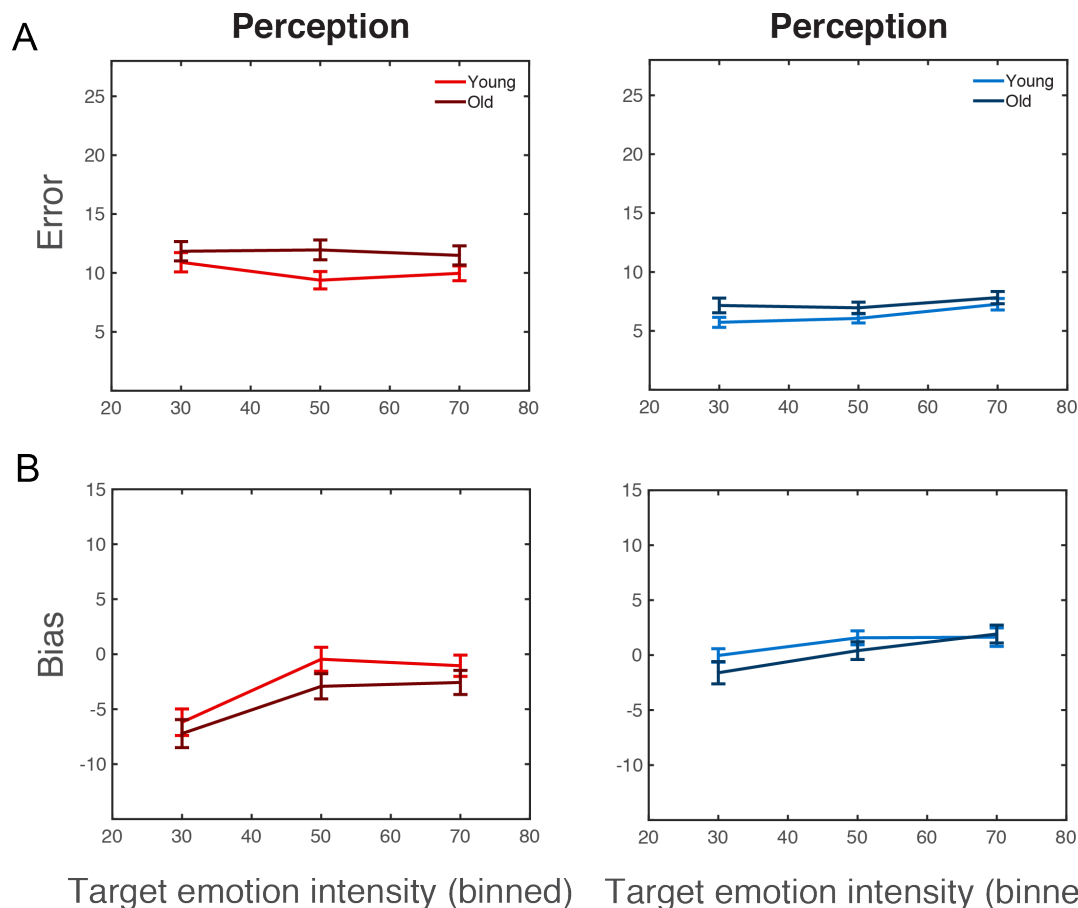


Figure 5.4. Effect of emotion type and emotional intensity on emotional expression-matching performance in younger and older adults. A) Perceptual matching error (unsigned) plotted as a function of emotional intensity for fearful faces (left) and happy faces (right) in younger (light red/blue) and older (dark red/blue) participants. B) Perceptual bias (signed error) plotted as a function of emotional intensity for fearful faces (left) and happy faces (right) in younger (light red/blue) and older (dark red/blue) participants. In all plots, the x-axis is the target face emotional intensity binned from 30% to 70% in 20% steps, the y-axis is the behavioural measure.

Older adults mistakenly report fearful faces as happy, young adults mistakenly report happy faces as fearful

On the emotional WM task, participants mistakenly reported the wrong emotion type on a sizable proportion of trials (proportion of happy faces reported fearful (young / old): 0.12 ± 0.01 / 0.11 ± 0.01 , proportion of fearful faces reported happy: 0.04 ± 0.004 / 0.07 ± 0.008 ; figure 5.5A). On the emotional expression-matching task, participants mistakenly reported the wrong emotion type on only a minority of trials (proportion of happy faces reported

fearful (young / old): $0.03 \pm 0.005 / 0.04 \pm 0.006$, proportion of fearful faces reported happy: $0.04 \pm 0.006 / 0.07 \pm 0.01$; figure 5.5B).

There was a main effect of age ($F(1,100) = 5.68$, $p = 0.02$, $\eta^2 = 0.02$), in which young adults had a smaller proportion of misreported responses ($t(98.0) = -3.04$, $p = 0.003$, effect size: -0.59). There was a main effect of emotion-type ($F(1,100) = 13.27$, $p = 0.0004$, $\eta^2 = 0.12$) reflecting participants' were more likely to misreport happy faces as fearful than misreporting fearful faces as happy ($t(104) = 3.13$, $p = 0.002$, effect size: 0.46). As reported in the previous experiments, the lower the emotional intensity, the more likely an emotion type was misreported ($F(1.76,176.10) = 288.81$, $p = 6.61 \times 10^{-53}$; $\eta^2 = 0.74$; mean slope: -0.05 ± 0.003 ; $t(104) = -21.97$, $p = 7.19 \times 10^{-41}$, effect size: -2.14). There was an effect of the Task ($F(1,100) = 99.89$, $p = 1.02 \times 10^{-16}$, $\eta^2 = 0.50$), where participants were more likely to misreport the emotion type in the WM task compared to the matching task ($t(105) = 10.51$, $p = 4.86 \times 10^{-18}$, effect size: 1.25).

Older adults exhibited a greater tendency to misreport a fearful face as happy (Age by Emotion-Type interaction: $F(1,100) = 12.53$, $p = 0.0006$, $\eta^2 = 0.11$; $t(76.5) = 3.67$, $p = 0.0005$, effect size: 0.72), whereas both age groups misreported happy faces as fearful to a similar extent ($t(102.9) = 0.56$, $p = 0.57$, effect size: 0.11). Both groups misreported happy faces as fearful more than misreporting fearful faces as happy (young: $t(53) = 7.27$, $p = 1.63 \times 10^{-9}$, effect size: 1.50 ; old: $t(50) = 2.77$, $p = 0.008$, effect size: 0.60), but this effect was stronger in the young adults ($t(97.1) = 2.38$, $p = 0.02$, effect size: 0.47). As shown in the previous experiments, there was an interaction between Emotion-Type and Intensity ($F(1.73,172.70) = 11.88$, $p = 4.11 \times 10^{-5}$, $\eta^2 = 0.11$), reflecting a greater tendency to misreport the emotion type with low emotional intensity relative to higher intensities, and this effect was stronger for happy compared to fearful faces (happy misreported as fearful:

mean slope: -0.06 ± 0.004 , $t(104) = -18.0$, $p = 1.17 \times 10^{-33}$, effect size: -1.75; fearful misreported as happy: mean slope: -0.045 ± 0.004 , $t(104) = -11.54$, $p = 2.40 \times 10^{-20}$, effect size: -1.13; mean slope difference: -0.02 ± 0.006 , $t(104) = -3.53$, $p = 0.0006$, effect size: -0.52). This effect was modulated by age (Age by Emotion-Type by Intensity interaction: $F(1.73,172.70) = 6.19$, $p = 0.004$, $\eta^2 = 0.06$), where young adults were less likely to misreport fearful faces with lower intensities as happy compared to older adults (mean difference in slope: 0.02 ± 0.04 ; $t(81.45) = 2.58$, $p = 0.01$, effect size: 0.51) but not for the happy faces (mean difference in slope: -0.002 ± 0.04 ; $t(102.7) = -0.38$, $p = 0.70$, effect size: -0.07 ; mean slope difference: 0.02 ± 0.05 , $t(87.2) = 2.02$, $p = 0.046$, effect size: 0.40).

There was an interaction between Emotion-Type and Task ($F(1,100) = 46.91$, $p = 6.14 \times 10^{-10}$, $\eta^2 = 0.32$), reflecting a larger proportion of happy faces misreported as fearful in the WM task compared with the emotional expression-matching task ($t(104) = 12.1$, $p = 1.64 \times 10^{-21}$, effect size: 1.53) but not for the fearful trials ($t(104) = 1.03$, $p = 0.30$, effect size: 0.13; difference between conditions: $t(104) = 7.03$, $p = 2.23 \times 10^{-10}$, effect size: 0.90). Finally, there was an interaction between Emotion-Type, Task, and Emotion-Intensity ($F(1.48,148.32) = 27.48$, $p = 5.92 \times 10^{-9}$, $\eta^2 = 0.22$), reflecting a greater tendency to misreport the emotion type with low emotional intensity relative to higher intensities in the WM task compared to matching task in the happy face trials (mean slope: -0.06 ± 0.006 , $t(104) = 9.54$, $p = 6.89 \times 10^{-16}$, effect size: -1.2) but not in the fearful face trials (mean slope: 0.002 ± 0.006 , $t(104) = 0.24$, $p = 0.81$, effect size: 0.03; mean difference between slopes: -0.06 ± 0.01 , $t(104) = 6.34$, $p = 6.12 \times 10^{-9}$, effect size: 0.79).

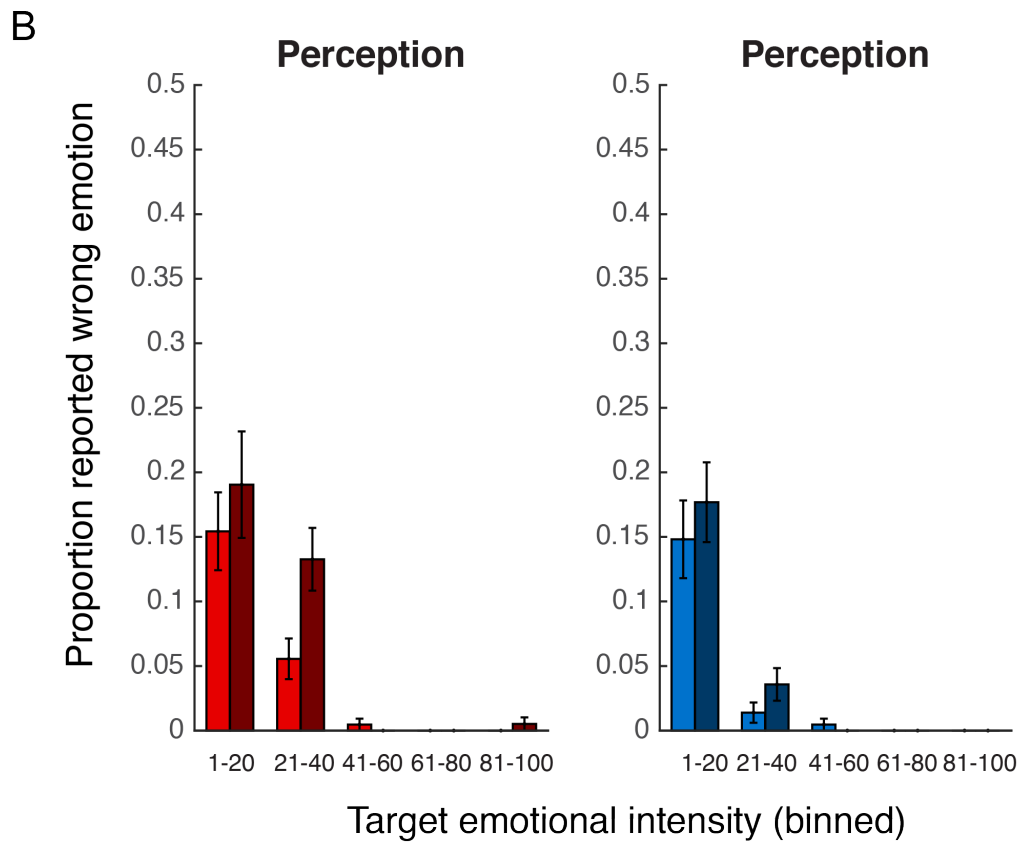
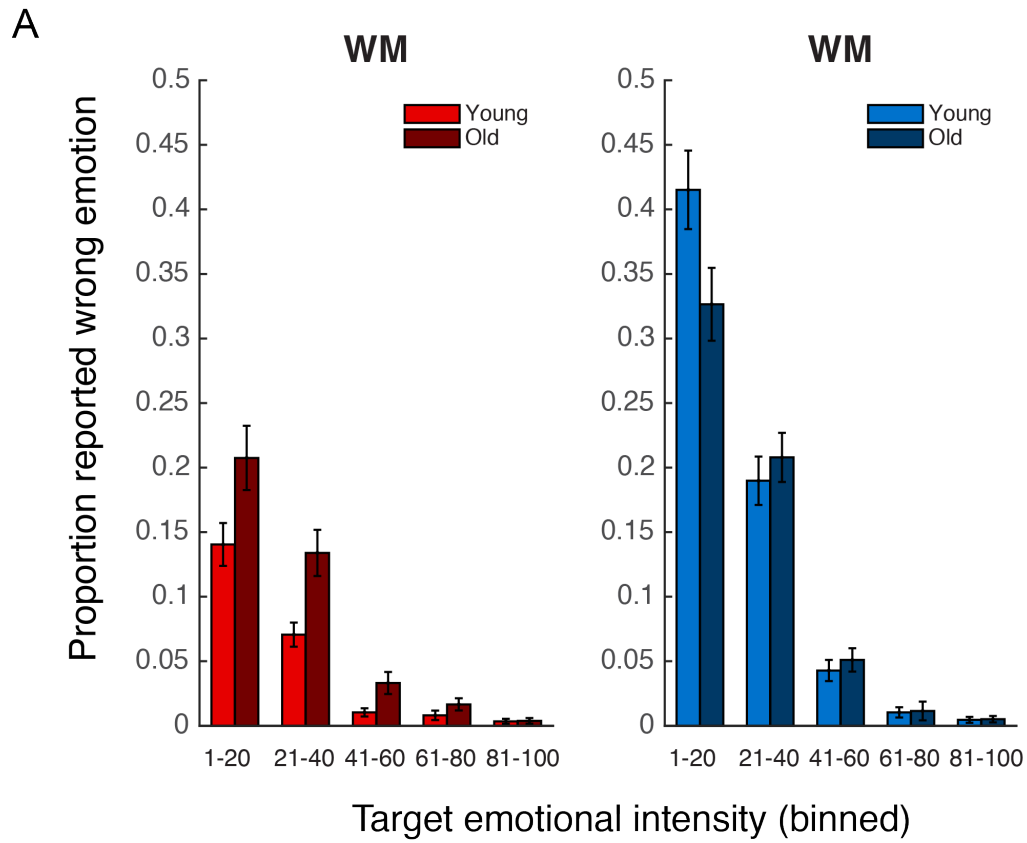


Figure 5.5. Proportion of trials where participants misreported the emotion type for each Emotion and Intensity value condition in the emotional WM task and emotional expression-matching task for younger and older adults. A) Bar plots showing the proportion of misreported-emotion trials for each emotional intensity bin from 1% to 80% in 20% steps for fearful (young: light red; old: dark red) and

happy (young: light blue; old: dark blue) faces in the emotional WM task. B) Bar plots showing the proportion of misreported-emotion trials for each emotional intensity bin for fearful (young: light red; old: dark red) and happy (young: light blue; old: dark blue) faces in the emotional expression-matching task.

Fearful faces are remembered as more fearful and happy faces are remembered as less happy in working memory

There was an effect of Emotion-Type by Task ($F(1,98) = 78.80$, $p = 3.30 \times 10^{-14}$, $\eta^2 = 0.45$), indicating the bias for the emotion type was different depending on the task type. Specifically, there was a greater negative bias in the happy compared to fearful faces in the WM task (mean bias fear: 0.49 ± 0.85 ; happy: -2.22 ± 0.68 ; $t(102) = 3.81$, $p = 0.0002$, effect size: 0.35), and a greater negative bias in the fearful faces compared to happy faces in the matching task (mean bias fear: -2.98 ± 0.55 ; happy: 0.79 ± 0.41 ; $t(102) = -6.02$, $p = 2.74 \times 10^{-8}$, effect size: -0.77). Indeed, participants' bias for fearful faces in WM was not significantly different from zero ($t(102) = 0.58$, $p = 0.56$, effect size: 0.06), but they reported fearful faces to be less emotionally intense than the target face in the matching task ($t(102) = -5.39$, $p = 4.45 \times 10^{-7}$, effect size: -0.53; difference between tasks: $t(102) = 4.02$, $p = 0.0001$, effect size: 0.48). WM bias for happy faces, however, was significantly less than zero ($t(102) = -3.25$, $p = 0.002$, effect size: -0.32) whereas the bias for happy faces in the matching task was not significantly different from zero ($t(102) = 1.95$, $p = 0.054$, effect size: 0.19; difference between tasks: $t(102) = -4.58$, $p = 1.32 \times 10^{-5}$, effect size: -0.53).

As reported previously, there was an effect of Emotion-Intensity on performance bias ($F(1.57,154.14) = 14.41$, $p = 1.31 \times 10^{-5}$, $\eta^2 = 0.13$), reflecting a greater tendency to under-report the emotional intensity of the facial expression with greater intensity (mean slope: -0.56 ± 0.28 , $t(102) = -2.05$, $p = 0.04$, effect size: -0.20). There was an Emotion-Intensity by Emotion-Type interaction ($F(1.89,185.17) = 6.20$, $p = 0.003$, $\eta^2 = 0.06$), reflecting a greater difference between fear and happy face conditions for the low

compared to medium intensities ($t(102) = 3.84, p = 0.0002, \text{effect size: } 0.55$) and low and high intensities ($t(102) = 2.07, p = 0.04, \text{effect size: } 0.25$) but not low and medium intensities ($t(102) = -1.23, p = 0.22, \text{effect size: } -0.18$). There was an Emotion-Intensity by Task interaction ($F(1.75,171.59) = 74.83, p = 4.23 \times 10^{-23}, \eta^2 = 0.43$), reflecting a greater negative bias with increasing intensity in the WM task (mean slope: $-1.49 \pm 0.19, t(102) = -7.85, p = 4.22 \times 10^{-12}, \text{effect size: } -0.77$) and a decrease in negative bias with increasing intensity in the matching task (mean slope: $0.94 \pm 0.17, t(102) = 5.54, p = 2.40 \times 10^{-7}, \text{effect size: } 0.55$; difference in slope: $-2.44 \pm 0.23, t(102) = -10.50, p = 6.47 \times 10^{-18}, \text{effect size: } -1.33$). Task type interacted with these factors (Task by Emotion-Type by Emotion-Intensity interaction: $F(1.92,188.07) = 13.55, p = 4.51 \times 10^{-6}, \eta^2 = 0.12$), in which there was a greater decrease in bias with increasing intensity for fearful faces versus happy faces in WM (mean difference in slope: $-2.38 \pm 0.35; t(102) = -7.73, p = 9.92 \times 10^{-10}, \text{effect size: } -0.73$) compared with an greater increase in bias with increasing intensity for fearful versus happy faces in the matching task (mean difference in slope: $1.18 \pm 0.59, t(102) = 2.00, p = 0.048, \text{effect size: } 0.26$; difference between effects: $-3.56 \pm 0.69, p = 1.09 \times 10^{-6}, \text{effect size: } -0.72$).

Relationship between emotional WM performance and depression/anxiety measures

I tested for correlations between behaviour and depression and anxiety measures (see figure 5.6 for distributions of depression and anxiety scores). Note that although there was an outlier in the young group with a BDI score of 50 (greater than three standard deviations from the young adults' group mean), Spearman rank correlation coefficients are largely insensitive to outliers. Performing the analyses after excluding the outlier left the results unchanged. In the young group, there was a good distribution for trait anxiety (mean: 37.9 ± 1.49 ; range: 22 – 67), state anxiety (mean: 32.6 ± 1.10 ; range: 20 – 51), and depression (mean: 6.37 ± 1.05 ; range: 0 – 50; without outlier, mean: 5.55 ± 0.65 ; range: 0 – 22), and slightly smaller range of scores for negative affect: mean: 8.41 ± 0.39 , range: 5 – 18) and positive affect (mean: $16.2 \pm$

0.51, range: 5 – 25). In the old group, there was also a good distribution for trait anxiety (mean: 36.0 ± 1.34 ; range 20 – 60), state anxiety (mean: 31.8 ± 1.14 ; range: 20 – 61), and depression (mean: 7.78 ± 0.67 ; range: 1 – 18), and slightly smaller range of scores for negative affect: mean: 7.57 ± 0.29 , range: 5 – 12) and positive affect (mean: 17.3 ± 0.44 , range: 9 – 25). The correlational analyses were kept to the key variables of interest of trait anxiety and depression, due to their relevance to mood disorders, and because trait anxiety was found to correlate with several behavioural measures in Chapter 4. There were no significant differences between age groups for trait anxiety ($t(102.4) = 0.97$, $p = 0.33$, effect size: 0.19) or depression scores ($t(89.8) = -1.14$, $p = 0.26$, effect size: -0.22).

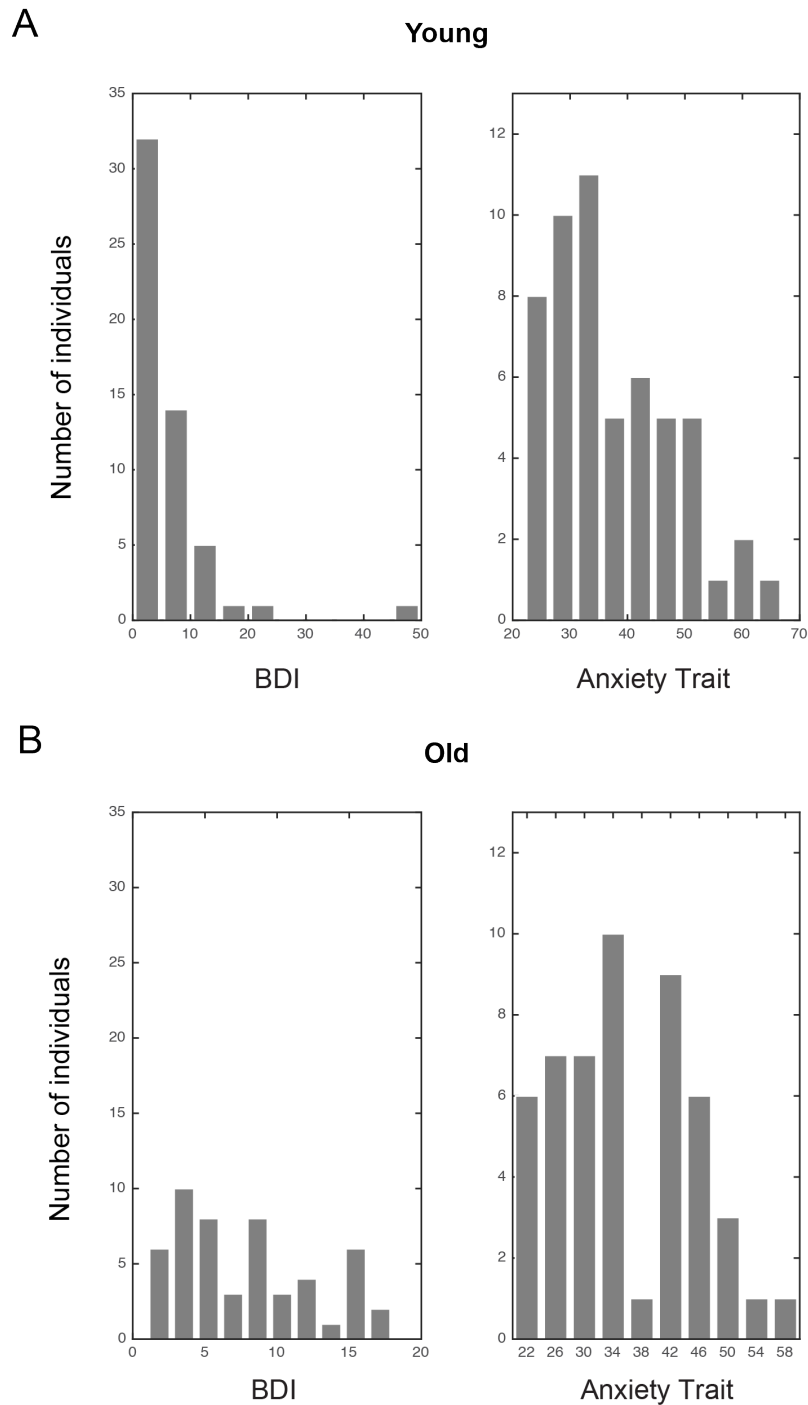


Figure 5.6. Distributions of depression/anxiety scores. Histograms showing the distribution depression (BDI) and trait anxiety (STAI) measures for A) young adults and B) old adults. X-axis is the depression/anxiety measure, y-axis is the number of individuals.

WM error for happy faces was positively correlated with depression scores ($r = 0.25$, $p = 0.01$; figure 5.7A, bottom left), with a similar trend for trait anxiety ($r = 0.17$, $p = 0.09$; figure 5.7A, bottom right). There were no significant correlations between error for happy faces on the expression-matching task and depression ($r = -0.05$, $p = 0.63$; figure 5.8A, bottom left) or

anxiety ($r = -0.02$, $p = 0.87$; see figure 5.8A, bottom right). Notably, this correlation was significant in the young adults but not in the older adults (young: $r = 0.38$, $p = 0.006$; old: $r = 0.028$, $p = 0.85$), and there was a strong trend for a difference between the correlation coefficients ($z = 1.85$, $p = 0.06$), suggesting that the group effect was driven by the younger adults. There was no difference between the correlation coefficients for WM for happy faces and anxiety between groups (young: $r = 0.17$, $p = 0.23$; old: $r = 0.18$, $p = 0.21$; difference: $z = -0.05$, $p = 0.96$).

To test for the specificity of the correlation of WM for emotional material with depression and anxiety (opposed to emotional processing in general), I compared the correlation coefficients of the correlations between tasks. Since performance error on the WM and matching task for happy faces were correlated ($r = 0.35$, $p = 0.0002$), the same analysis was performed on each variable after regressing the other ones out. WM error was still correlated with depression ($r = 0.25$, $p = 0.01$), matching error was not ($r = -0.11$, $p = 0.29$) and there was a trend for a difference between the two effects ($z = 1.09$, $p = 0.057$).

I performed a similar analysis to test whether WM for happy faces predicted depression scores over and above trait anxiety. Since depression and trait anxiety scores were highly correlated ($r = 0.65$, $p = 7.74 \times 10^{-14}$), the correlational analysis was performed on each measure after regressing each other out. Depression showed a trend to correlate with WM performance for happy faces ($r = 0.19$, $p = 0.061$), whereas trait anxiety was not correlated ($r = 0.003$, $p = 0.98$). Comparing the two correlation coefficients showed no significant difference ($z = 1.34$, $p = 0.18$).

All other correlations with emotional WM and matching (error and bias) were not significant (see figure 5.7 and 5.8; $p > 0.085$). Furthermore, all control correlations with emotional

expression matching, visual WM, and visual matching also yielded no significant correlations with depression or anxiety scores (see figure 5.10; $p > 0.082$).

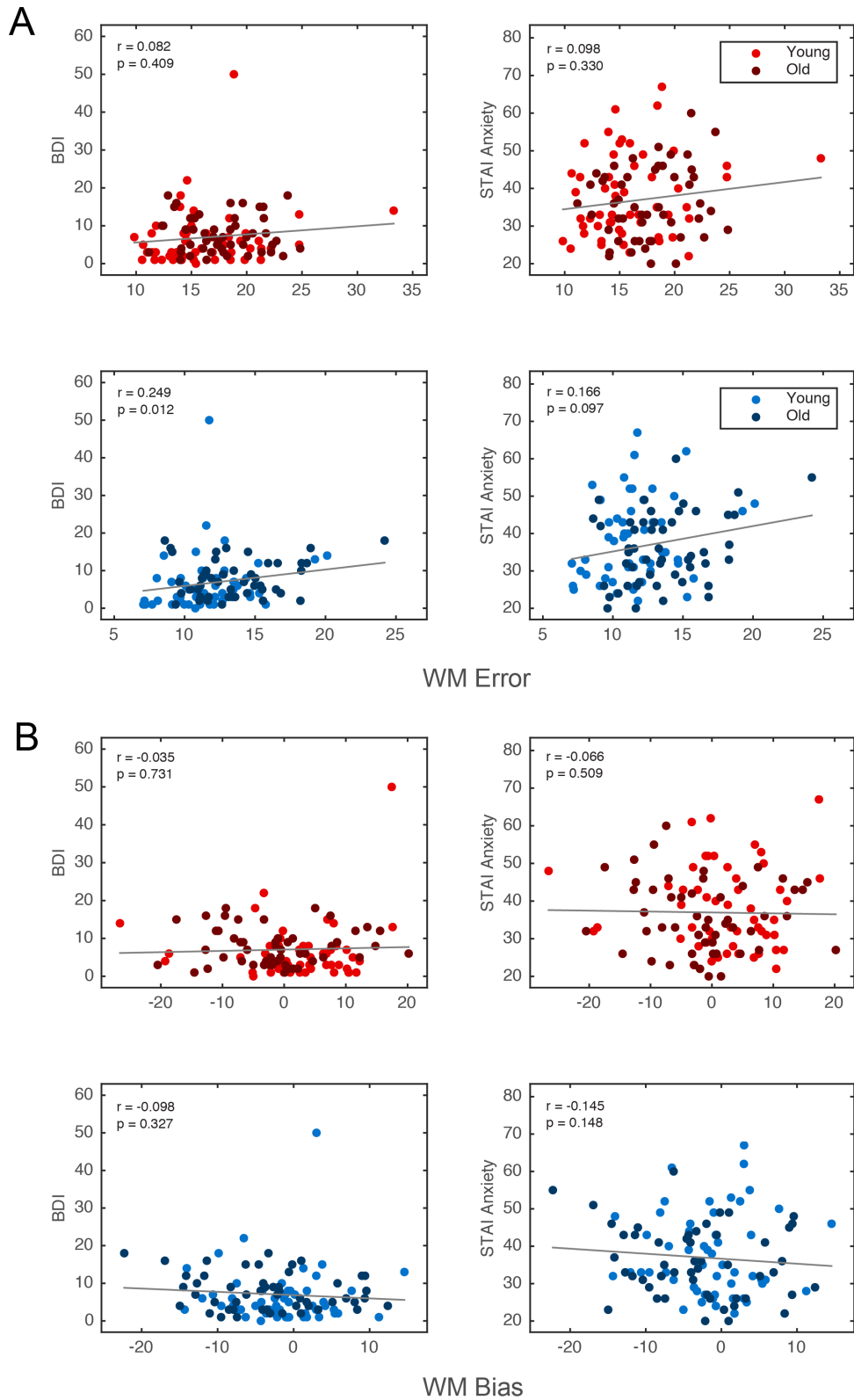


Figure 5.7. Correlations between depression/anxiety and WM performance. *A*) Scatter plots of depression/anxiety measures as a function of WM error for fearful faces (top, red) and happy faces (bottom, blue), averaged over emotional intensities. X-axis is WM error averaged over emotional intensity conditions, y-axis is the depression/anxiety measure. *B*) Scatter plots of depression/anxiety measures as a function of WM bias for fearful faces (top, red) and happy faces (bottom, blue), averaged over emotional intensities. X-axis is WM bias averaged over emotional intensity

conditions, y -axis is the depression/anxiety measure. In all plots, each point is an individual participant, and correlation values are Spearman's partial rank correlation coefficients. Light red/blue dots denote young adults, and dark red/blue dots denote older adults.

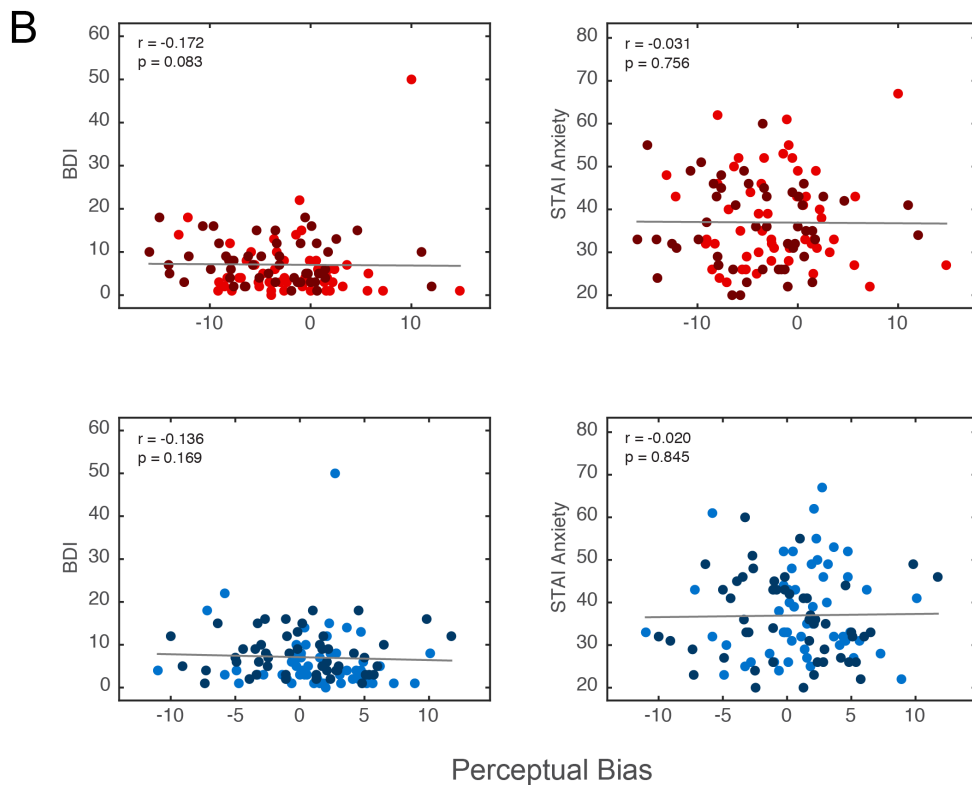
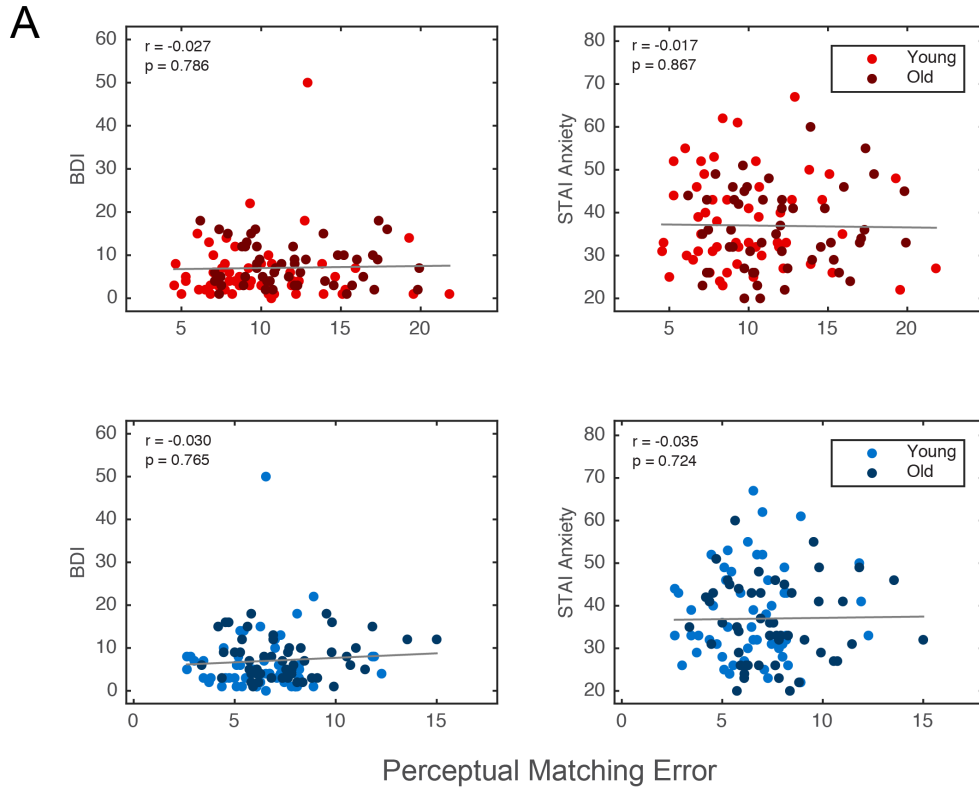


Figure 5.8. Correlations between depression/anxiety and emotional expression-matching performance. A) Scatter plots of depression/anxiety measures as a function of matching error for fearful faces (top, red) and happy faces (bottom, blue), averaged over emotional intensities. X-axis is matching error averaged over emotional intensity conditions, y-axis is the depression/anxiety measure. B) Scatter plots of depression/anxiety measures as a function of matching bias for fearful faces (top, red) and happy faces (bottom, blue), averaged over emotional intensities. X-axis is matching bias averaged over emotional intensity conditions, y-axis is the depression/anxiety measure. In all plots, each point is an individual participant, and correlation values are Spearman's partial rank correlation coefficients. Light red/blue dots denote young adults, and dark red/blue dots denote older adults.

Visual WM and visual matching

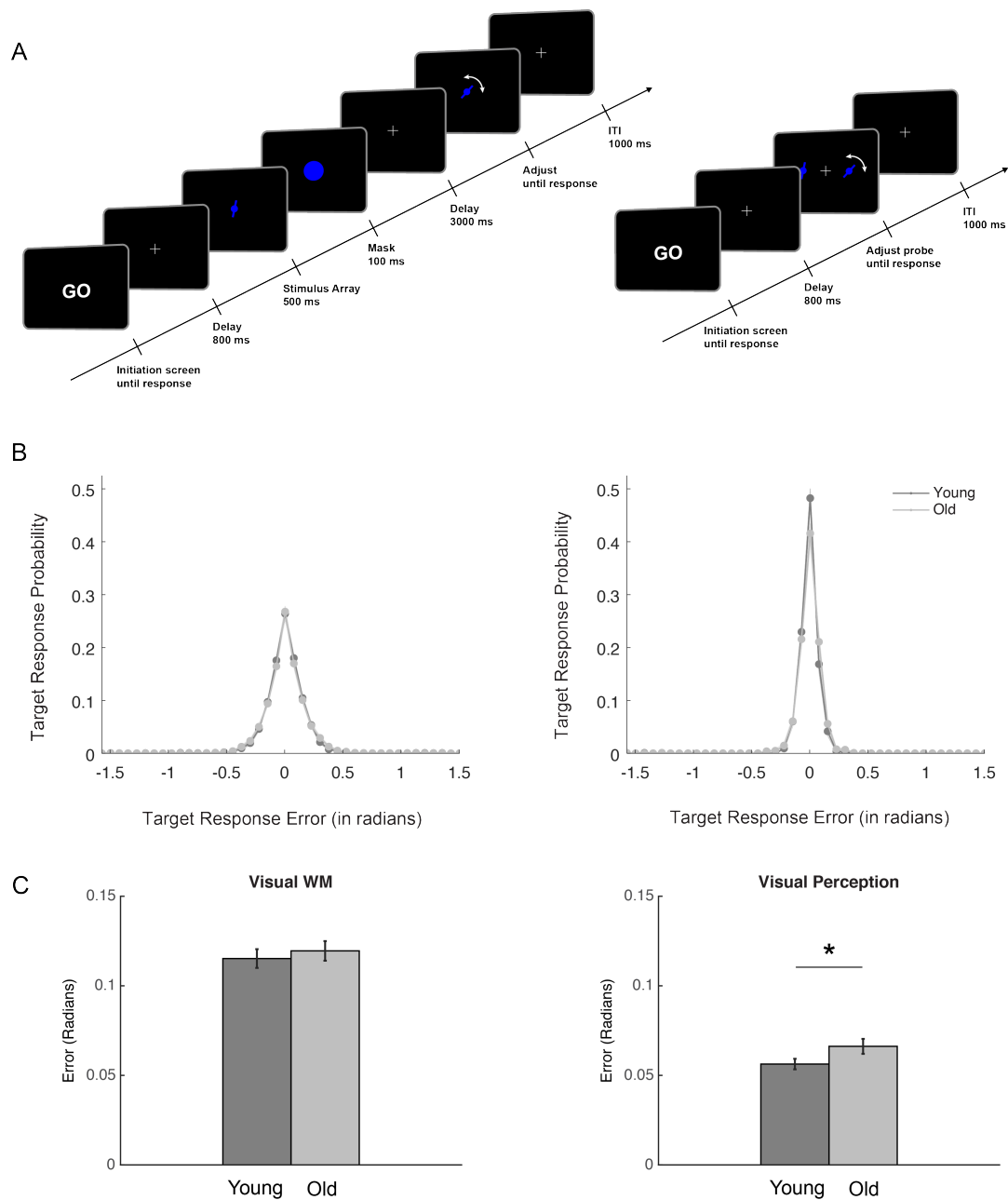


Figure 5.9. Task schematics and behavioural performance for non-emotional visual WM and visual matching. A) Left: Task schematic for visual WM. After initiating the trial with a mouse click,

participants encoded an orientation into memory. After a fixed delay of 3000 ms, a probe stimulus appeared at a random orientation. Participants made their response by changing orientation of this stimulus to match the orientation in memory using a trackball mouse. The inter-trial-interval was 800 ms. Right: Task schematic for visual matching. After initiating the trial with a mouse click, participants are simultaneously presented with two orientation stimuli on the left and right of the screen and adjust the right stimulus to match the orientation of the stimulus on the left. The inter-trial-interval was 800 ms. B) Left: Error distributions for visual WM centred on the target orientation for young (dark grey) and old (light grey) participants. Right: Error distributions for visual matching task centred on the target orientation for young (left, dark grey) and old (right, light grey) participants. For all histograms, the error probability is plotted at each bin and connected by the lines, and the shaded areas show the standard error of the mean. Bins are equally spaced from $-\pi/2$ to $\pi/2$ in steps of 0.075, x-axis is the response error in radians, y-axis is the response error probability. C) Error (mean of the unsigned error distributions in B) for the young (dark grey) and old (light grey) participant groups. * denotes $p = 0.028$, one-tailed.

Participants performed very well on the visual WM (mean unsigned error in radians (young / old): 0.115 ± 0.005 / 0.120 ± 0.006) and visual matching task (0.056 ± 0.003 / 0.066 ± 0.004 ; figure 5.9). All participants performed better for the visual matching task compared to the visual WM task ($F(1,102) = 267.13$, $p = 3.01 \times 10^{-30}$, $\eta^2 = 0.72$; $t(104) = -16.14$, $p = 4.30 \times 10^{-30}$, effect size: -1.70), a trend for a main effect of Age ($F(1,102) = 3.26$, $p = 0.07$, $\eta^2 = 0.03$), and no interaction between Task and Age ($F(1,102) = 0.24$, $p = 0.63$, $\eta^2 = 0.002$). I hypothesised that younger participants should be better at visual WM, and this difference should be greater than the effect on age on visual matching. Young adults were numerically better but not significantly better than old adults at the visual WM task ($t(102.5) = -0.56$, $p = 0.29$, one-tailed, effect size: -0.11). However, young adults were significantly better at the visual matching task compared to the older adults ($t(90.8) = -1.93$, $p = 0.028$, one-tailed, effect size: -0.38).

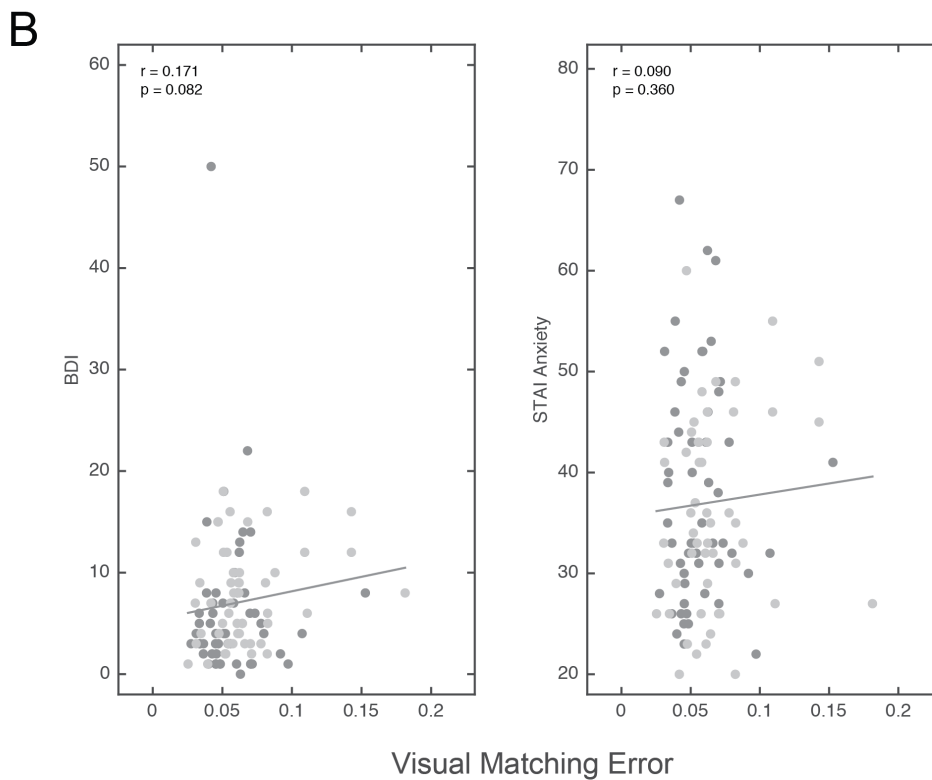
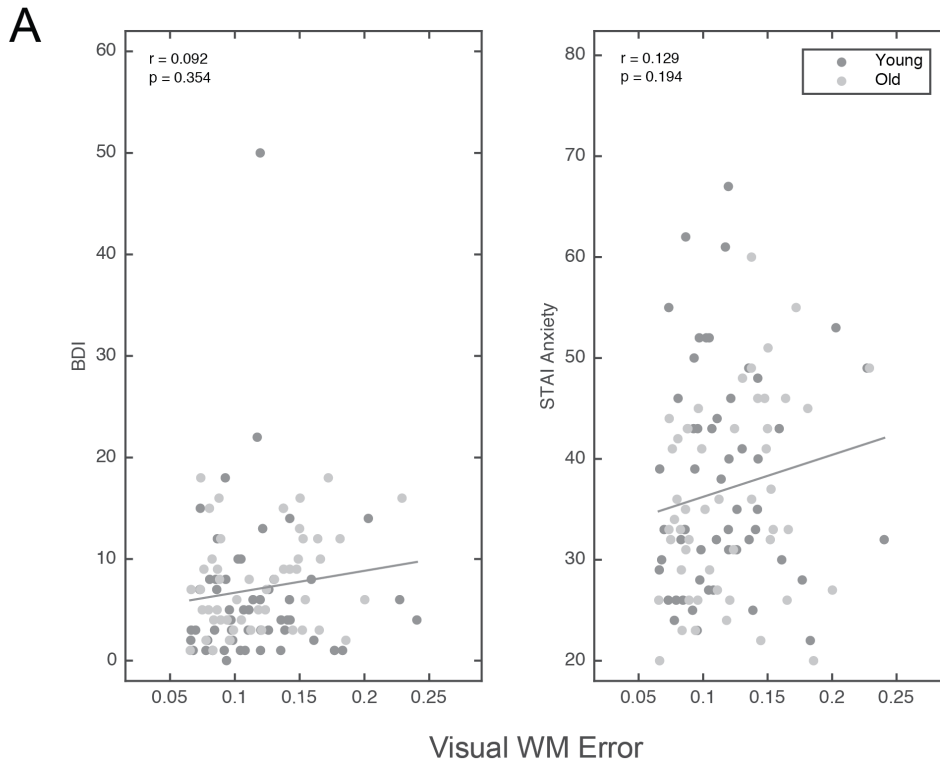


Figure 5.10. Correlations between depression/anxiety and non-emotional WM and perceptual matching performance. A) Scatter plots of depression/anxiety measures as a function of non-emotional WM error. X-axis is non-emotional WM error, y-axis is the depression/anxiety measure. B) Scatter plots of depression/anxiety measures as a function of non-emotional perceptual matching. X-axis is non-emotional perceptual matching error, y-axis is the depression/anxiety measure. In all plots, each point is an individual participant, and correlation values are Spearman's partial rank correlation coefficients. Dark grey dots denote young adults, and light grey dots denote older adults.

Discussion

Using a novel emotional working memory and emotional expression-matching task in a large sample of younger and older adults, I found that older adults were impaired in the ability to match emotional expressions for perception and WM, they under-reported the emotional intensity of fearful faces and misreported fearful faces as happy to a greater extent than their younger counterparts. In younger adults, WM abilities for happy faces were correlated with depression scores.

Older adults were impaired in both the WM and matching task with emotional facial expression stimuli, indicating a decline in emotion recognition (Ruffman et al., 2008). I hypothesised that WM for emotional material, independent of visual abilities, would be impaired with ageing (e.g. Nilsson, 2003), and that there could be a particular memory benefit for positive stimuli (Mather & Carstensen, 2005). However, there was no additional detriment in the WM task compared to perceptually matching the emotional expressions. This is consistent with previous studies which have suggested that WM for emotional content is preserved in healthy ageing regardless of the valence (D'Argembeau & van der Linden, 2004; Hartley et al., 2013; Mammarella et al., 2013). However, I found that this effect is not specific to WM. In this study, I tested both WM and visual abilities for emotional material, whereas others have only compared emotional and non-emotional stimuli. I note that it is difficult to conclude that there is in fact a benefit for emotional material for WM with the lack of an effect, but it raises the important point that emotion researchers should also test for visual abilities in processing emotional material as well as non-emotional WM and visual perception in order to test whether their effects are specific to WM for emotional material.

Older adults underestimated the emotional intensity of fearful faces and misinterpreted low intensity fearful faces as happy faces more than young adults, suggesting an attenuated representation of negative information, and a positive interpretation bias. Previous theoretical and empirical work has suggested that older adults show a 'positivity bias', in which older adults selectively attend to positive stimuli to a greater extent to negative stimuli (Carstensen et al., 2003; Mather & Carstensen, 2005). In contrast, young adults exhibit a 'negativity bias', and preferentially attend to threat or fear-related stimuli more than positive or neutral stimuli (Rozin & Royzman, 2001). As outlined in the introduction, findings on the positivity bias in older adults are, however, mixed (Murphy & Isaacowitz, 2008). In the present study, older adults tended to underreport the emotional intensity of fearful faces. In addition, older adults misreported fearful faces as happy to a greater extent to their younger counterparts. These data suggest that older adults exhibit an attenuated representation of negative information in both perception and WM, and a positive interpretation bias when there is a categorical decision to be made (making a judgment as to whether a face was happy or fearful at the response). Young adults, on the contrary, showed no significant bias in the representation of negative information, and had a greater tendency to misreport happy faces as fearful more than misreporting fearful faces as happy compared to older adults (although note that the proportion of misreporting happy faces as fearful itself was not significantly different to the older adults). The mixed results in the literature may stem from different sources of error in participant responses that traditional measures of behavioural performance cannot separate. Measures of 'bias' have ranged from reaction-time measures in attentional tasks (how much attention do you allocate to a certain location) to accuracy measures (how much better are participants at remembering or recalling emotional material from memory), which might conflate biases for the perceptual or mnemonic representation of emotional information versus interpretation biases. The current paradigm was able to characterise how participants represent emotional information and their categorical interpretation of stimulus valence

(happy, fear). It is worth noting that the reduced negative bias was a weak effect: there was no Emotion by Age interaction in the main analysis, but the effect was significant in the hypothesis-driven comparisons. This is consistent with the weak effects in the literature. However, the tendency for older adults to misinterpret fearful faces as happy was statistically robust, suggesting a positive bias in the older adults when faced a categorical judgement when interpreting affective valence.

There was a dissociation between emotional WM and perceptual matching, in which participants, as a group, underestimated the intensity of fearful faces in perception and underestimated the intensity of happy faces in WM, but showed no such effect in WM for fearful faces or perceptual matching of happy faces. If we take perceptual matching performance 'bias' as the emotional intensity that participants actually perceive, this suggests that fearful faces are remembered as more fearful when recalled from memory, and happy faces are remembered as less happy when recalled from memory. This is consistent with the idea that negative stimuli attract more attention, and it is important to prioritise the intensity of the negative stimulus in memory in case it becomes behaviourally relevant later on (LeDoux, 2003; Phelps, 2006; Vuilleumier & Driver, 2007). On the other hand, a positive stimulus would signal that pleasant things could be in the environment, but nothing of immediate behavioural importance. It might be a better strategy to overestimate the negative information in case a negative event is to happen, especially when there are memory constraints. However, there is no potential disadvantage of underestimating the intensity of a happy face, and the intensity simply reduces with memory degradation. Future work should test whether there are differences in the way we represent information in perception compared to those in memory, and the brain systems that might correspond to these differences.

I found a significant correlation between depression scores and WM for happy faces, but not with emotional expression matching of happy faces. Inspecting this correlation for younger and older adults separately showed that the effect was mainly driven by the young group. Interestingly, depression scores (BDI) were not correlated with the tendency to report emotions as more or less emotionally intense than they were perceived (bias), which is what one might have expected. In fact, it was the performance error, which corresponds to a greater mean deviation from the target intensity irrespective of overestimating or underestimating the intensity. This means that participants with higher depression levels seemed to report happy faces as more happy than they actually were on some trials, and less happy than they actually were on other trials; they were more variable. One intriguing possibility could be that participants with higher depression scores in general might show greater fluctuations in performance that correspond to fluctuations in mood. It would be interesting to record mood state after each individual trial to test if the trial-by-trial variability could be explained by trial-by-trial fluctuations in mood over short time-scales. I note that our group has relatively low depression scores compared with individuals with clinical depression. It will be interesting for future studies to use this paradigm in a group with higher depressive symptoms to test whether this result holds up.

In previous studies testing WM for emotional content in healthy ageing, non-emotional WM and perceptual abilities were not assessed, which could differ markedly between age groups. I tested these abilities here using a simple load-1 orientation visual WM task and a perceptual matching task with the same orientation stimuli. Unexpectedly, there was no age-related WM deficit for non-emotional material in our group, even though such deficits are well documented (Salthouse, 2010). The current task required participants to hold one orientation stimulus in memory, which was likely very easy. Some researchers have found that when interference from irrelevant information is minimised, older adults perform as well as young

adults (May et al., 1999; G. Rowe et al., 2008, 2010). Since there was only one simple stimulus (no interference between multiple items in WM) and no distractor stimuli, one might expect older adults no age-related impairment. However, performance values were still numerically different between groups, so it was still useful as a measure of non-emotional WM performance as covariates in the main analysis. There was, however, a significant difference between age groups in the visual matching task. I hypothesised a difference in visual WM, and that differences in visual matching performance could account for the in visual acuity in the WM task. One possibility is that the visual WM task was low in cognitive load, and it was also straightforward in that participants simply had to monitor the centre of the screen for the target and response. In the visual matching task, participants were instructed to keep their head still, even though the stimuli were on the left and right of the screens. Therefore they had to move their eyes from left to right and back in order to match the orientations of the bars. This involves eye movements and therefore a combination of motor skills and visual skills, which might have been more difficult for the older adults. Future studies should include measures of non-emotional WM and visual perception in order to account for potential age-related differences that are not specific to emotion.

Using a novel emotional WM task and expression-matching task to assess age differences emotional processing, I found that older adults exhibited general deficits in cognitive tasks with emotional material, and showed an attenuated representation of fearful faces and a tendency to interpret ambiguous, low intensity fearful faces as happy to a greater extent than younger adults. The new task and response method provides rich behavioural data for individual participant's perceptual and memory representation on each trial. Future work should use more sophisticated behavioural measures to characterise how individuals represent emotional information, and test for the neural mechanisms that underlie these abilities using human neuroimaging. It will also be highly informative to investigate how the cognitive and

neural mechanisms are altered in patient groups with mood disorders. The current results show that older adults show a general deficit in cognitive tasks with emotional material and a tendency to report facial expressions more positively compared to young adults, which suggests that, as we grow older, we start downplaying our negative experience, and interpret things in a more positive light.

6. General discussion

Chapter Abstract

This general discussion outlines the key findings from the work presented in this thesis and their broader implications, and suggests how future studies can build on this work to reach a better understanding of WM in healthy ageing. This thesis has examined several aspects of WM and its associated functions that change with age, and the individual differences in brain function that correspond to differences in successful cognitive ageing. The key finding is that the neural mechanisms that support flexible control over WM can be relatively preserved in healthy ageing, and that attentional control can enhance behavioural performance in elderly adults and thereby mitigate some of the age-related deficits in WM function.

6.1 Overview of the Thesis

In Chapter 2, I presented evidence from an fMRI study which showed that older adults successfully recruit cognitive control networks during selective WM encoding, and that regions in the IFC play a role in modulating activity in the relevant sensory areas for attended and ignored stimuli according to task demands. In Chapter 3, I presented behavioural evidence that WM maintenance declines with age, but that the ability to orient attention within WM to enhance memory is preserved. In line with these results, older adults exhibited similar neural activity patterns to those found in younger adults during attentional orienting, and the temporal dynamics of these signals corresponded to the attentional benefits in WM performance. The second part of the thesis was concerned with whether the nature of the content of the information to be held in WM, focussing on affective stimuli, influences age-related changes in WM. In Chapter 4, I described how I developed a novel emotional WM task. In Chapter 5, I reported findings from testing younger and older adults in a series of WM experiments with and without emotional content. Although older adults showed general deficits in behavioural performance on tasks with emotional stimuli, they were not specific to WM. Overall, the work in this thesis has shed some light on the differential changes of WM functions in healthy ageing, with relatively intact control functions that can be used to support WM, and changes in WM performance for both non-emotional and affective stimulus content.

6.2. Selective attention can help mitigate working-memory deficits in ageing

Preserved mechanisms of top-down attention enabled older adults to prioritise items within WM to enhance behavioural performance. In Chapter 3, I presented a study showing that older adults experience strong attentional enhancements in WM performance with the help of spatially informative retro-cues. I found that WM maintenance (without cues) declined with age within the cohort of older participants I tested (60-87 years old). This age-related

impairment was significantly alleviated by the deployment of attention within WM. Even within the relatively narrow age range in the current study, there was a significant decline in WM performance with increasing age. However, the ability to use the retro-cue to enhance WM performance was not significantly correlated with age. That is, how well you can use the cue to enhance behavioural performance does not seem to be affected by increasing age. The benefits from a retro-cue were largely attributed to an increase in the probability that the target item was remembered, a reduction in the probability of reporting a non-target item, and, to a much lesser degree, the precision with which that item was recalled. The finding that a spatial cue helps reduce the proportion of non-target responses is particularly interesting, since older adults show higher proportions of erroneously reporting a non-target item (e.g. Cowan et al., 2006; Peich et al., 2013). Indeed, elderly adults in my study showed larger proportions of non-target responses when no informative retro-cue was available compared to younger adults in similar studies (e.g. Bays et al., 2009, 2011). Hasher and colleagues proposed that inhibition of task-irrelevant information was the key factor linked to age-related impairments in WM span tasks, in which items on past memory lists interfere with the current memory task (e.g. May et al., 1999; G. Rowe et al., 2008, 2010). In my study, older adults had a large proportion of non-target responses in trials where there was no retro-cue, suggesting that there was interference between memory items during WM maintenance. Consistent with these data and other 'prefrontal' deficits in ageing, researchers have suggested that impairments in executive function are responsible for WM deficits in old age (e.g. Hasher & Zacks, 1988; West, 1996). However, I found that attentional control for orienting within WM is preserved in older adults, suggesting that not all control functions related to WM are impaired. Indeed, when such control functions are preserved, they can be used to enhance WM performance. Since older adults seem to be prone to interference from other memory items, retro-cues could help by reducing interference within WM

representations. Therefore, reducing interference may be one of the key factors to minimising cognitive decline caused by reductions in WM capacity.

These results raise the intriguing possibility of training older adults to improve WM by reducing interference between items in memory. Retro-cues may help individuate and separate the representations in WM, thus reducing the rate of incorrect non-target responses. This suggests that training this individuation of representation might improve older adults' WM performance. Studies have shown that WM capacity for visual items can be enhanced when items can be grouped together (Woodman, Vecera, & Luck, 2003), but this type of strategy might also lead to more interference between items. This strategy can sometimes be used in the task here, since the orientation stimuli can be grouped as a single object depending on their orientations (e.g. four bars into the shape of a diamond). Older adults could be trained to separate items in WM and avoid using grouping strategies to minimise interference between items. In such a study, I would first determine the individuals' WM capacity, and start the cognitive training with a WM precision task (without cues) at or below their capacity. The key is to encourage the participant to remember each item individually and separate the memory items as much as possible in mind. As performance improves, I would increase the number of items and keep training the participant in the same way. Feedback would be given as to how much they are reporting the non-target items over a block of trials, as well as average WM accuracy. Separating the memory items could help stabilise representations in WM, rather than being in a 'fragile' state prone to between-item memory interference, and in turn decrease the non-target responses. Stabilisation of the memory items could also help to enhance the precision of the WM items. This cognitive training study could try to train participants to reduce between-item interference within WM and maintain a more robust memory representation during cognitive tasks. Relatedly, some studies have shown multitasking training can lead to benefits in WM (Anguera et al., 2013), and it could

be that multitasking training improved their ability to deal with interference in WM, since multitasking requires storing multiple task rules and avoiding confusion between the two tasks while performing each task.

6.3. Preserved neural mechanisms of selective attention for working memory in ageing

In accordance with the behavioural enhancements in WM by attentional cues in older adults, the imaging results presented in Chapter 2 and 3 indicate that the neural mechanisms that underlie top-down attention are relatively preserved in healthy ageing. In both studies, there were remarkable similarities in the neural mechanisms recruited during top-down attention for WM in older adults compared to those found in younger adults in other studies, but with some interesting differences. In Chapter 2, older adults recruited the fronto-parietal and cingulo-opercular networks during top-down attention for selective WM encoding that was qualitatively similar to the networks recruited in younger adults (Dosenbach et al., 2008; Petersen & Posner, 2012). There were also similar attentional modulations in category-sensitive areas in visual cortex during selective WM (e.g. Ranganath, Cohen, et al., 2004), with the strongest attentional modulations in the left PG (Gazzaley, Cooney, McEvoy, et al., 2005). However, in this group of older adults, activity in purported control regions in the IFC was more reliable in the left compared to the right, whereas other studies in younger adults with feature-based attention recruit more bilateral regions of the PFC (e.g. Chadick & Gazzaley, 2011) or only in the right hemisphere (e.g. Zanto et al., 2010, 2011). It would be interesting to investigate the changes in the degree of PFC lateralisation during selective WM by comparing activations in older and younger adults directly in the same study. One speculative possibility for any putative difference in lateralisation is that older adults may employ a verbal strategy to support good performance, such as reminding themselves of the block they are in by verbalising “face” or “house” in mind during the task. The activations in the left IFC included the IFG pars opercularis and triangularis (Broca’s area), which is

implicated in semantic processing. Semantic abilities are maintained through old age (e.g. Hedden et al., 2004; Nyberg et al., 2012), and it could be that older adults in this study employed these preserved abilities in semantic processing to support attentional control for selective WM. Although this is highly speculative, future studies could test this by employing a similar WM paradigm with articulatory suppression, in which participants have to store visual images in WM whilst producing irrelevant speech (e.g. counting from one to ten).

It would have been useful to include a subsequent memory test for the study presented in Chapter 2, to look at the individual differences in the degree to which the attended stimuli were remembered and the ignored stimuli were forgotten. This could have lent support to Hasher and colleagues' idea that older adults are impaired in ignoring irrelevant information by showing greater recollection of ignored stimuli (e.g. Campbell et al., 2010; Hasher & Zacks, 1988; J. B. Rowe et al., 2006; R. T. Zacks et al., 1996). Furthermore, attentional modulations during selective WM are related to whether or not stimuli are subsequently remembered, and correspond to individual differences in the cognitive health of attentional mechanisms in ageing.

In the study presented in Chapter 2, IFC activity was coupled with the activity in category-sensitive cortex, suggesting the IFC is involved in modulating the sensory representations in visual cortex (c.f. Higo et al., 2011; Nelissen et al., 2013; Zanto et al., 2010, 2011). This could be tested more specifically by employing multivariate decoding methods to investigate the representational content in ventral visual cortex (e.g. Kriegeskorte et al., 2008; Kriegeskorte, Formisano, Sorger, & Goebel, 2007) and testing whether the magnitude of the IFC response correlates with the representational distance between attended and ignored stimuli (e.g. activation distance between attended faces and ignored faces, and between attended houses and ignored houses; c.f. Nelissen et al., 2013). This would indicate that

control mechanisms in the IFC play a role in separating the representations of the attended and ignored stimuli during selective WM, and not only showing activity coinciding with sensory cortex. This was not possible in the current study since there were few trials in each condition per participant, and a large number of trials are required to successfully implement these techniques.

When older adults oriented attention within WM following retro-cues (Chapter 3), there was a transient lateralisation of alpha power in posterior cortices, similar to what has been observed in younger adults (Myers et al., 2015; Poch et al., 2014; Wallis et al., 2015). However, the signals related to spatial attention also exhibited some changes. First, the lateralised signals were not only in the alpha band but also in the beta band. Furthermore, the topographies differed markedly between frequency bands. Alpha lateralisation was mainly found in the posterior sensors, and beta lateralisation was mainly found in the motor and frontal sensors. Beta oscillations in motor and premotor cortex are often associated with movement preparation or execution. In this task, however, participants were not required to respond at the time of the cue and the cue did not allow them to prepare a specific movement, so this activity is unlikely to have reflected motor preparation or execution. The hand responsible for making the response was also not associated with the cued location. Another possibility is that older adults recruited additional neural activity in motor and frontal areas in order to perform the task. Beta oscillations have been recently proposed to play a key role in top-down attention (e.g. Bastos et al., 2015; Engel & Fries, 2010; X. J. Wang, 2010). Other studies have found that older adults seem to recruit additional activity from motor networks during cognitive and motor tasks (Deiber et al., 2013; Kopp et al., 2011; J. B. Rowe et al., 2006). Since the ability to orient attention within WM was relatively preserved in this group of elderly adults, the additional beta activity could reflect compensatory processes in the motor system to support flexible control for WM. How could the motor system help with this

task? What mechanisms for selecting memories could draw on beta oscillations? It has been suggested that orienting attention within WM using retro-cues involves the sequential activation of several cognitive control networks, with the fronto-parietal network first activated for spatial selection within WM, followed by the cingulo-opercular network that may be involved in selection of relevant representations for action – for output gating (Chatham, Frank, & Badre, 2014; Wallis et al., 2015). Parallel to a movement-based action-planning network in the PFC and basal ganglia, there is a cognitive action-planning network that is involved in selecting information that is likely to guide the upcoming behaviour (Dosenbach et al., 2008). This network is distinct from that which represents items in WM, so rather than changing the memory representation, it could move the cued item into a distinct state for action preparation via an ‘output gate’ (Chatham et al., 2014; Dosenbach et al., 2008; Wallis et al., 2015). One possibility is that older adults need to engage this system more than younger adults to prepare the relevant representations for action. Future studies will have to test whether the lateralisation of beta oscillations found here is related to compensatory processes, or is in fact an epiphenomenon that accompanies ageing but has no relevance to task performance.

To test whether the pattern of alpha/beta lateralisation in older adults is related to cognitive performance and if the beta oscillations are in fact compensatory mechanisms, one could use a longitudinal design and test the same participants again after a short time interval. If performance is maintained at a similar level with an increase in beta lateralisation, and poor performance coincides with a decrease in beta lateralisation, this would suggest that the beta lateralisation observed in the study presented here is related to compensatory processes that support flexible attention for WM in ageing.

Another way to test the role of alpha and beta oscillations in orienting attention within WM in older adults is to use neuro-feedback training with EEG or MEG to increase alpha or beta lateralisation related to the task. Neuro-feedback involves measuring and displaying brain signals to participants, who try to self-regulate their own brain function by trying to modulate the specific brain signal in the way instructed (Gruzelier, 2014). The idea is that if individuals can train themselves to enhance a brain signal related to a particular cognitive function, they could potentially improve the performance that relies on that function. In this case, participants might be asked to perform the spatial cueing task and are shown the amount of alpha or beta lateralisation recruited after each trial, and told to try to increase this type of activity during orienting attention within WM. Another way to train the participant could be to ask them to orient their attention to a certain location and show them the current degree of alpha or beta lateralisation, and train them to increase this signal of neural activity before training with the actual task. I would train participants to enhance alpha or beta lateralisation. After training, I would inspect whether the degree of change in alpha or beta lateralisation depends on whether the group was trained on increasing alpha or beta oscillations, and whether the effect in one or both of the frequency bands contributed to changes in performance. This training could be used in both younger and older adults, to explore whether the lateralisation of beta oscillations during attention is an age-specific effect or if it can also benefit younger adults.

Some researchers have suggested that older adults have a specific impairment in inhibiting irrelevant information in WM (e.g. Gazzaley, Cooney, Rissman, et al., 2005; Hasher & Zacks, 1988). Hasher and colleagues have suggested inhibitory deficits for WM including those around the time of stimulus encoding, and the deletion of items no longer relevant for behaviour (Hasher et al., 2007; Hasher & Zacks, 1988). Retro-cues might work by enabling the directed inhibition or deletion of irrelevant information in WM (e.g. Williams &

Woodman, 2012). Indeed, the retro-cueing paradigm shares features with directed forgetting tasks (cues that indicate items are to-be-remembered and to-be-forgotten items shortly after memory encoding) by Hasher and Zacks (Zacks et al., 1996). For instance, some work has shown that retro-cues essentially reduce the load or the number of items that are held in WM (Kuo et al., 2012). Behavioural and neural markers of older adults during retrospective attention (Chapter 3) are relatively preserved, suggesting no deficit in the ability to remove items from WM. However, the way in which the retro-cue produces behavioural benefits continues to be investigated (Souza & Oberauer, 2016). Some suggest that the cue allows protection of memory items from decay (Pertzov, Bays, Joseph, & Husain, 2013), others that the cued items change from a 'fragile' state that is more prone to interference to a more robust state (Sligte et al., 2008), still others that the cue allows re-distribution of resources between memory items (e.g. Bays & Husain, 2008; Ma et al., 2014). There might also be a role for rehearsal or 'refreshing' functions (e.g. Souza, Rerko, & Oberauer, 2015) since incidental retro-cues also improve WM (e.g. Zokaei et al., 2014). Retro-cues could also enhance performance by selecting the relevant representation to facilitate subsequent actions, also termed output gating (Wallis et al., 2015). Since older adults were not impaired as using retro-cues to enhance WM performance, retro-cues may not work by inhibiting irrelevant items but rather by one of these alternative mechanisms, which are preserved in healthy ageing.

6.4. Inter-individual differences in the neural markers of selective attention for WM in healthy ageing

I employed an inter-individual differences approach to study the neural processes that correspond to better versus worse behavioural performance during tasks of selective attention for WM. The wide range in behavioural scores and neural markers allowed the exploration for neural markers that corresponded to healthy cognitive ageing.

In the MEG study (Chapter 3), the individuals that had a larger benefit in WM performance with a retro-cue relative to a neutral cue exhibited a strong increase of alpha/beta lateralisation, which quickly returned to baseline; mirroring what has been found in younger adults (Wallis et al., 2015). However, those who had smaller benefits with a retro-cue showed a moderate increase of alpha, which lasted for a longer time period before returning to baseline. This was interpreted as a difficulty in orienting within WM, reflected in a lengthened period of neural activity that corresponds to selection or retrieval of WM.

In the fMRI study, there was a positive correlation between age and the coupling strength between the left IFC and the relevant category-sensitive visual areas during selective attention for WM encoding. More specifically, in the old-old adults, activity in the left PG was coupled with a larger – or spatially more distributed – region of the IFC compared to the young-old adults. Behavioural performance did not vary as a function of age, likely because it was an easy task with performance levels near ceiling. The younger subgroup of old adults might have found the task relatively easy, recruiting a moderate level of IFC activity to modulate sensory cortex, whereas the older subgroup may have exerted slightly more cognitive effort in order to reach good performance, linked to more IFC activity to modulate sensory cortex effectively during selective WM. The additional recruitment in the older old adults could reflect additional neural resources required for good performance in the face of neural declines (e.g. Reuter-Lorenz & Cappell, 2008).

However, there is another possible interpretation. It could be that the additional activity in the older old adults is not related to the task, but instead reflects inefficient recruitment of unnecessary neural resources, and that only the centre of the IFC activation is really task-relevant. To choose between the two accounts, let us consider the relationship between

behaviour and functional activity. For instance, if the activity in older old adults in this region correlated positively with behaviour, this would suggest the additional activity reflects good use of neural resources to support behaviour. However, if the activity correlated negatively with behaviour, the additional recruitment would reflect an inefficient use of neural resources. Finally, if there were no correlation with behaviour, but with performance at ceiling level as observed here, this would point more toward the compensation account, since the old group exhibits matched performance with the young group with greater activity in the brain region of interest, suggesting a compensatory mechanism. A compensation account would be especially convincing if there were a positive correlation with performance in this area independent of age, but since there is not even a trend for a negative correlation suggests that it is likely not due to inefficiency (with the caveat that it is difficult to conclude this with the absence of an effect).

It would have been useful to include a young comparison group to test whether they would recruit as much activity as the younger subgroup of old adults tested, with the older subgroup showing more activity than both young and young-old adults, which would point toward the compensation hypothesis. However, a younger group may show differences for other reasons, such as less activity because the task was too easy and they did not need to recruit top-down neural resources to perform the task. Age-related vascular differences would also be impossible to avoid and differences are hard to interpret. Ideally, a longitudinal study could tell us whether or not older adults show increased brain activity with unchanged good performance corresponding to compensation, or unchanged (maintained at the same) neural activity with the same level of performance reflecting brain maintenance, or a decrease in the level of activity with reductions in performance levels corresponding to cognitive decline in ageing (e.g. Nyberg et al., 2010; Persson et al., 2012).

6.5. Discussion of fMRI results in light of recent reports of false-positives in fMRI cluster-wise inference

Eklund, Nichols, & Knutsson (2016) recently reported that common statistical packages that perform statistical inference on fMRI data (including FSL) produce a higher proportion of false positives than expected when using cluster-based statistics. In light of this recent paper, it is appropriate to discuss how my study should be viewed and what steps to take in the future. In the past, researchers have attempted to control error rates by simulating data with the temporal and spatial structure of fMRI data and testing how well the packages fared in terms of false positives. In this study, they used real resting-state fMRI data, selected epochs of the data assigned to condition A and condition B or condition A versus rest, and if error rates are controlled appropriately, there should be a 5% chance of false positives in this data (there should be no reliable differences between conditions since they are random epochs of resting-state data). They found that all commonly used packages (FSL, SPM, AFNI) had much higher false-positive rates than the 5% expected, with the highest at 70% (probability of having a false positive in the experiment; not that 70% of the results were false positives). There are several important points to note. At a more conservative cluster-forming threshold ($p = 0.001$ rather than $p = 0.01$), the probability of false positives reduced dramatically, with FSL FLAME (group analysis) reaching below the target 5% false-positive rate. Using voxel-wise inference rather than cluster-wise inference, error rate was controlled at approximately 5% for all packages, and using permutation statistics, error rate was properly controlled even with the more liberal cluster-forming threshold of $p = 0.01$). It is notable that FSL's FLAME (as used in the fMRI study here) had one of the lower false positive rates even for the cluster-forming threshold of $p = 0.01$, at approximately 10%.

The authors do not claim that all fMRI studies that have used these packages have produced false results, but that some of them could be called into question. Importantly, if the study is well powered and the statistics are reliable, then the main conclusions of the study will likely hold. The fMRI study I presented in Chapter 2 was well powered, and there were some strong hypotheses as to what we would be looking for, so I was able to perform both whole-brain analyses and ROI-based analyses for the attentional-modulation effects on the category-sensitive visual areas as well as the IFC (based on coordinates in the literature). In the future, it will be important to use a more conservative cluster-forming threshold for performing statistical inference, or alternatively use permutation testing or voxel-based inference – both of which control error rates sufficiently. Given these problems, it is also important to have strong hypothesis about our data when possible and define ROIs, which are more principled and are less likely to show false positives. In conclusion, I believe that the conclusions of my fMRI study are relatively well grounded, given that it is a well-powered study, I was able to confirm the validity of my results by having a priori hypotheses about certain brain regions of interest, and that I used FSL FLAME which had relatively better error rate control compared to other software packages.

6.6. Changes in WM and perception for emotional content in healthy ageing

The way in which emotional information is processed changes as we age (Grady, 2008; Mather, 2012). In contrast to many cognitive functions that exhibit declines in old age (Hedden & Gabrieli, 2004), older adults seem to be relatively unimpaired on tasks with emotional content (e.g. Calder et al., 2003; Keightley et al., 2006; Mammarella et al., 2013; Mikels, et al., 2005). In Chapter 4, I developed a new experimental task to test WM for

emotional content. In Chapter 5, I tested a large group of young and older adults to investigate how WM for emotional content changes with age.

I found that older adults were impaired at emotional WM. However, they were also impaired at making perceptual comparisons about the same stimuli, indicating that there was no specific deficit in WM for emotional content. There are several possible interpretations given these results. First, it is possible that older adults have deficits in perception, being less able to match emotional faces precisely. Since the accuracy impairment in WM for emotional content is completely explained by the accuracy differences in the perceptual tasks, it is unclear whether the older adults show a deficit in WM for emotional content. It is possible that older adults are relatively unimpaired in WM for emotional content after considering perceptual differences. Another possibility for the lack of a difference between WM and perceptual abilities for emotional content could be that there were significantly fewer trials in the perception task than in the WM tasks, since the focus of the study was on emotional WM. That is, a larger number of trials for the perception condition would make the statistical comparison more reliable and potentially show a difference. Future studies that aim to test WM for emotional content should put more emphasis on the perceptual version of the task. I used a non-emotional WM task in order to test for the age-related differences in WM for emotional versus non-emotional content. Unfortunately, the task chosen was too easy, and produced no differences in WM performance between the age groups. Future studies should use a sufficiently demanding non-emotional WM task (e.g. more complex visual stimuli similar to faces) in order to better compare WM for emotional versus non-emotional content. Although it is unclear whether affective content has a special status in WM for older adults, this study has shown how important it is to include a perceptual control of the WM tasks to ensure whether age-related changes are related to WM or actually already surface at the level of perception. Future studies should examine the question with different task parameters such

as higher WM loads, intervening distractors during WM encoding, or stimuli that match faces in visual complexity but not in emotion.

Interestingly, there were marked differences in how emotional information was reported between age groups. Older adults underestimated the emotional intensity of fearful faces to a small degree, and misinterpreted low intensity fearful faces as happy faces more than young adults. These results suggest that older adults do show an attenuation of negative information, and have a tendency to interpret information as more positive than younger adults. Researchers have suggested that older adults show a general ‘positivity bias’ across multiple domains of cognition (e.g. Carstensen & Mikels, 2005; Mather & Carstensen, 2005), but the studies that apparently lend support to this hypothesis have shown different patterns of effects, such as a reduced negative bias but not a positive bias, a positive bias but no reduced negative bias, or a greater positive bias than a negative bias. Here, in the same set of tasks (Chapter 5), I could separate two measures of bias. First, I found that when examining how emotionally intense a face is reported to be (continuous measure), older adults show a (weak) reduced negative bias compared to young adults. However, when examining the reported valence of an emotional face (happy or fearful), older adults reliably reported fearful faces to be happy faces more often than the younger adults. This tells us that the bias measure can be quite different and can be interpreted differently depending on the task instruction, the response method (e.g. two-alternative forced-choice, free recall), and the judgement (match/non-match, matching to an item in WM). That is, effects could be diluted because different opposing biases could be measured in the same response (see the next paragraph for examples of the different measures of bias). This could be part of the reason why studies on the positivity bias in ageing are mixed (e.g. Murphy & Isaacowitz, 2008), and it might be important for the field to provide clearer hypotheses on the specific pattern of bias, and the

types of biases one might expect in different tasks, rather than simply refer to a 'positive' or 'negative' bias.

The task used in Chapter 5 was able to separate different types of bias, providing measures of two different aspects of emotional processing to understand the features of WM and perceptual performance. This could be useful to test groups with mood disorders in order to separate the different types of emotional biases they might experience. Previous tasks have used the attentional dot-probe task, which focuses on characterising the *attentional* biases to positive or negative stimuli indexed by the relative difference between RTs for affective versus neutral stimuli (e.g. Fox et al., 2001). The idea is that the faster participants make a detection or discrimination response to a probe stimulus that followed an affective stimulus relative to the neutral stimulus, the more they preferentially process stimuli of that affective valence (greater positive/negative bias). This is an indirect measure of bias (since the response is not a judgment on the stimuli but on the probe that follows it), which also relates to individual differences in selective attention and inhibition of irrelevant information. This task only tests attentional bias for affective information, one aspect of affective bias. Furthermore, the reliability of the dot-probe task as measuring allocation of spatial attention has also been questioned (Schmukle, 2005). Another problem is that the task is highly dependent on RTs, which may be unsuitable for certain populations such as older adults and clinically depressed patients. There are benefits of these tasks, in which participants make a judgement independent of the affective value of the stimulus, so that the effect might be less dependent on subjective biases and more dependent on automatic, unconscious biases that occur in the brain (e.g. E. Fox, 2002). However, the shortcoming of these tasks is that it does not test subjective judgment, which is a useful measure for understanding affective changes in mood disorders. Another task that has been used is an emotion categorisation task in which participants are presented with an emotional face and asked to judge which of six emotions

the face belongs to (anger, disgust, fear, happiness, sadness, surprise). This has been used to test negative biases in patients with mood problems and the changes in affective biases after antidepressant medication (e.g. Chan, Harmer, Goodwin, & Norbury, 2008; Chan, Norbury, Goodwin, & Harmer, 2009; Harmer et al., 2003, 2009). For example, Harmer et al., (2009) showed that a single dose of antidepressant medication (reboxetine, a norepinephrine reuptake inhibitor) increased depressed patients' ability to recognise happy faces, even with no immediate change in mood. However, this task mainly tests how participants interpret the affective valence of the faces. It is still a categorical judgement that does not tell us how positive or negative they interpret a face to be. It might be interesting to combine the emotion categorisation task with the WM precision task presented here to add an additional measure of bias to the original categorisation task. For instance, individuals could be presented with faces with varying emotional intensities from any of the six emotion categories, and they have to make a judgement as to which emotion it was, then adjust the face to how emotionally intense they remembered it to be. This could tell us the interpretation of the emotion type and then the intensity to which each emotion was perceived. In the task developed in this thesis, it is possible to measure both the interpretation bias like in the emotion categorisation task, but also the intensity to which individuals perceive the affective stimuli. The intensity judgment provides a direct measure of affective judgment bias, rather than an indirect measure such as an affective RT difference. The task I developed also emphasises accuracy over fast responses, which is more appropriate for older adults and clinical populations with mood disorders. I aimed to test individual differences in WM for emotional faces related to trait anxiety, but found that the task seemed to correlate more with depression scores. It would be interesting to use this task in a group of participants with a larger range of BDI scores to test whether this task actually taps into the affective changes in depression rather than anxiety. Overall, studies would benefit from applying several tests rather than a single

test in order to assess different types of affective biases, which could tell us more about the differences in processing biases between age groups or individuals with mood problems.

The work in this thesis involved developing a new emotional WM precision task and testing a group of younger and older adults on a simple version of the task. Future studies can build on this paradigm and test questions about WM for emotional content. For instance, one could include distractor faces that are to be ignored, and test if the distractor faces influence the emotional intensity of the target faces, and if they influence the probability of recalling the target to be one valence or the other. Would predictive cues help with deficits that older adults experience with emotional WM and perceptual tasks?

6.7 Concluding remarks

In healthy ageing, a reasonable number of cognitive functions will show significant decline. However, there are some cognitive functions that are relatively preserved in old age, which can be utilised to support other domains of cognition that experience decline. The work in this thesis has shown that top-down attentional control functions are relatively preserved in healthy ageing and can help support good WM function. Emotional stimuli may also have a special status in perceptual and WM function. Future work should keep exploring the cognitive control functions that are preserved in age and their neural bases, in order to discover the mechanisms of 'healthy' cognitive ageing rather than focussing on its declines. These preserved functions can be used to improve cognition in normal ageing, and knowledge of the mechanisms that underlie healthy ageing may potentially help with the development of treatments and therapies for age-related disorders, such that instead of trying to revive the mechanisms that are destined to decline, we should train and exploit those that are preserved, and so capitalize on the strongest aspects of cognition in the ageing brain.

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7. Appendix



Figure S2.1. All face stimuli used in the main task.



Figure S2.2. All house stimuli used in the main task.



Figure S2.3. Face and house stimuli used in the practice session.

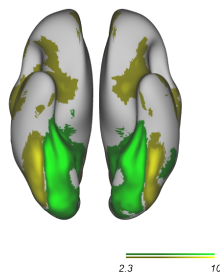


Figure S2.4. Localising face and place sensitive brain areas. The green clusters display the brain areas that showed greater BOLD activity for houses versus faces (parahippocampal gyri) and the yellow clusters display the brain areas that showed greater BOLD activity for faces versus houses (fusiform gyri at the lower part of this image). Note that the bilateral frontal operculum and a part of the orbital frontal cortex, also show greater BOLD activity for faces relative to houses.

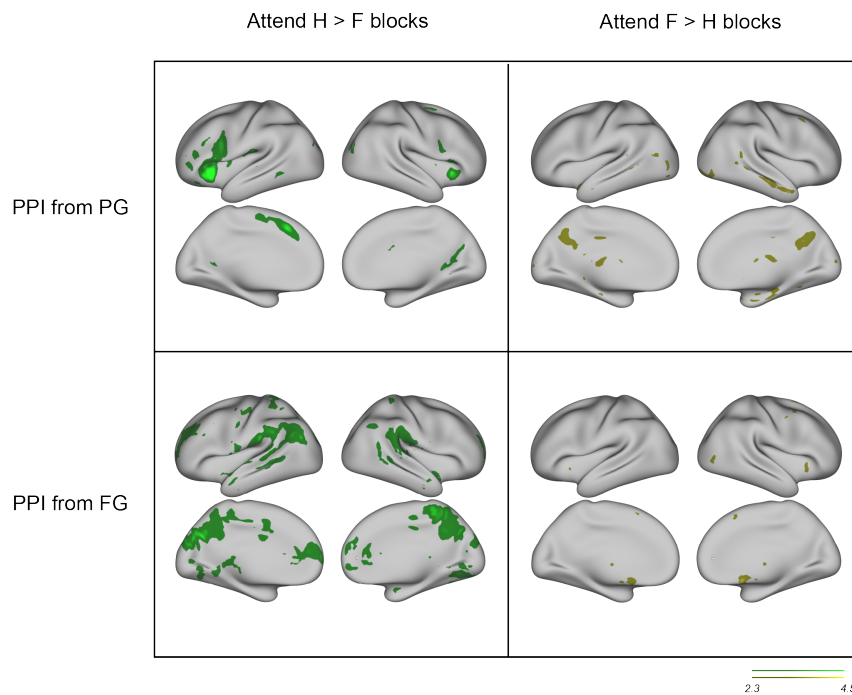


Figure S2.5. Uncorrected z-statistic images showing functional connectivity (psychophysical interaction) between category-sensitive visual areas (parahippocampal gyri, fusiform gyri) during selective encoding of houses versus faces.

Location	Cluster number	Z value (peak)	x	y	z
Left occipital pole	1 (cluster extent: 69375 voxels; $p = 5.61 \times 10^{-45}$)	7.73	-20	-94	4
Left superior LOC	1	7.01	-34	-84	24
Left fO, insular	1	6.94	-30	24	-2
Paracingulate gyrus (cluster extends inferior to ACC, and superior to SMA)	1	6.59	-8	14	46
Left inferior LOC	1	6.59	-48	-64	-8
SFG (extends inferior to ACC, and posterior to SMA)	1	6.46	-2	18	54

Table S2.1. MNI coordinates and peak Z values from the significant cluster during encoding house stimuli into WM (house stimulus, attend houses) relative to ignoring house stimuli (house stimulus, attend-face blocks). The cluster is significant at the whole-brain level, $p = 5.61 \times 10^{-45}$. ACC: anterior cingulate cortex; fO: frontal operculum; LOC: lateral occipital cortex; SFG: superior frontal gyrus; SMA: supplementary motor area.

Location	Cluster number	Z value (peak)	x	y	z
Paracingulate gyrus / ACC, extends superior to SMA	1 (cluster extent: 10747 voxels; $p = 8.4 \times 10^{-15}$)	5.78	-6	20	44
Left fO / insular	1	5.45	-30	20	2
Left inferior LOC	1	5.34	-48	-70	4
Left temporal occipital fusiform cortex, posterior temporal fusiform cortex	1	4.64	-40	-46	-20
Left ITG,	1	4.59	-44	-52	-12

temporal occipital fusiform cortex					
MFG, SFG	1	4.52	-26	0	54
Right ITG, temporal occipital fusiform cortex	2 (cluster extent: 2336 voxels; $p = 7.8 \times 10^{-5}$)	5.64	46	-46	-16
Right inferior LOC	2	4.35	50	-70	-2
Right inferior LOC	2	4.12	50	-62	6
Right ITG, MTG.	2	4.01	54	-58	-6
Right inferior LOC	2	3.27	54	-82	2
Right inferior LOC	2	2.57	52	-74	-16

Table S2.2. MNI coordinates and peak Z values from the significant clusters during encoding face stimuli into WM (face stimulus, attend-face blocks) relative to ignoring face stimuli (face stimulus, attend-house blocks). Clusters are significant at the whole-brain level, $p < 7.8 \times 10^{-5}$. ACC: anterior cingulate cortex; fO: frontal operculum; ITG: inferior temporal gyrus; LOC: lateral occipital cortex; MFG: middle frontal gyrus; MTG: middle temporal gyrus; SFG: superior frontal gyrus; SMA: supplementary motor area.

Cluster number	Z value (peak)	x	y	z	Location
2 (cluster extent: 4384 voxels, $p = 1.49 \times 10^{-6}$)	3.91	-22	-60	-10	Left temporal occipital fusiform cortex, OFG
1	3.85	-32	-42	-22	Left posterior temporal fusiform cortex, temporal OFG
1	3.82	-32	-46	-24	Left temporal occipital fusiform cortex, posterior

					temporal fusiform cortex
1	3.58	-18	-68	-8	Left lingual gyrus, OFG
1	3.56	-36	-60	-16	Left temporal occipital fusiform cortex
1	3.56	-44	-50	-8	Left ITG, posterior temporal fusiform cortex
2 (cluster extent: 1176 voxels, $p = 0.025$)	3.71	34	-48	-24	Right temporal occipital fusiform cortex
2	3.66	34	-62	-24	Right temporal occipital fusiform cortex
2	3.61	30	-58	-24	Right temporal occipital fusiform cortex
2	3.58	30	-60	-20	Right temporal occipital fusiform cortex
2	3.39	26	-70	-24	Right OFG
2	3.16	36	-78	-4	Right inferior LOC

Table S2.3. MNI coordinates and peak Z values from the significant clusters which exhibited a significant correlation between attentional modulation in the PG (attend houses > ignore houses) and digit span. Clusters are significant at the whole-brain level, $p < 0.025$. ITG: inferior temporal gyrus; LOC: lateral occipital cortex; OFG: occipital fusiform gyrus.

Cluster number	Z-value (peak)	x	y	z	Location
1 (cluster extent: 3746, $p = 5.36 \times 10^{-7}$)	4.11	-34	22	2	Left fO, insular cortex
1	3.83	-38	22	-4	Left frontal

					orbital cortex, insular cortex, fO
1	3.6	-50	-22	18	Left central opercular cortex
1	3.52	-36	0	26	Left precentral gyrus
1	3.34	-44	10	22	Left IFG pars opercularis
1	3.32	-48	10	24	Left IFG pars opercularis

Table S2.4. MNI coordinates and peak Z values from the significant clusters showing areas that were functionally coupled with bilateral PG during encoding house stimuli into WM (house stimulus, attend-house blocks) relative to ignoring house stimuli (house stimulus, attend-face blocks). Clusters are significant at the whole-brain level, $p = 5.36 \times 10^{-7}$. fO: frontal operculum; IFG: inferior frontal gyrus.

Cluster number	Z value (peak)	x	y	z	Location
1 (cluster extent: 14199 voxels, $p = 1.36 \times 10^{-16}$)	6.87	22	-86	-6	Right OFG
1	6.81	-22	-94	2	Left occipital pole
1	6.35	20	-92	2	Right occipital pole
1	5.8	-30	-88	26	Left superior LOC
1	5.69	-26	-90	18	Left superior LOC
1	5.34	-20	-88	-10	Right OFG
2 (cluster extent: 4958 voxels, $p = 5.96 \times 10^{-8}$)	3.99	-30	-26	64	Left postcentral gyrus, (extends to precentral gyrus)
2	3.7	-56	10	28	Left precentral gyrus, extends to left fO
2	3.66	-64	-26	36	Anterior SMG, postcentral gyrus
2	3.59	-66	-26	32	Anterior supramarginal gyrus, post-

					central gyrus
2	3.58	-6	8	62	SMA (extends superior to SFG and inferior to ACC)
2	3.5	-10	-10	64	SMA, SFG
3 (cluster extent: 1592 voxels, $p = 0.0028$)	3.96	-30	24	-6	Left fO
3	3.94	-34	24	-8	Left fO
3	3.9	-42	20	-4	Left fO
3	3.84	-38	26	-4	Left frontal orbital cortex, fO
3	3.8	-50	20	0	Central opercular cortex
3	3.76	-18	18	-12	Left putamen, extends to caudate

Table S2.5. MNI coordinates and peak Z values from the significant clusters for attending to house blocks (attend-house blocks, all stimuli) relative to attending to face blocks (attend-face blocks, all stimuli). The clusters are significant at the whole-brain level, p 's < 0.0028. fO: frontal operculum; SMA: supplementary motor area; SFG: superior frontal gyrus; OFG: occipital fusiform gyrus.

Cluster number	Z value (peak)	x	y	z	Location
1 (cluster extent: 988 voxels, $p = 0.035$)	4.79	2	-64	34	Precuneus

Table S2.6. MNI coordinates and peak Z values from the significant clusters for attending to attending to face blocks (attend-face blocks, all stimuli) relative to attending to house blocks (attend-house blocks, all stimuli). The cluster is significant at the whole-brain level, $p = 0.035$.

Cluster number	Z value (peak)	x	y	z	Location
1 (cluster extent: 3745 voxels, $p = 8.94 \times 10^{-7}$)	5.41	-30	24	0	Left fO/insular
1	4.1	-36	0	24	Left precentral gyrus
1	4	-50	-22	18	Left central/parietal operculum
1	3.84	-46	6	24	Left precentral gyrus/IFG pars

					opercularis
1	3.81	-46	12	2	Left fO, IFG pars opercularis
1	3.62	-42	-2	14	Central operculum

Table S2.7. MNI coordinates and peak Z values from the significant clusters showing areas that were functionally coupled with bilateral PG during house attention (all stimuli, attend-house blocks) relative to face attention (all stimuli, attend-face blocks). Clusters are significant at the whole-brain level, $p = 8.94 \times 10^{-7}$. fO: frontal operculum; IFG: inferior frontal gyrus.

Cluster number	Z value (peak)	x	y	z	Location
1 (cluster extent: 6726 voxels, $p = 5.49 \times 10^{-11}$)	4.6	-10	-72	32	Precuneus
1	4.37	6	-74	38	Precuneus, cuneus
1	3.97	14	-40	54	Right postcentral gyrus, precuneus
1	3.9	12	-40	58	Right postcentral gyrus
	3.87	-8	-88	32	Left cuneus, occipital pole
1	3.86	0	-82	26	Cuneus
2 (cluster extent: 4094 voxels, $p = 1.19 \times 10^{-7}$)	4.57	-18	48	20	Frontal pole
2	3.94	-14	60	4	Frontal pole
2	3.65	-6	64	8	Frontal pole
2	3.56	0	34	20	ACC, paracingulate gyrus
2	3.56	-10	44	14	Paracingulate gyrus, ACC
2	3.56	-14	58	10	Frontal pole, medial frontal cortex
3 (cluster extent: 3043 voxels, $p = 3.93 \times 10^{-6}$)	3.96	-26	-70	-16	Left OFG
3	3.93	28	-60	-16	Left temporal fusiform gyrus, OFG

3	3.81	24	-74	-14	Left, OFG
3	3.61	16	-68	-6	Left lingual gyrus
3	3.51	16	-72	-10	Left lingual gyrus
3	3.47	-14	-48	-4	Right lingual gyrus
4 (cluster extent: 2817 voxels, p = 8.76×10^{-6})	4.05	-62	-30	22	Left anterior SMG, parietal operculum
4	3.8	-46	-68	24	Left superior LOC
4	3.77	-56	-42	32	Left posterior SMG
4	3.57	-44	-58	28	Left angular gyrus
4	3.37	-42	-28	-4	Left posterior MTG
4	3.32	-60	-36	2	Left STG, posterior MTG
5 (cluster extent: 2108 voxels, p = 0.0001)	3.48	54	-30	30	Right parietal operculum, anterior SMG
5	3.45	62	-22	12	Right planum temporale
5	3.35	60	-28	-2	Right posterior STG, posterior MTG
5	3.34	56	-32	0	Right posterior STG, posterior MTG
5	3.29	62	-22	18	Right parietal operculum, planum temporale
5	3.28	64	-42	26	Right posterior SMG

Table S2.8. MNI coordinates and peak Z values from the significant clusters showing areas that were functionally coupled with bilateral FG during house attention (all stimuli, attend-house blocks) relative to face attention (all stimuli, attend-face blocks). Clusters are significant at the whole-brain level, p 's < 0.0001. ACC: anterior cingulate gyrus; MTG: middle temporal gyrus; SMG: supramarginal gyrus; STG: superior temporal gyrus; OFG: occipital fusiform gyrus.

Cluster number	Z-value (peak)	x	y	z	Location
1(cluster extent: 1237 voxels, $p = 0.008$)	3.38	-42	16	-4	Left fO, insular
1	3.38	-46	6	10	Left central opercular cortex
1	3.29	-44	16	0	Left fO
1	3.15	-44	14	6	Left fO, IFG pars opercularis
1	3.13	-30	20	-10	Left frontal orbital cortex, insular
1	3.07	-44	14	12	IFG pars opercularis

Table S2.9. MNI coordinates and peak Z values from the significant clusters which exhibited a significant positive correlation between the functional coupling strength with bilateral PG during house attention (all stimuli, attend-house blocks) relative to face attention (all stimuli, attend-face blocks) and age. Clusters are significant at the whole-brain level, $p = 8.94 \times 10^{-7}$. fO: frontal operculum; IFG: inferior frontal gyrus.

Cluster Index	Z	x	y	z	Location
1 (cluster extent: 1768 voxels, $p = 0.0008$)	3.6	38	-30	6	Right planum temporale
1	3.43	-14	-32	12	Left thalamus
1	3.37	16	-30	14	Right thalamus
1	3.35	24	-28	16	Right thalamus
1	3.32	14	-24	16	Right thalamus
1	3.29	36	-46	-10	Right temporal occipital fusiform cortex
2 (cluster	3.99	-48	-86	2	Left inferior

extent: 1032 voxels, p = 0.02)					LOC
2	3.65	-70	-46	-2	Left MTG
2	3.15	-60	-70	-4	Left inferior LOC
2	3.15	-40	-90	-8	Left inferior LOC, occipital pole
2	3.04	-34	-98	10	Left occipital pole
2	2.98	-60	-68	8	Left inferior LOC
3 (cluster extent: 957 voxels, p = 0.029)	3.37	10	-52	32	Precuneus
3	3.28	6	-62	38	Precuneus
3	3.16	-8	-60	34	Precuneus
3	3.14	-8	-58	42	Precuneus
3	3.13	-8	-60	38	Precuneus
3	2.92	0	-50	28	Posterior cingulate gyrus, precuneus

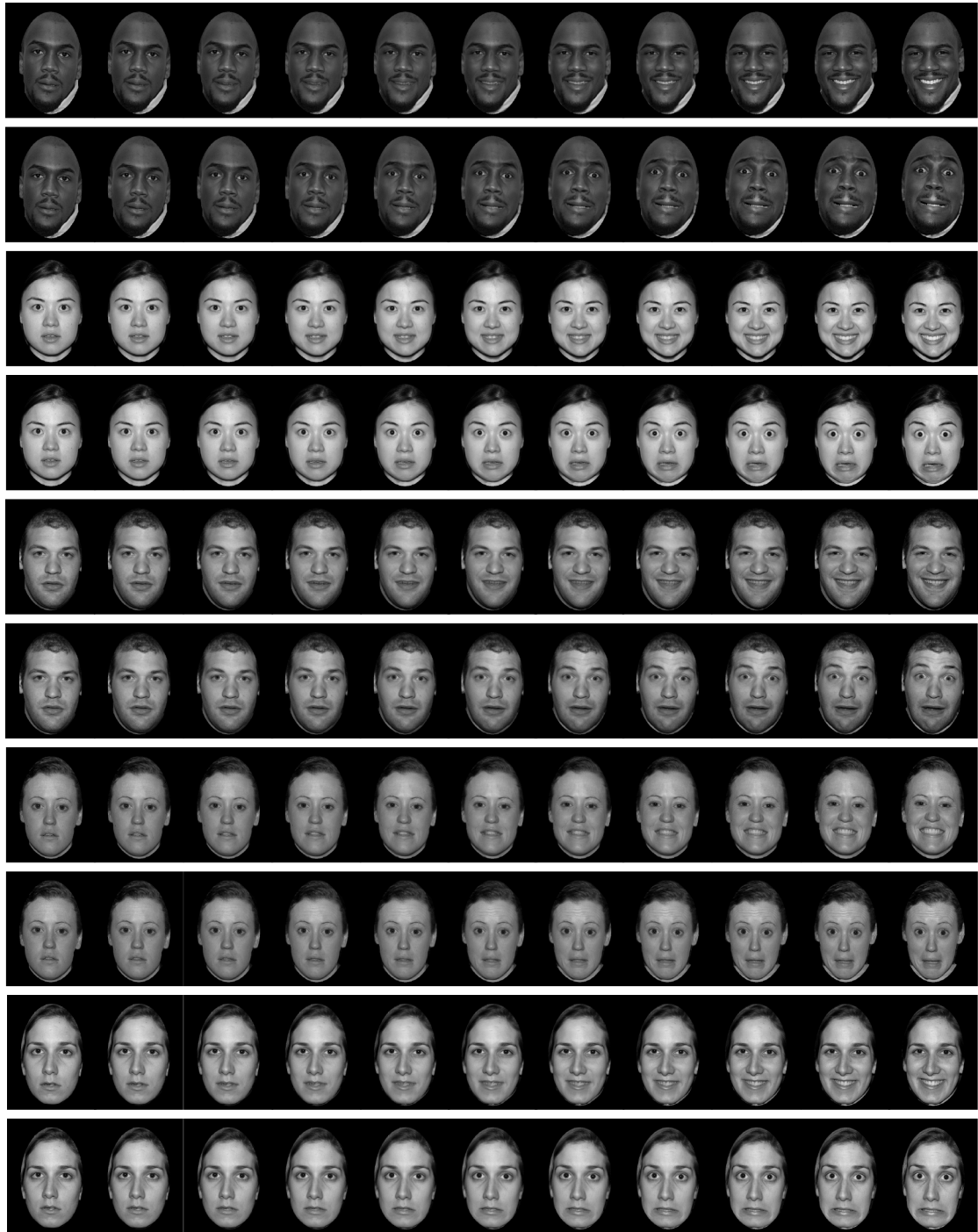
Table S2.10. MNI coordinates and peak Z values from the significant clusters showing areas that were functionally coupled with bilateral PG during face attention (all stimuli, attend-face blocks) relative to house attention (all stimuli, attend-house blocks). Clusters are significant at the whole-brain level, p 's < 0.029. LOC: lateral occipital cortex; MTG: middle temporal gyrus.



Figure S4.1A. Face stimuli used in the emotional WM and perceptual tasks.



Figure S4.1B. Face stimuli used in the emotional WM and perceptual tasks (continued from S4.1A).



S4.1C. Face stimuli used in the practice session of the emotional WM and perceptual tasks.



S4.1D. A selection of the face stimuli that were not used in the emotional WM and perceptual tasks.

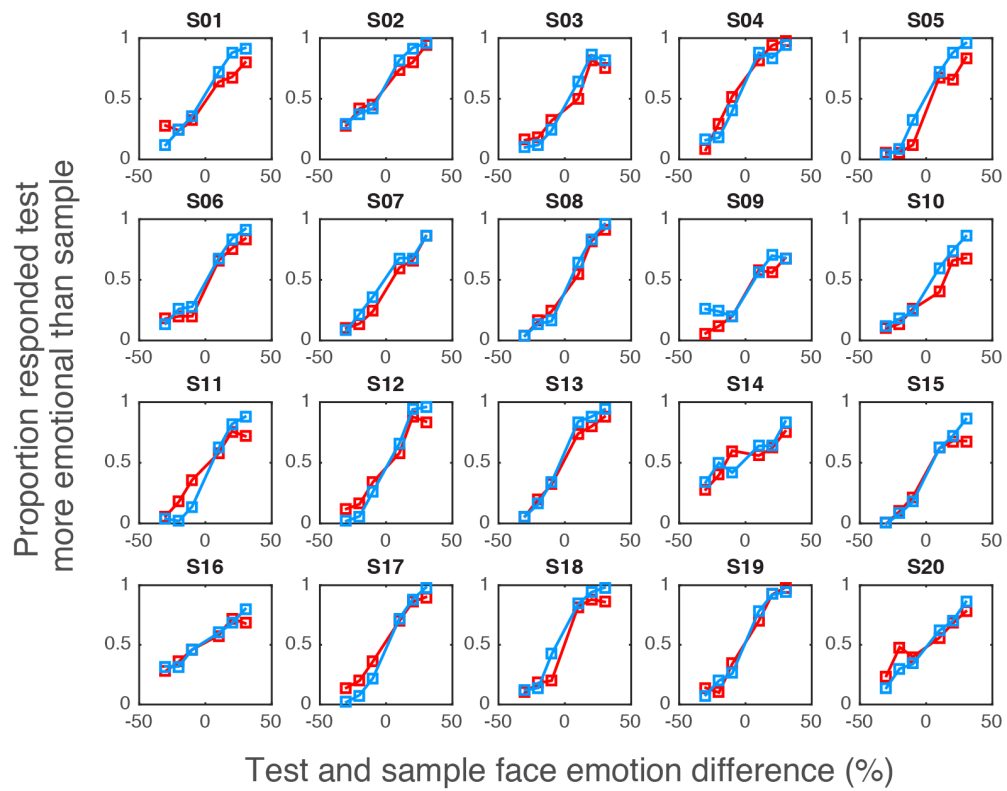


Figure S4.2. Psychometric functions for each individual participant in the emotional WM task.

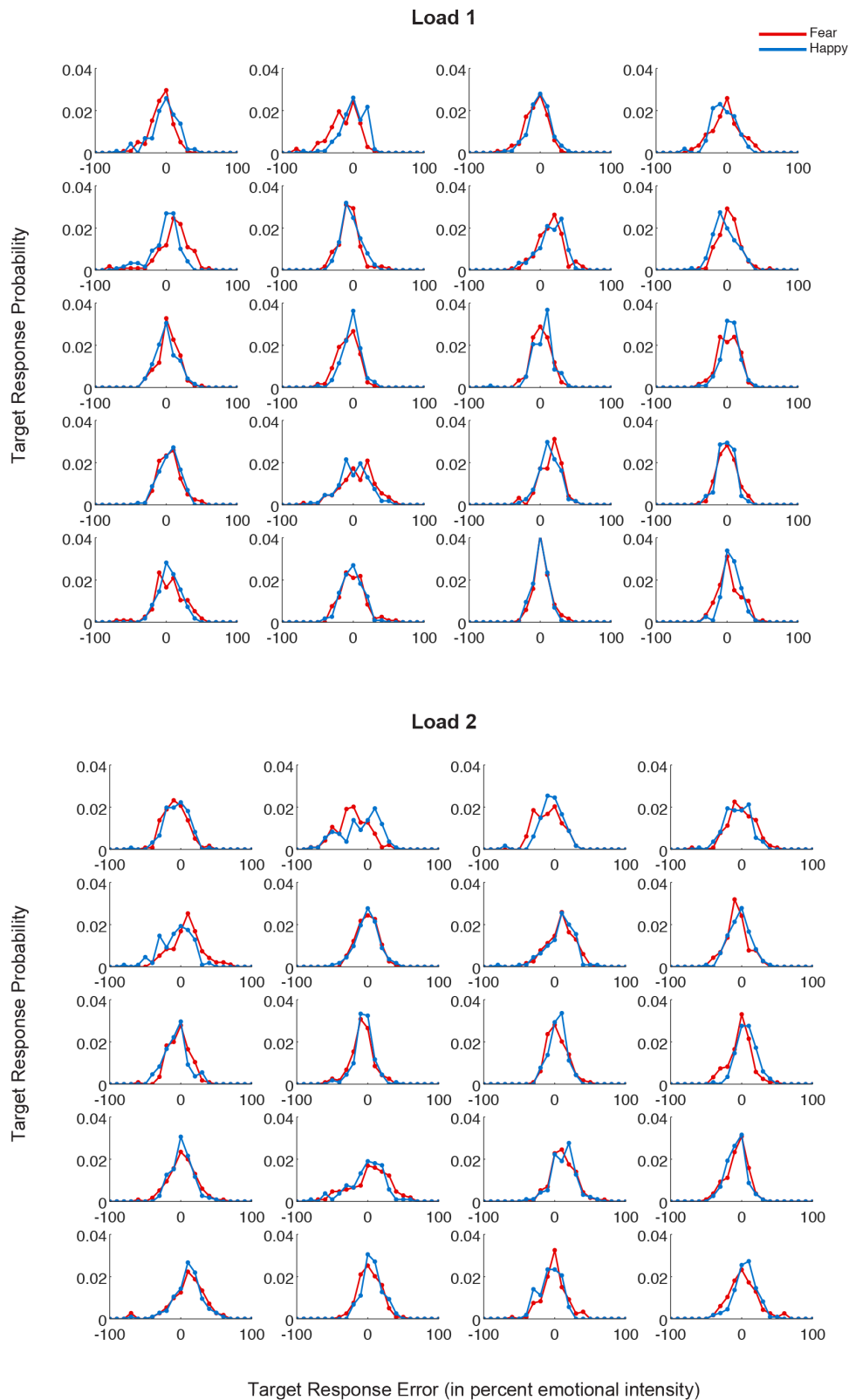


Figure S4.3. Error distributions for emotional WM centred on the target face emotional intensity for load one (top) and load two (bottom) conditions for individual participants. The error probability is plot at each bin and connected by the lines for fear (red) and happy (blue) WM conditions. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, Y-axis is the response error probability.

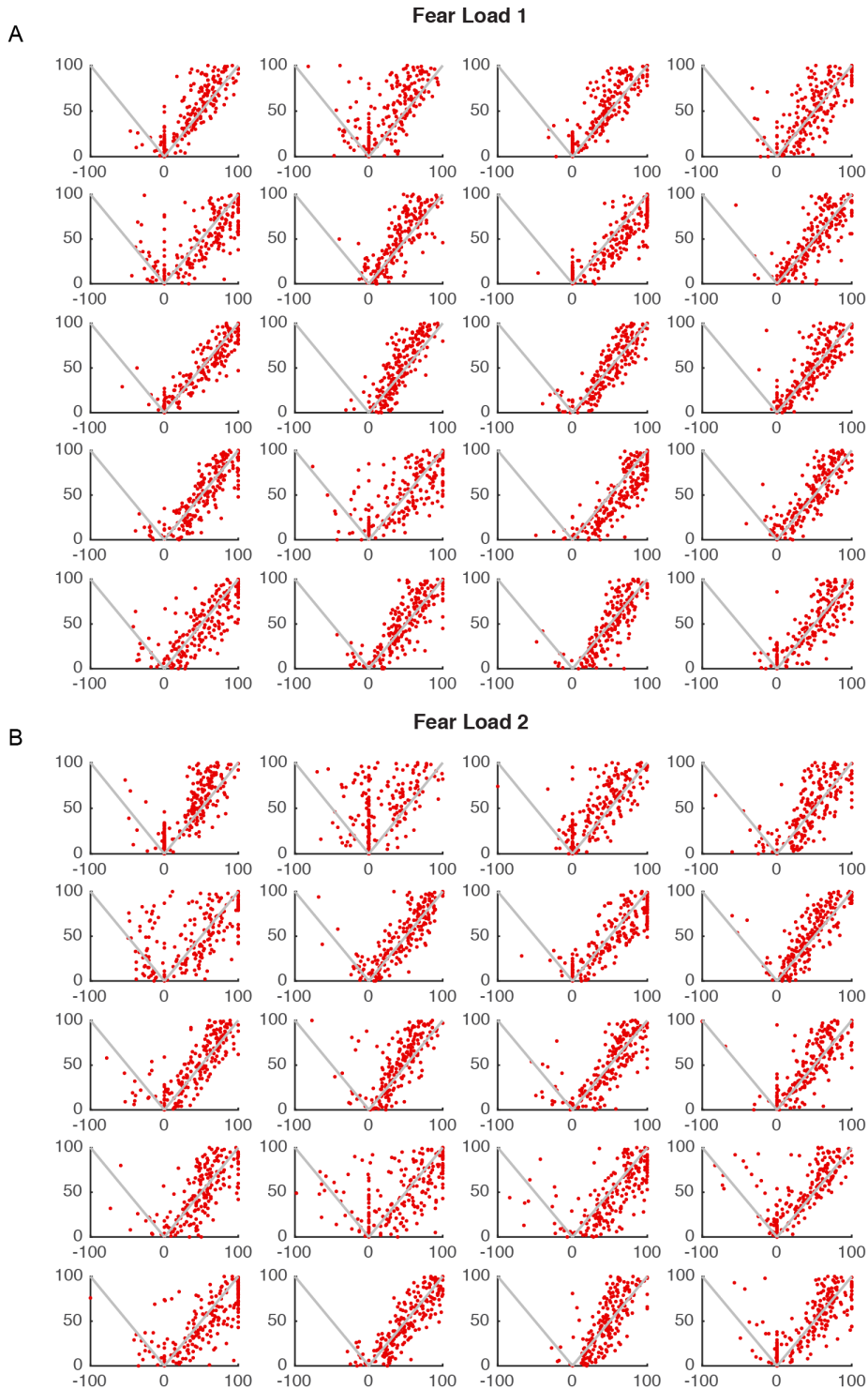


Figure S4.4A. Scatterplots of fearful target face emotional intensities plot as a function of responses for individual participants for emotional WM. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. Incorrect responses that reflect a 'mirrored' response (e.g. reported 50% fearful when it was a 50% happy face) would lie on a 'mirrored' version of the identity line ($y = -x$). Each subplot shows the data for an individual participant, and each point is an individual trial.

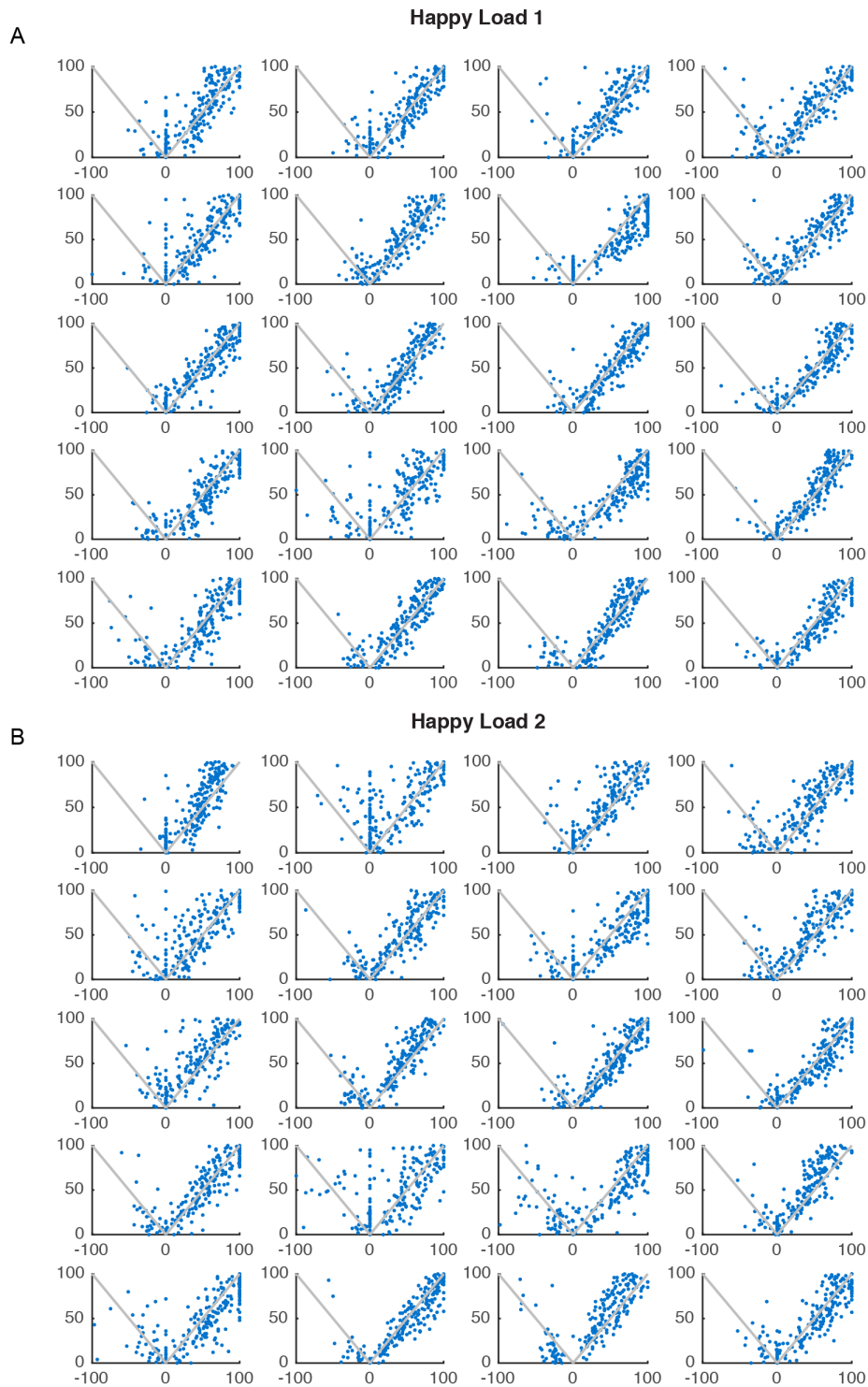
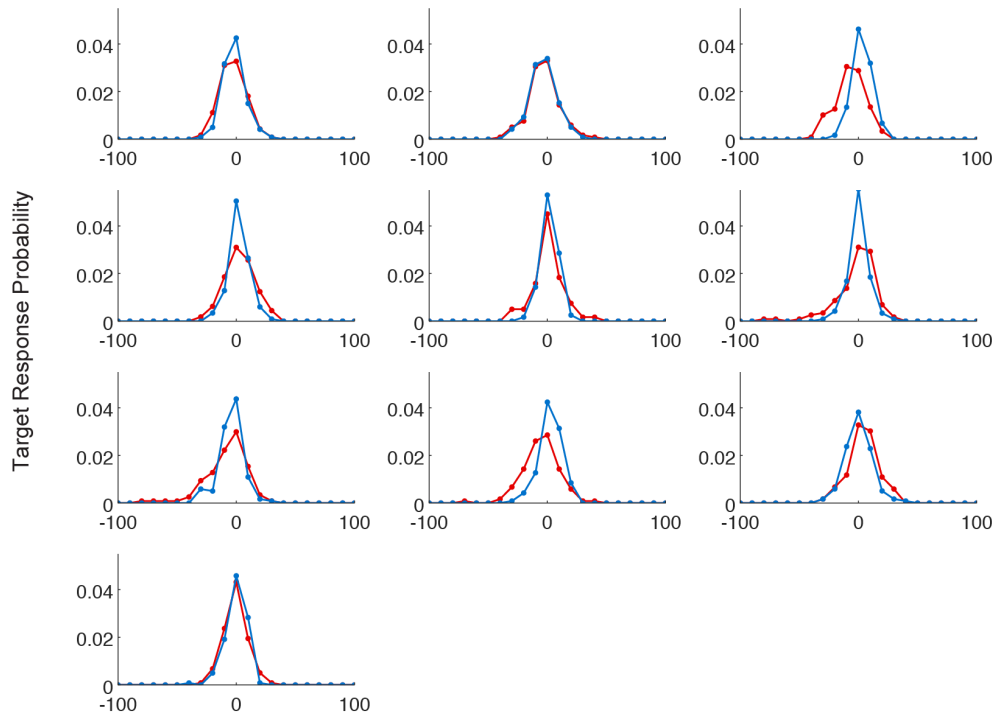


Figure S4.4B. Scatterplots of happy target face emotional intensities plot as a function of responses for individual participants for emotional WM. Conventions are the same as in figure S4.4A.



Target Response Error (in percent emotional intensity)

Figure S4.5. Error distributions for emotional-expression matching centred on the target face emotional intensity for individual participants. The error probability is plot at each bin and connected by the lines for fear (red) and happy (blue) WM conditions. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, Y-axis is the response error probability.

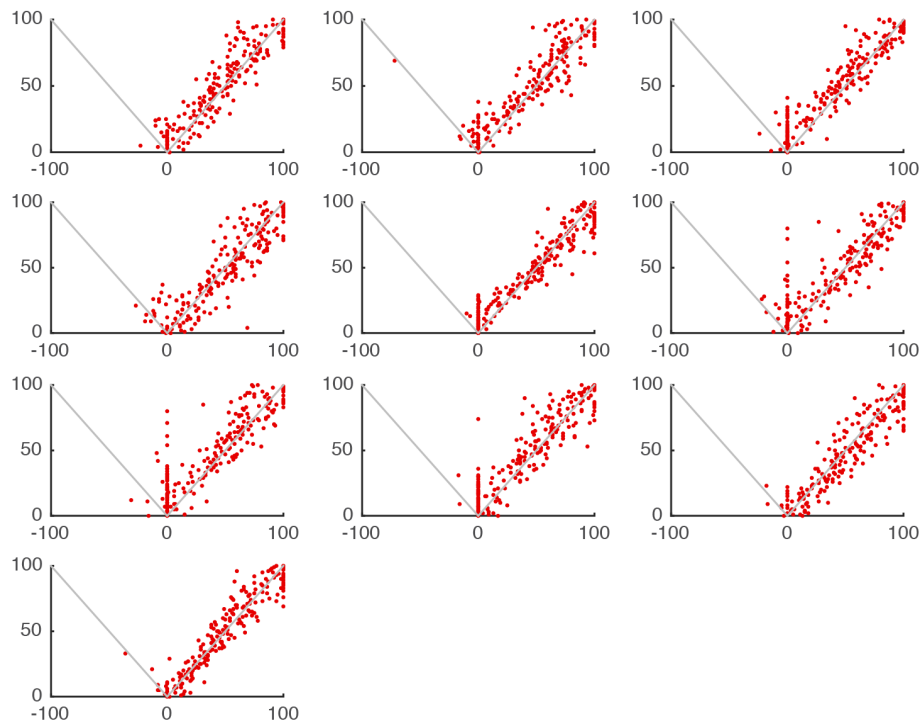


Figure S4.6A. Scatterplots of fearful target face emotional intensities plot as a function of responses for individual participants for emotional-expression matching. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. Incorrect responses that reflect a 'mirrored' response (e.g. reported 50% fearful when it was a 50% happy face) would lie on a 'mirrored' version of the identity line ($y = -x$). Each subplot shows the data for an individual participant, and each point is an individual trial.

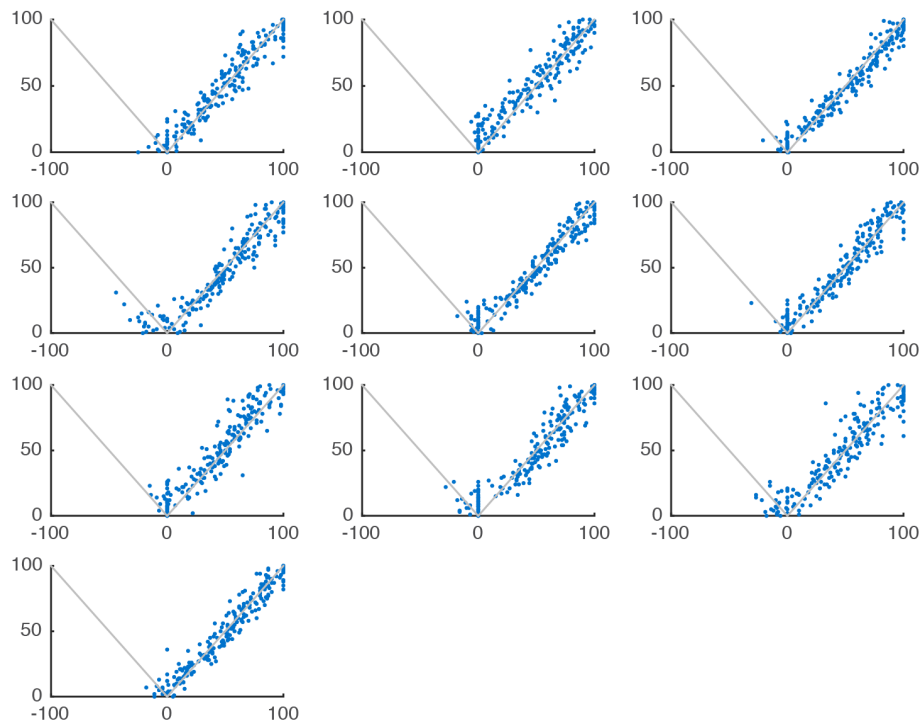


Figure S4.6B. Scatterplots of happy target face emotional intensities plot as a function of responses for individual participants for emotional-expression matching. Conventions are the same as in figure S4.6A.

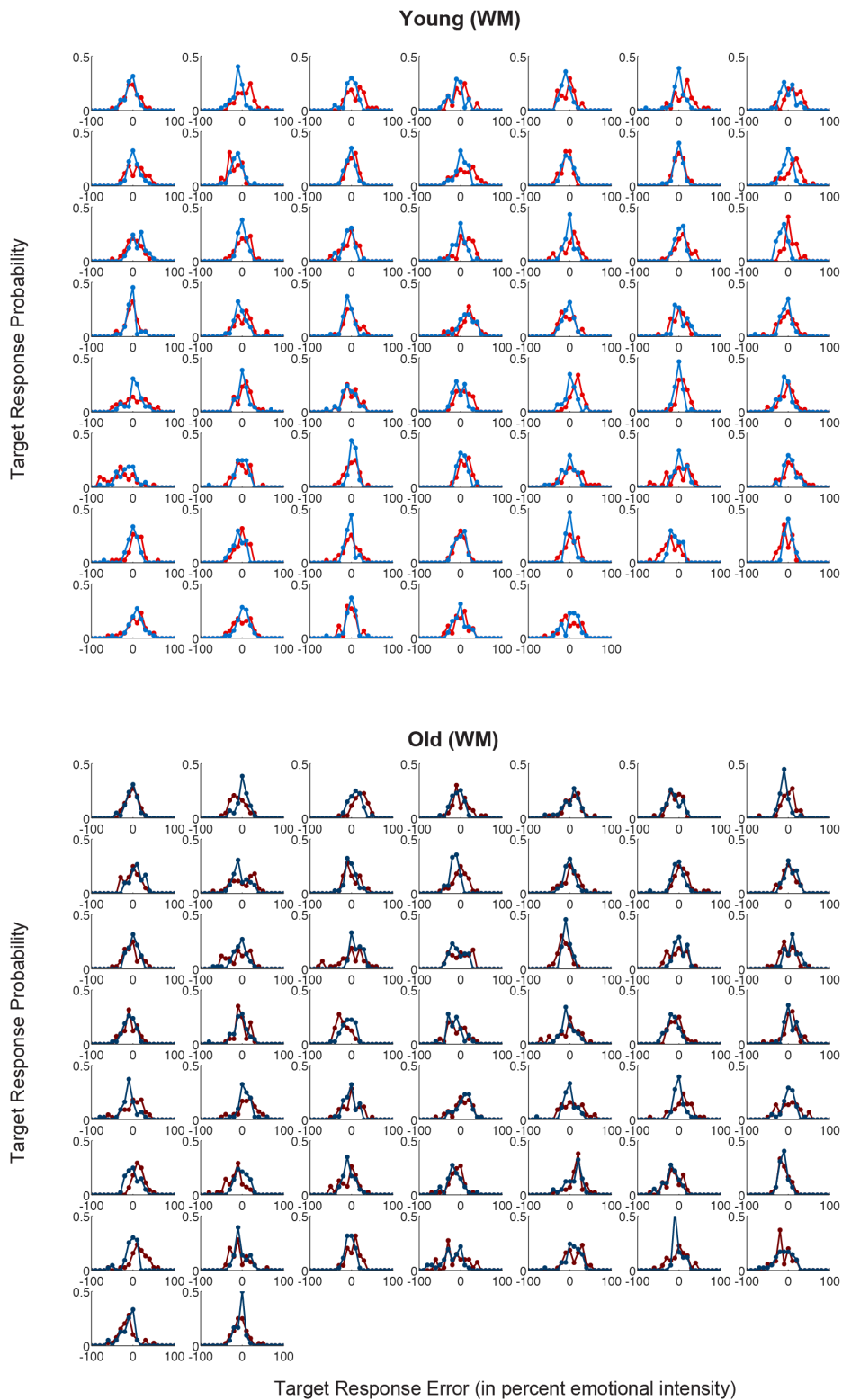


Figure S5.1. Error distributions for emotional WM centred on the target face emotional intensity for individual participants, separated into younger (top) and older (bottom) adults. The error probability is plot at each bin and connected by the lines for fear (young: light red, old: dark red) and happy (young: light blue; old: dark blue) WM conditions. Bins are equally spaced from -100% to 100% in 10% steps. X-axis is the response error in percent emotional intensity, Y-axis is the response error probability.

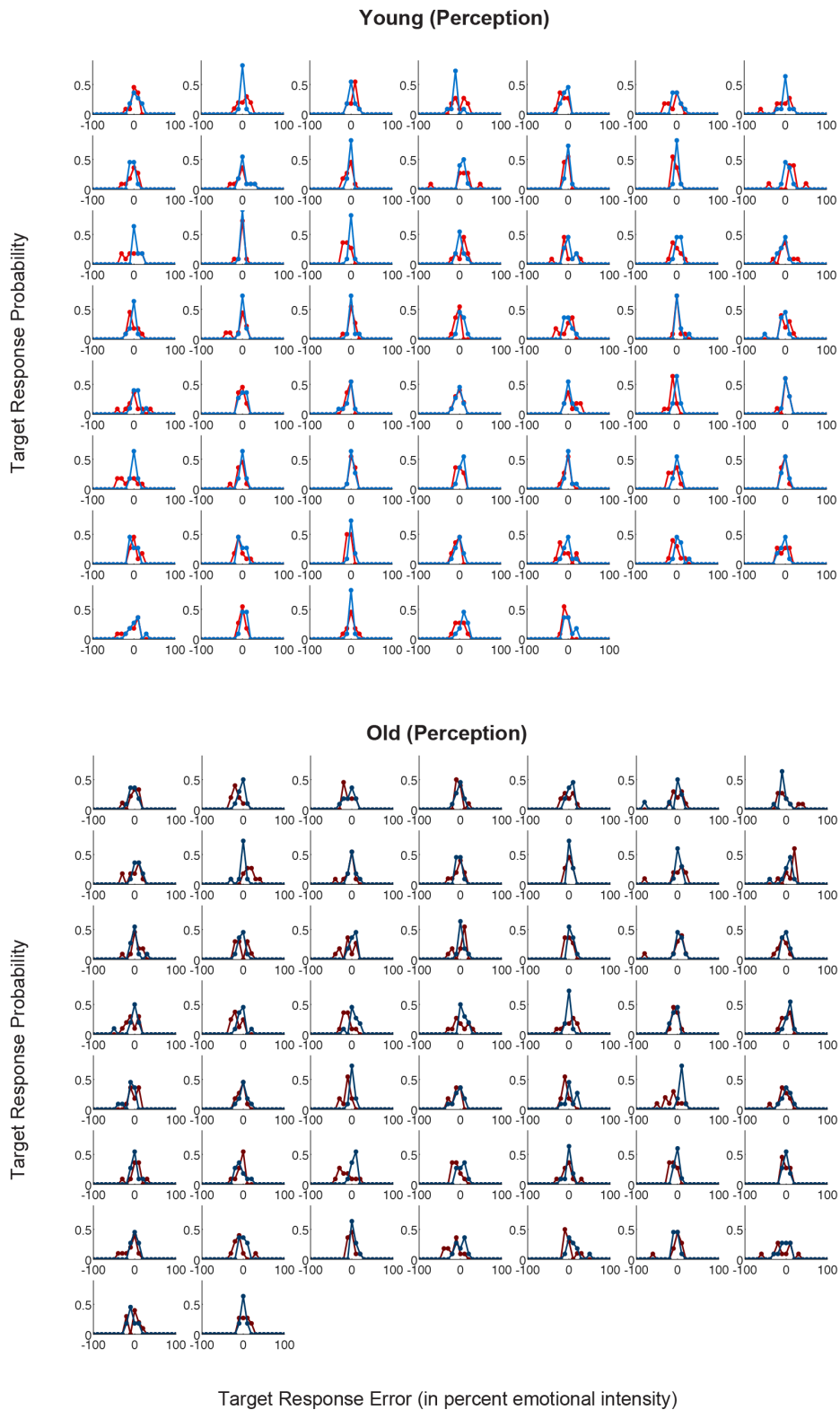
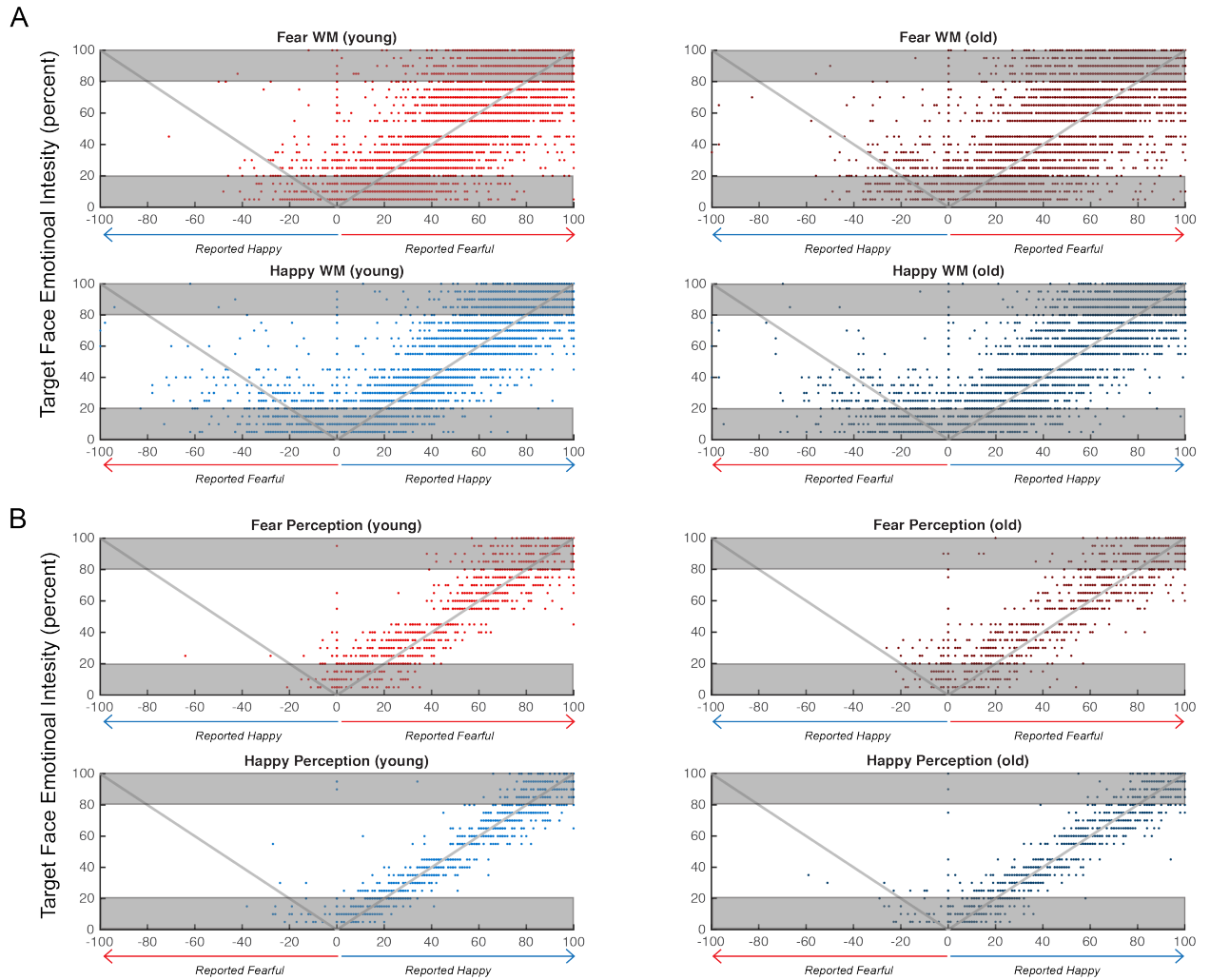


Figure S5.2. Error distributions for emotional-expression matching centred on the target face emotional intensity for individual participants, separated into younger (top) and older (bottom) adults. Conventions as in S5.1.



Emotional Intensity Responded (percent)

Figure S5.3. Scatterplots showing trials where participants correctly reported and misreported the emotion type for each Emotion and Intensity value condition. A) Target face emotional intensities plot as a function of participant responses for emotional WM for fearful (top, red) and happy (bottom, blue) faces, for young (left; light red/blue) and older (right; dark red/blue) adults. X-axis is the target emotional intensity value, y-axis is the reported emotion; positive values correspond to the target emotion type intensities, negative values correspond to the other emotion type intensities. Responses to the correct emotion type lie to the right of zero, and responses to incorrect emotion type lie to the left of zero. Correct responses would lie on the identity line ($y = x$) on the right of each plot. A 'mirrored' version of the identity line ($y = -x$) is plot on the left side for reference. Each point is an individual trial, and each scatter plot includes all the trials in the specified condition for all participants. The areas in grey are trials from 0% – 19% and 81% – 100% emotional intensity, which were removed from the main analyses. B) Target face emotional intensities plot as a function of participant responses for emotional-expression matching. Conventions as in A.

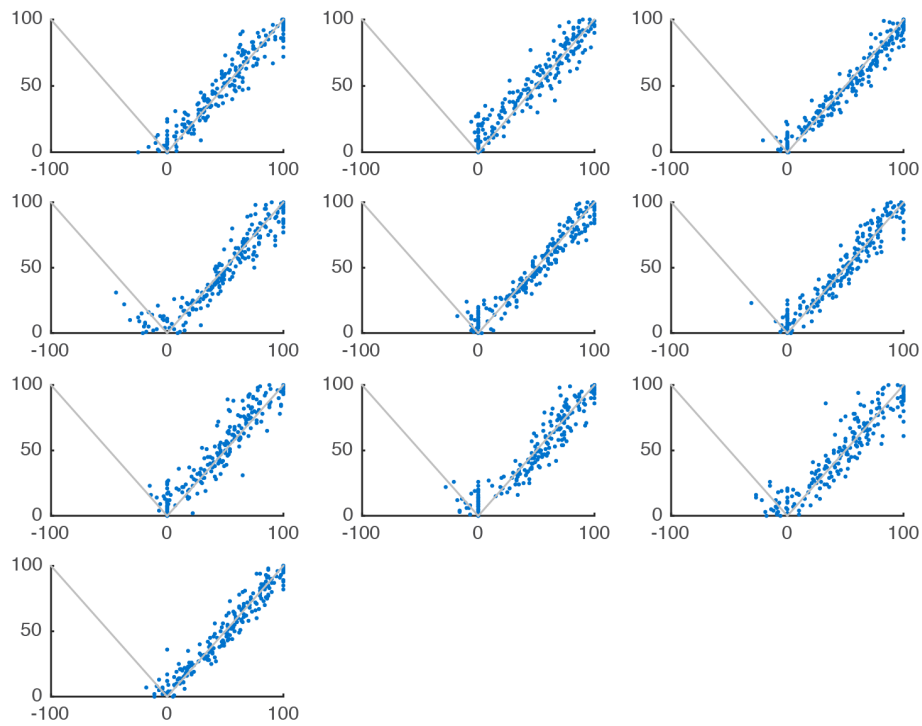


Figure S4.6B. Scatterplots of happy target face emotional intensities plot as a function of responses for individual participants. Conventions are the same as in figure S4.6A.

Neuropsychological Tests and Questionnaires

The Positive and Negative Affect Schedule (PANAS)

State-Trait Anxiety Inventory (SSAI)

Montreal Cognitive Assessment (MoCA)

Trail Making Task A

Trail Making Task B

Category fluency

Hopkins Verbal Learning Test (HVLN)

Boston Naming Test (BNT)

Digit Span - Forward Span

Digit Span - Backwards Span

Digit Span- Sequential

Digit Coding

Test of Premorbid Functioning

Prospective Imagery Task (PIT)

Fishing Game VAS

Rey-Osterrieth Complex Figure Test (ROCF)

Scrambled Sentences Task