Understanding the mechanisms underlying ignoring distractions at working memory encoding and during maintenance

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Abstract

Working Memory (WM) is necessary for performing daily skills and WM performance is highly correlated with a number of cognitive skills (Kyllonen & Christal, 1990; Conway, Kane & Engle, 2003). The ability to ignore distraction may be an important factor underlying visual working memory capacity (VWMC)(Vogel & Machizawa, 2004) and separate mechanisms may be involved with ignoring distractors presented at WM encoding (Encoding Distraction; ED) and during maintenance (Delay Distraction; DD)(McNab & Dolan, 2014). The aim of this thesis was to understand the mechanisms underlying ED and DD filtering; How ED and DD filtering ability change over development and healthy ageing, whether they generalise across WM tasks and their underlying neural mechanisms. Behavioural experiments using laboratory tests and smartphone games, as well as fMRI were used to address these questions.

Novel findings identified were:

1. Evidence for unique ED and DD filtering mechanisms during development. DD filtering became less predictive of VWMC over development, whilst there was a trend towards ED filtering becoming more predictive of VWMC.
2. DD filtering ability correlated across different WM tasks, however ED filtering ability did not. This might reflect a task-specific filtering mechanism for ED and a more general filtering mechanism for DD.
3. A novel suppression mechanism was identified, in task-specific visual regions, which relies on comparison with a passive baseline *and* a no distraction condition. This likely extends a previously identified suppression mechanism, which relies on comparing activity only to a passive condition.
4. This suppression mechanism was only observed for ED and not DD, suggesting distinct neural mechanisms for ED and DD filtering.

These studies advance our understanding of ED and DD filtering. The insights can inform future research into conditions where WMC is impaired (e.g. developmental disorders), as well as healthy ageing and inform training tailored to the individual.

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Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter 1: Introduction

Working Memory (WM) is defined as a limited-capacity system, which maintains and stores information over a short period of time (Baddeley, 2003) and WM performance is highly correlated with a number of cognitive skills, such as cognitive reasoning, control of attention and general fluid intelligence (Kyllonen & Christal, 1990; Conway, Kane & Engle, 2003). The number of items an individual can store in WM is known as their Working Memory Capacity (WMC) and this varies between individuals. The average number of items that can be held simultaneously in WM is debated, with estimates ranging from four (Luck & Vogel, 1997; Cowan, 2010) to seven items (Lisman & Idiart, 1995; Miller, 1956). The number of items that can be held in WM also differs between groups of people; for example, research has found that children, older adults and people with schizophrenia have a lower WMC (Gathercole, Pickering, Ambridge & Wearing, 2004; Craik & Salthouse, 2000; Gold, Wilk, McMahon & Buchanan, 2003).

Behavioural and neuroimaging research suggests that the ability to ignore distraction may be an important factor underlying Visual WMC (VWMC) as the ability to ignore irrelevant information predicts VWMC and research suggests that distractors may be unnecessarily stored in those with a low VWMC (Vogel & Machizawa, 2004; McNab & Klingberg, 2008). Recent behavioural research has made a distinction between two types of distraction; 1) Encoding Distraction (ED); distractors that appear when relevant information should be encoded into WM (i.e. distractors and relevant stimuli are presented simultaneously) and 2) Delay Distraction (DD), distractors that appear when relevant information is no longer displayed, but is being maintained within WM, and each uniquely contribute to VWMC (McNab & Dolan, 2014). The research presented in this thesis focusses on understanding the mechanisms underlying ignoring distractions presented at encoding and during the delay, comparing across development and healthy ageing, and across different WM tasks. Finally, the neural mechanisms underlying ED and DD filtering ability will be investigated. The insights from these studies can be used to understand more about what limits WM and by gaining a better understanding of what limits VWMC, we can then investigate how this might differ in people with a low WMC. For example, it could be useful in understanding developmental disorders in which WM is impaired, such as ADHD (Barkley, 1997; Martinussen, Hayden, Hogg-Johnson, & Tannock, 2005). This could lead to techniques to improve WM in these populations.

Models of WM

Generally, models of WM can be split into two categories: systems models and state-based models. Systems models, which make a distinction between short-term memory (STM) and long-term memory (LTM), became popular in the 1960's, with Atkinson and Shiffrin (1968) modal model of WM, which made a distinction between a short-term store and LTM. This was the basis for the multi-component model (Baddeley & Hitch, 1974), which is still a popular model of WM. The multi-component model of WM proposes that WM consists of four components: the central executive for attentional control, the phonological loop to store and manipulate speech information, the visuo-spatial sketch pad to store and manipulate visual and spatial information, and the episodic buffer to temporarily store and bind information together (Baddeley, 2003).

However, over the past few decades state-based models have also gained popularity. State-based models suggest differing levels of priority in WM, depending on the allocation of attention; at the highest level of priority there is a 'spot-light' of attention on particular items , that is often termed the focus of attention (FoA), and lower priority items are held in a state of activated LTM (Cowan, 1988). It has been suggested that these state-based models account for research indicating close associations between STM, LTM and attention (e.g. Postle, 2006). A popular state-based model is the three-embedded-component theory (Oberauer, 2002; 2009). In this model three levels of priority/ states were proposed: The FoA, which acts as a 'selection device', selecting items or chunks of information, the region of direct access, a limited-capacity state which represents items and their relations in temporary bindings, and the activated part of LTM, which represents items that are not in WM, in an easily-retrievable part of LTM. This model suggests that the FoA is a selection device, and that the limits of WM, suggested in this model are due to interference between objects in WM (Oberauer & Kliegl, 2006; Oberauer 2013). The relationship between WM and distraction will be discussed further in the next section.

WM and distraction

There are many measures of WM performance used in the literature, such as reaction times, precision and non-target responses that are thought to indicate mis-binding (e.g. Bays, Wu & Husain, 2011). However, the research presented in this thesis will focus mainly on WMC, as measures of WMC have reliably given differences between the groups previously mentioned, for example between older adults and younger adults and between schizophrenia patients and healthy controls (Craik & Salthouse, 2000; Gold, Wilk, McMahon & Buchanan, 2003). WMC has also been shown to correlate with cognitive skills previously mentioned (Kyllonen & Christal, 1990; Conway, Kane & Engle, 2003). Studies in cognitive psychology often measure WMC using a battery of WM tasks, often including both visual and verbal WM tasks. However, the studies in this thesis will focus on VWMC tasks, which is often used in cognitive neuroscience studies. For example, previous cognitive neuroscience studies have established differences between distractions during WM encoding and distractions during the delay period, using VWMC (McNab & Dolan, 2014) and so in order to replicate this approach, the research presented will focus mainly on VWMC.

WM and the ability to ignore distraction are closely linked with attention (see review by Oberauer, 2019). In everyday life we often see scenes which contain irrelevant information, and we must search for the relevant, using attention to guide our search. For example, picking someone we know out of a crowd. During WM tasks, similar mechanisms are required to selectively attend to and encode relevant information (e.g. Pessoa & Ungerleider, 2004; Mayer, Bittner, Nikolic, Bledowski, Goebel & Linden, 2007; Anderson, Mannan, Rees, Sumner, & Kennard, 2010). Attention is thought to be a limited capacity mechanism, where only some of the information in a scene is stored or perceived (Treisman, 1969; Duncan, 1980). Therefore, stimuli in a scene must compete for attention, as suggested in the bias competition model (Desimone & Duncan, 1995) which suggests that all visual inputs compete, although this can be guided or biased by bottom-up, and top-down information. Research using visual search tasks, where participants have to pick out relevant stimuli in a scene with irrelevant stimuli, support the theory that search is guided by bottom up factors, such as saliency of distraction and top-down factors such as feature guidance (Duncan & Humphreys, 1989; Beck & Kastner, 2007; Henderson, Malcom & Schandl, 2009; Barras & Kerzel 2017; Wolfe & Horowitz, 2017). Factors such as priming with targets or distraction (Wolfe, Horowitz, Kenner, Hyle & Vasan, 2004; Wolfe, Butcher, Lee & Hyle, 2003; Kristjansson & Driver, 2008), or value of items (Anderson, Laurent & Yantis, 2011), can also improve search time. These factors are important when considering how distraction presented at the same time as relevant stimuli, compared with distractions presented after relevant stimuli is encoded, might affect how attention is directed to the relevant information and how this might affect the contents of WM. Studies often focus on how relevant information is enhanced and stored, however there is also an important role of suppression or inhibition in attention and WM tasks, as indicated by the studies discussed below.

WM research finds that inhibitory control, is linked to WMC (Conway & Engle, 1994; Kane & Engle, 2003; Unsworth et al., 2004, Redick, Calvo, Gay & Engle, 2011). Inhibitory control is a broad term which can refer to any inhibition of stimuli, cognition, or motor responses. For example, Redick, Calvo, Gay and Engle (2011) found a relationship between inhibition of motor responses (or response-inhibition) and WMC. However, the focus of this thesis will be on the relationship between the ability to ignore irrelevant stimuli and VWMC. One example of this relationship is shown in Conway, Cowen, and Bunting (2001) where they investigated whether low WMC individuals were more susceptible to distraction, using an experiment based on the cocktail party effect. This is the idea that in a cocktail party you attend to the conversation you are having whilst ignoring the rest of the conversations in the room, however if for example your name is called in a different conversation, this might capture your attention. In this study participants were instructed to attend to the message being given in one ear and ignore the message in the other ear. They found that individuals with low WMC were more likely to detect their name in the unattended stream. This suggests that low WMC individuals are more susceptible to distraction. However, from these studies it is not known what the direction of the relationship between WM and inhibitory ability is e.g. whether WM influences inhibitory ability or vice versa. For example, WM might maintain what is relevant and suppress the irrelevant, or inhibitory ability might affect what is stored in WM.

Research by Vogel and McCollough (2004) and Vogel, McCollough and Machizawa (2005) investigated this further. First, Vogel and McCollough (2004) showed that Contralateral

Delay Activity (CDA); the mean amplitude of the difference between the contralateral and the ipsilateral Event Related Potentials (ERPs), gave a measure of the number of items held in WM. In a second study they used this to compare activity in low and high VWMC participants, when a distractor is added to the cued hemifield (Vogel, McCollough & Machizawa, 2005). In the task, participants were asked to remember the orientation of red rectangles in the cued hemifield and in some conditions they were additionally asked to ignore blue rectangles. As in the first study, they found that in both high and low VWMC individuals the CDA was greater for four items than two items, confirming that the amplitude reflects the number of items stored in WM. For the condition where two items needed to be remembered, and two items needed to be ignored, they found that in high VWMC individuals the CDA was similar to the CDA for the condition where only two items needed to be remembered without distraction. This suggests that they were only holding the relevant items in WM. However, for the low VWMC individuals they found that the CDA was similar to the CDA for the condition where four items needed to be remembered. This suggests that in the condition where they should have been remembering two items and ignoring two items, individuals with low VWMC may store the relevant *and* irrelevant information in WM. From this it could be suggested that individuals with a low VWMC may struggle to efficiently ignore distractors and so during WM tasks, the limited resources available in WM might be partly used up by irrelevant information and this could contribute to their lower performance in WM tasks (Vogel, McCollough & Machizawa, 2005).

Further evidence of an association between distraction filtering and WM, comes from cognitive load theory; cognitive load theory suggests that high load on cognitive control functions (WM tasks), can increase interference from distractors (Lavie, Hirst, DeFockert & Viding, 2004). In this study, participants were presented with a short-term memory recognition task, where they were given a memory set, then a selective attention task, followed by a memory probe. At the response, participants had to indicate whether the probe was present or absent in the memory set. WM load varied from one (low) to six (high) items. They found that interference from distractions was significant in both low and high WM load, however this was greater for high WM load. They suggest that this gives evidence that in both conditions the distractors were perceived, but under high WM load distractor interference was greater. A study by Lavie and DeFockert (2003), supports the idea that this is due to WM load and not simply task-difficulty, as they found that when you reduce the target size or contrast of the targets, performance in task-difficulty measures, such as reduced speed and accuracy are seen, however distractor interference does not increase. A more recent study by Shimi, Woolrich, Mantini and Astle (2015), investigated the interaction between the effects of the perceptual similarity of distraction and VWM load. They did this through grading perceptual similarity through 40 different levels, from very similar to dissimilar. Consistent with cognitive load theory (Lavie, Hirst, DeFockert & Viding, 2004), they found that there were different effects, of perceptual similarity, depending on WM load. These studies suggest an influence of WM load in distractor interference.

The timing at which distraction is presented could also influence distraction filtering ability. Previous research shows that the timing in which stimuli are presented has also been found to play an important role in influencing WM performance. This may be due to competition between stimuli. Effects of competition between stimuli were first seen in visual search paradigms, where studies find that when targets and distractors have greater similarity, there is an increase in visual search time (e.g. Duncan & Humphrey, 1989). This suggests that the increased competition can impair performance. This finding also extends to WM research, as Ihssen, Linden and Shapiro (2010) found that individuals can remember more items when memory items are presented sequentially rather than simultaneously. This suggests that when competition between stimuli is increased (in the simultaneous condition), the number of items that can be held in WM is reduced. In the case of this study the competition is seen between relevant stimuli held in WM, however there could also be competition between relevant and irrelevant information. Therefore, the timing of the distractor could affect performance in WM tasks.

McNab and Dolan (2014) investigated how presenting a distractor at different times affects WM performance. They made a distinction between ED and DD, as described previously. In this study they used a visual-spatial task where participants had to remember positions of red circles and in some conditions ignore yellow circles. They had a No Distraction (ND), ED and DD condition. In the ND condition red circles were presented without any overt distraction. In the ED condition yellow circles were presented at the encoding period (at the same time as the red circles), and in the DD condition yellow circles were presented during the delay period (after the red circles had gone off the screen). They found that the ability to ignore ED and the ability to ignore DD made a significant and unique contribution to VWMC. This suggests that these are dissociable mechanisms that contribute to WMC (McNab & Dolan, 2014). In a later study it was shown that the contribution of ED and DD to WMC also differentially changes during healthy ageing (McNab et al., 2015). The current findings associated with distraction filtering in WM tasks during healthy ageing are discussed next.

Behavioural findings during healthy ageing

Ageing has been associated with a decline in WMC (Craik & Salthouse, 2000; Bopp & Verhaeghen, 2005). This could be due to the decline of several components of cognition, a few examples being processing speed (Salthouse & Babcock, 1991), storage capacities (Babcock & Salthouse, 1998), or inhibitory processes (Hasher & Zachs, 1988). As previously discussed, studies have found the ability to ignore distraction to play an important role in WM (Ploner et al., 2001; Vogel & Machizawa, 2004) and so as the ability to ignore distraction declines with ageing (Kane et al., 1994), this will have a negative effect on WM ability.

It is important to study what limits WMC in ageing, as different processes might underlie the lower ability in older adults and low WMC younger adults. Several studies have shown that inhibitory control is impaired in healthy ageing. For example, the presence of irrelevant information has a greater effect on WM performance in older adults, compared with younger adults (e.g. West, 1999; Hasher & Zachs, 1988, Connely, Hasher & Zachs, 1991) and older adults are more likely to maintain this irrelevant information in WM (Hartman & Hasher, 1991). Jost, Bryck, Vogel and Mayr (2010) investigated to what degree the ability to ignore distraction underlies WM performance in older adults as well as younger adults. They used ERPs to get a measure of filtering efficiency, during a change-detection task. They found that in older adults, differences in filtering abilities compared with younger adults were mostly early in the retention period (the period between the memory array and the probe) and so it may be that filtering ability is delayed. Whereas individual differences in younger adults were mostly later during the retention period. This provides evidence that whilst the behavioural measures of WMC in older adults and low performing younger adults may appear similar, different neural processes may be limiting their WM performance.

Recent research has investigated how the presentation of distractors at different times might differently affect performance in ageing (McNab & Dolan, 2015). As previously described, McNab and Dolan (2014) made a distinction between encoding and delay distractors. These are two types of distractors that were found to uniquely contribute to VWMC. McNab and Dolan (2015) investigated how performance on tasks with ED and DD are differently affected by ageing. They found that there was a decrease in the number of items successfully remembered on both ED and DD tasks with increasing age, however the decline was greater for delay distraction. This suggests that older adults are worse at ignoring distractors presented during the delay, than distractors presented at encoding. They also found that performance in the encoding distraction task was more similar to performance in the VWMC task without overt distraction for older adults. It was suggested that the greater similarity between encoding distraction and WM performance suggests more focused attention during encoding in older adults, preserving their performance on the encoding distraction task. This may suggest that older adults are compensating at encoding for a decline in ability to hold items in WM. This is something that younger adults presumably would not need to do as they can more successfully hold items in WM over the delay period. Older adults may also need to apply more focussed attention at the encoding of memory items to make up for the delay in filtering efficiency observed in Jost, Bryck, Vogel and Mayr (2010). Mitchell, Cusack and Cam-CAN (2018) have also suggested other techniques that older adults might use in order to compensate for the decline in WM, such as attention to context and metacognitive awareness, which would allow older adults to adopt better strategies in WM tasks. These findings might relate to the compensation mechanism proposed in McNab et al. (2015) as, if participants are more aware of their decline in ability to hold items in working memory, or their decline in ability to ignore distraction, this might make them more likely to apply more focussed attention to items that need to be encoded. In chapter 2, ED and DD filtering in healthy ageing is further investigated and compared to ED and DD filtering during development.

Behavioural findings during development

During development, it is well-established in the literature that WM performance improves (e.g. Gathercole, Pickering, Ambridge & Wearing, 2004; Westerberg, Hirvikoski, Forssberg & Klingberg, 2004; Conklin, Lucian, Hooper & Yarger, 2007). For example, Gathercole et al., (2004) tested children ages 6-15 on a battery of WM tests, associated with three components of the WM model (Baddeley & Hitch, 1974; Baddeley, 2000; Baddeley, 2003); participants completed three tests associated with the phonological loop, three tests associated with the visuospatial sketchpad, and three tests associated with the central executive). They found that performance on each component of WM improved linearly from ages 6 to 15. These improvements in performance have been associated with increases in factors such as storage capacity and processing efficiency or speed (Gathercole, 1999; Bayliss, Jarrold, Gunn & Baddeley, 2003). For example, in Gathercole (1999), it was found that improvement in phonological WM measures were related to increased efficiency in storage of item and order information, and rehearsal and retrieval of memory traces. Whereas improvements in complex WM, such as backward digit span and counting span, were related to processing efficiency and attentional capacity.

It has also been found that children are worse at ignoring distraction than adults and ability to ignore distraction increases over development (e.g. Tipper, Bourque, Anderson, & Brehaut, 1989; Dempster, 1992; Hale, Bronik & Fry, 1997; Olesen, Macoveanu, Tegner & Klingberg, 2007). For example, Olesen et al. (2007) found that accuracy in both a no distraction and distraction condition, was lower in children than adults, and for both children and adults, accuracy was lower for distraction than no distraction. However, relative to the no distraction condition, children were less accurate in the distraction condition compared with adults, suggesting that children were more distracted by the distraction than adults. Additionally, Olesen et al. (2007) suggested that increased activity in the superior frontal sulcus in children compared with adults, when distraction was on screen might be associated with maintenance of the irrelevant material. This is in line with previous research that finds that adults with a low VWMC appear to store irrelevant material (Vogel, McCollough & Machizawa, 2005).

Additionally, regions such as dorsal frontal and parietal cortex are associated with WM in both children and adults (e.g. Thomas et al., 1999; Nelson et al., 2000; Olesen, Macoveanu, Tegner & Klingberg, 2007; Darki & Klingberg, 2015) and increases in WM performance during development have been associated with the maturation of these brain regions, in white matter density (Nagy, Westerberg, & Klingberg, 2004) and increases in functional brain activity (Klingberg, Forssberg & Westerberg, 2002; Ullman, Almeida & Klingberg, 2014; Darki & Klingberg, 2015). Ullman, Almeida & Klingberg (2014) also found that future WMC could be predicted from structural and functional data in the basal ganglia and thalamus. This might be important as McNab and Dolan (2014) speculate that ED filtering but not DD filtering is associated with the basal ganglia, and if activity in the basal ganglia predicts future WMC in children, it may be that ED filtering becomes more predictive of WM during development. However, it is unknown how ED and DD filtering ability changes over development, or how they might differentially predict WMC over development. This will be addressed in chapter 2.

Findings across different subtypes of WM

Previous studies investigating ED and DD filtering have used visuo-spatial WM tasks (McNab & Dolan, 2014; McNab et al., 2015), however there are many sub-types of WM. A popular model of WM proposes that WM consists of four components: the phonological loop, the visuo-spatial sketch pad, the episodic buffer, and the central executive (Baddeley & Hitch, 1974; Baddeley, 2000; Baddeley, 2003). The phonological loop is thought to be for storage and articulatory rehearsal of speech information for a few seconds, and is often measured using lists of letters, digits, or words. Similar to the phonological loop, the visuo-spatial sketch pad is thought to be for storage and manipulation of visual and spatial information, and this is measured in a variety of visual tasks including recalling images and patterns, as well as spatial locations of blocks. The episodic buffer is thought to be for temporarily storing and binding information together into integrated episodes and finally, the central executive is thought to be for attentional control, and coordinating information from the phonological loop, visuo-spatial sketch pad and the episodic buffer. Based on this model of WM, there are sub-types of WM such as verbal WM (thought to be processed by the phonological loop) and visual-spatial WM (thought to be processed by the visuo-spatial sketchpad) and behavioural research suggests that performance on verbal WM and visual-spatial WM tasks are relatively independent of each other (Hanley, Young, & Pearson, 1991; Wang & Ballugi, 1994; Farah, Baddeley & Logie, 1999; Baddaley, 2000).

However, further distinctions within these modalities have also been made, for example the phonological loop can be split into storage and phonological rehearsal (Vallar & Baddeley, 1984; Baddeley & Wilson, 1985) and visual-spatial WM can be split into visual and spatial sub-categories (Logie & Marchetti, 1991; Logie, 1995; Della Sala, Gray, Baddeley, Allamano & Wilson, 1999). Evidence of a distinction between visual and spatial WM comes from evidence of a double-dissociation between spatial and visual tasks (Logie & Marchetti, 1991; Della Sala, Gray, Baddeley, Allamano, & Wilson, 1999). For example, in Della Sala et al. (1991) they found that visual interference affected the visual task more than the spatial task, and spatial interference affected the spatial task more than the visual task. Other evidence comes from studies showing greater improvements in performance with development for visual patterns than spatial tasks (Pickering, 2001; Logie & Pearson, 1997). Additionally, Della Sala et al. (1999) found significantly lower correlation coefficients between visual-object and visual-spatial tasks, than between two visual-object tasks.

However, during development, Gathercole, Pickering, Ambridge, & Wearing (2004) found a moderate correlation between a visual-pattern and a visual-spatial WM task, and did not find that performance on visual-pattern tasks increased more rapidly than on spatial tasks, as found previously (Pickering, 2001; Logie & Pearson, 1997). They suggest that this discrepancy is due to previous findings of more rapid improvements in performance on visual pattern tasks compared with spatial tasks, reflecting differences in the scales, as visual pattern tasks are associated with higher performance scores. They suggest that when these scaling differences are taken out, these differences are no longer present. This suggests that whilst there might be some differences in the mechanisms underlying visual and spatial WM, there are also commonalities. This dissociation between visual and spatial WM is important as previous research using ED and DD paradigms has focussed on visual-spatial WM tasks (McNab & Dolan, 2014; McNab et al., 2015), and so it is unknown whether findings would generalise to other visual WM tasks, without a spatial element e.g. visual-object WM. This will be addressed in chapter 3.

Neuroimaging findings

A popular theory in WM over the last few decades was that storage of items in WM is reflected in persistent neural activity across the delay period of WM (between the encoding period and response period) (Funahashi, Bruce & Goldman-Rakic, 1989; Funahashi, Chafee, Goldman-Rakic, 1993; Chafee & Goldman-Rakic, 1998). For example, in a study by Vogel and McCollough (2004), described previously, they found that as WM load increases, so does contralateral delay activity, and in those with a lower WMC this curve reached an asymptote earlier than in those with a higher WMC, which was interpreted as reflecting storage or maintenance of items in WM. Persistent delay period activity has been found in many studies, and in a variety of regions, including the prefrontal cortex and posterior parietal cortex (e.g. Curtis & D'esposito, 2003; Ranganath & D'esposito, 2001; Todd & Marois, 2004). Another theory, termed 'sensory recruitment theory' suggests that the sensory regions that are involved in the perceptual processing of information are also involved in WM storage (Postle et al., 2006). Evidence for this comes from research finding persistent neural activity, during the delay period, in these sensory regions (e.g. Super, Spekreijse, & Lamme, 2001; Harrison & Tong, 2009; Serences, Ester, Vogel & Awh, 2009).

However, not all studies find this persistent delay activity (e.g. Sreenivasan, Curtis, & D'esposito, 2014; Shafi, Zhou, Quintana, Chow, Fuster, 2007), and this has been taken as evidence that during these 'activity silent' periods, items in WM must be maintained through other mechanisms. In Stokes (2015), a dynamic coding framework was put forward, where it was suggested that items might be maintained through a pattern of synaptic weights, rather than through persistent neural activity. This theory was supported in a recent study which used an impulse stimulus to 'ping' the brain, during the WM delay period, and used the response to investigate the information held in the ‘activity silent’ mechanisms (Wolff, Jochim, Akyurek & Stokes, 2017). They found that WM items were decodable from this impulse response, even when persistent delay period activity was not present.

Some evidence suggests that the active neural trace might represent what is in the focus of attention rather than all items in WM (according to state-based models of WM) (Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012). Using Multivariate Pattern Analysis (MVPA) Lewis-Peacock et al. (2012) found that only items in the focus of attention elicited persistent neural activity, and when items became temporarily irrelevant (and so no longer in the focus of attention), the persistent neural activity disappeared. However, when this was then cued the neural activity could be restored. This would also fit in with Stokes (2015) dynamic coding model, which suggests that temporarily irrelevant items are maintained in activity silent mechanisms, and so it may be that these items are maintained in activity silent mechanisms when they are not in the focus of attention, but can be brought into the focus of attention, where they are held in active neural states. WM research has also found many brain regions associated with ignoring distraction, including the basal ganglia, prefrontal cortex (PFC), inferior frontal gyrus (IFG), and stimuli-specific visual regions (McNab & Klingberg, 2008; Toepper et al.,2010; Dolcos, Miller, Kragel, Jha & McCarthy, 2007; Gazzaley, Cooney, Rissman, & D’Esposito, 2005). The role of these regions in ED and DD filtering in younger adults will be discussed next. It is important to understand the neural basis of ignoring distraction in order to understand how distraction interferes with WM and how it might differently affect high and low WM individuals. However, little is known yet about the neural basis for the dissociation between ED and DD filtering.

Studies have found that the basal ganglia is associated with ED-filtering (McNab & Klingberg, 2008; Baier et al., 2010; Haeger, Lee, Fell, & Axmacher, 2015), but possibly not DD filtering (Cools, Miyakawa, Sheridan & D'esposito, 2010; Mehta et al., 2004). For example, McNab and Klingberg (2008) used functional Magnetic Resonance Imaging (fMRI), to investigated preparatory activity for ignoring ED. They presented participants with red and yellow circles in certain positions of a circle and then presented a question mark in a certain position of the circle and asked if there had been a coloured circle at that position. Participants were cued to ignore the yellow circles in some trials. They then identified unnecessary storage activity, by locating a load-sensitive parietal region and extracting the difference in activity between the no distractor and distractor conditions (both with the same load) for each participant. They suggest that this represents the extent to which irrelevant information is unnecessarily stored. This unnecessary storage activity was then correlated with activity in regions found to be significantly different between tasks. They found an increase in activity in the basal ganglia prior to ignoring the yellow dots and they found that this increase in activity predicted the extent to which only relevant information was stored in WM. This study suggests that the basal ganglia plays an important role in ED-distractor filtering. However, studies using DD paradigms do not support the role of the basal ganglia in distractor filtering (Cools, Miyakawa, Sheridan & D'esposito, 2010; Mehta et al., 2004). For example, Mehta et al. (2004) found that after participants ingested Sulpiride, a dopamine antagonist, reducing levels of dopamine in the striatum, distractor filtering improved rather than declined. The latter would have been expected if the basal ganglia plays an important role in distraction filtering. McNab & Dolan (2014) suggested that a possible explanation for this inconsistency could be that the basal ganglia is involved in distractor filtering at encoding, but not when distractors are presented during the delay period.

Frank, Loughry, and O'Reilly (2001) put forward a model suggesting that the basal ganglia acts as a gating mechanism, which is necessary to update information in WM and that when the gate is 'open' information held in WM can be easily and rapidly updated. Therefore, the disinhibitory gating allows information held in WM in frontal regions of the brain to be updated when it is necessary. Additionally, Gruber, Dayan, Gutkin and Solla (2006) also argue that modulations of dopamine in the basal ganglia, may be involved in selectively gating items from entering WM, protect memory from distractions. McNab and Dolan (2014) suggest that this process may underlie ED filtering. However, for DD filtering, when according to this model the gates are 'closed', a different process may underlie distraction filtering to prevent distractions presented during this period interfering with items being held in WM.

More frontal regions have also been associated with both ED (McNab & Klingberg, 2008; Toepper et al., 2010) and DD filtering (Artchakov et al., 2009; Dolcos, Miller, Kragel, Jha, & McCarthey, 2007; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). For example, McNab and Klingberg (2008) presented targets and distractions simultaneously during the encoding period, as described above (ED paradigm). They found increased activity in the middle frontal PFC preceding distractor filtering. They also found that the increase in frontal distractor filtering activity predicted VWMC. This suggests that the PFC might be important in encoding distractor filtering for ignoring distraction and only holding the relevant items in WM. Evidence for the role of frontal regions in delay distraction filtering comes from multiple studies, including single neuron recordings, fMRI and Transcranial Magnetic Stimulation (TMS) research (Sakai, Rowe & Passingham, 2002; Artchakov et al., 2009; Dolcos, Miller, Kragel, Jha, & McCarthey, 2007; Minamoto et al., 2010; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). For example, Minamoto et al. (2010) presented participants with three faces to remember and then during the delay period presented faces or scenes as distractors. At the response screen participants had to say whether the face they were being shown was one of the to-be-remembered faces. The behavioural findings show that performance was better for those with a high VWMC compared to those with a low VWMC. They found increased activity in the IFG in the stronger distraction condition (when faces were shown), suggesting the IFG has a role in inhibiting irrelevant information. However, there was not a difference in activity between participants with high and low VWMC. They also found greater activity in the Middle Frontal Gyrus (MFG) in individuals with high VWMC compared to low VWMC, suggesting the MFG may be important for the increased performance in VWMC tasks.

The MFG and frontal cortices might also be important for top-down modulation to task-specific visual regions (Minamoto et al., 2010; Gazzaley et al., 2007; Gazzaley, Cooney, McEvoy, Knight & D'Esposito, 2005a; Gazzaley, Cooney, Rissman, & D'Esposito, 2005b; Clapp & Gazzaley, 2012). Gazzaley et al. (2005b) asked participants to either remember scenes and ignore faces or remember faces and ignore scenes. They found an enhancement of activity in the parahippocampal place area (PPA - a scene processing region) when participants were instructed to remember scenes and a suppression of activity in the PPA when they were asked to ignore scenes. This suggests top-down modulation to task-specific visual cortices plays a role in ignoring distractions and remembering relevant information. However, it is not known whether this target enhancement and distractor suppression will be seen for encoding and delay distractors. The way in which the distractors are presented in Gazzaley et al. (2005a & b), means they could act as both encoding and delay distractors as targets and distractors are presented sequentially in a random order. For encoding distractors, filtering needs to be highly selective in order to specifically ignore or remember certain information presented on the screen and so it might be that selective target enhancement and distractor suppression is necessary. However, for delay distraction when filtering can be less selective as anything presented on screen can be ignored regardless of what it is, suppression of activity may not be as selective and so the selective suppression seen in Gazzaley et al. (2005) may not be observed in DD filtering. Enhancement and suppression in task-specific visual regions for ED and DD filtering will be directly compared in chapter 4.

Summary

The ability to successfully ignore distraction is one possible basis for the variability seen in WMC between individuals and WMC changes associated with development and healthy ageing. Behavioural findings using visual-spatial WM tasks have made a distinction between encoding and delay distractions and suggest that they require separate mechanisms which uniquely contribute towards WMC. These might represent separate bases for limited VWMC. WM performance and ability to ignore distraction changes over development and healthy ageing, however it is unknown whether distinct ED and DD mechanisms are present during development, and if so, how these might differentially contribute to predicting VWMC. Additionally, studies comparing visual-spatial and visual-object WM have found a dissociation between the two types of WM, however performance in these WM tasks are often still (moderately) correlated, which suggests there are also more general WM mechanisms underlying both types of WM. It is not known whether ED and DD filtering mechanisms will generalise to other types of WM such as visual-object WM, as previous research has only focussed on visual-spatial WM. Finally, target-enhancement and distractor-suppression has been observed in stimuli-specific visual regions, when participants are asked to remember or ignore stimuli, respectively. However, it is not known whether this target-enhancement and distractor-suppression is involved in both ED and DD distractor filtering, as this has not been directly tested. In this thesis, I aim to: (1) understand how ED and DD filtering mechanisms change over development and healthy ageing and in particular how the contribution of ED and DD filtering ability to VWMC might change; (2) Investigate whether ED and DD filtering mechanisms generalise to other types of WM beyond visuo-spatial WM, in particular investigating whether ED and DD mechanisms are common to visual-object WM tasks; (3) understand differences in the underlying neural mechanisms associated with ED and DD filtering, in particular whether enhancement and suppression in task specific regions are associated with both ED and DD filtering, and how this relates to performance.

Chapter 2: ED and DD filtering over development and healthy ageing

Introduction

It is well established that during development WM improves (e.g. Gathercole, Pickering, Ambridge & Wearing, 2004; Westerberg, Hirvikoski, Forssberg, & Klingberg, 2004; Conklin, Luciana, Hooper & Yarger, 2007). These improvements in WM performance have been attributed to differences in storage capacity and processing speed compared with adults (Bayliss, Jarrold, Gunn, & Baddeley; 2003). In particular, Gathercole (1999) made a distinction between improvement in phonological WM and executive function/ complex WM, finding that improvement in phonological WM, such as digit span and non-word repetition, is related to increased efficiency in processes such as storage of item and order information, as well as rehearsal and retrieval of memory traces. Whereas improvement in complex WM, such as backward digit span and counting span, are related to processing efficiency and attentional capacity.

Research also finds that the ability to ignore distractions to WM is lower in children than in adults (e.g. Tipper, Bourque, Anderson, & Brehaut, 1989; Ridderinkhof, van der Molen, Band, & Bashore, 1997) and that children might unnecessarily store irrelevant information (Olesen, Macoveanu, Tegner & Klingberg, 2007), similar to findings in low VWMC adults (Vogel, McCollough & Machizawa, 2005). For example, Oleson, Macoveanu, Tegner and Klingberg, (2007) presented participants with grey circles to remember, and then at the response period a white line was presented, and participants were asked to indicate where one of the previously presented grey circles intersected the line. In the no distraction condition, they were not presented with any overt distraction, however in the distraction condition they were presented with white circles to ignore during the delay period. Accuracy was recorded as distance from the grey circle. They found that in both the no distraction and distraction condition, accuracy was lower in children than adults, and for both children and adults, accuracy was lower for distraction than no distraction. However, children were more distracted by the distraction than adults i.e. relative to the no distraction, children were less accurate in the distraction condition compared with adults. The finding that children are more distracted by distraction than adults is similar to findings in older adults, which find that WM declines during healthy ageing and that there is a greater decline in performance in distraction tasks, suggesting older adults are more affected by distraction, than younger adults (e.g. Brown et al., 2014).

Previous research in adults also suggests that there are separate mechanisms underlying ignoring distractions presented during WM encoding (encoding distraction -ED) and during the delay period (delay distraction -DD) (McNab and Dolan, 2014). However, currently research into ED and DD filtering has focussed on adults. McNab and Dolan (2014) recruited participants aged 20-29 and found that ED and DD significantly and uniquely predicted VWMC. Following on from this, McNab et al. (2015) used a smartphone game to collect a large number of data sets, sampling across adulthood (ages 18-69). They found that whilst VWMC decreases and performance on ED and DD deteriorates, this decline is greater for DD i.e. as people get older performance dropped more for DD than ED. They also found that ED performance became more predictive of VWMC with healthy ageing. They suggest that this is possibly due to some compensation at the encoding period in older adults, even when no distractions are present. However, it is not known whether similar ED and DD filtering mechanisms would be seen in children as seen in adults, or how ED and DD filtering might contribute to VWMC over development. As we see some similar findings in older adults as seen in children e.g. both children and older adults are more affected by distraction than younger adults (Brown et al., 2014; Oleson, Macoveanu, Tegner & Klingberg,, 2007), it might be that ED and DD contribute to VWMC in a similar way in children as in older adults.

During development, improvements in WM can be linked to the maturation of certain brain regions. Regions such as dorsal frontal and parietal are associated with WM in both children and adults (e.g. Thomas et al., 1999; Nelson et al., 2000; Oleson, Macoveanu, Tegner & Klingberg, 2007; Darki & Klingberg, 2015 etc.) and increases in WM ability over development have been associated with changes in white matter density (Nagy, Westerberg, & Klingberg, 2004) and increases in functional brain activity in these regions (Klingberg, Forssberg & Westerberg, 2002; Ullman, Almeida & Klingberg, 2014; Darki & Klingberg, 2015). Klingberg et al. (2002) used a spatial WM task and measured BOLD activity using fMRI. They found increases in VWMC during development (ages 9-18) positively correlated with activity in the superior frontal and intraparietal cortex. Following on from this, Ullman, Almeida & Klingberg (2014) again found that VWMC correlated with activity in frontal and parietal regions, however they also found that future VWMC could be predicted from structural and functional data in the basal ganglia and thalamus. McNab and Dolan (2014) speculate that the basal ganglia might be important for ED, but not DD filtering, therefore if the basal ganglia plays an important role in predicting future WMC in children, it may be that ED filtering becomes more predictive of WM during development.

Within this study we investigate whether ED and DD filtering make a unique contribution to VWMC in children, and how this contribution changes over development. We also aim to replicate previous findings in older adults (McNab et al, 2015). In order to investigate this, this study uses an approach similar to McNab et al (2015). In the current study, we used a smartphone game, in order to collect data from a large number of participants. Participants were presented with a visuo-spatial WM task, with three conditions: 1) no distraction (ND), where they were not presented with any overt distraction, in order to get a measure of VWMC, 2) ED, where they were presented with distraction during the encoding period and, 3) DD, where they were presented with distraction during the delay period (when relevant information was no longer on screen).

Firstly, it is expected that during development VWMC will increase and performance in distraction-filtering will improve, in line with previous research. Next, it is hypothesised that ED and DD will uniquely contribute to predicting VWMC, if there are similar distractor-filtering mechanisms in children, as seen in adults. It is less clear how ED and DD might contribute to predicting VWMC over development. If performance in children is similar to older adults (as seen with other distraction effects), we would expect ED to be more predictive of WM in younger children and become less predictive over development. However, if ED filtering relies on the basal ganglia, and activity in the basal ganglia predicts future VWMC (Ullman, Almeida & Klingberg, 2014), it may be that ED filtering becomes more predictive over development. During healthy ageing in adults, we predict that ED and DD filtering ability will decline with age and that ED, DD and age will significantly and uniquely predict VWMC. However, we predict that performance in DD will decline more rapidly than ED, and that ED will become more predictive of VWMC, as found in McNab et al. (2015).

Methods

Participants

All participants gave informed consent for their data to be used before playing the smartphone game and the study was approved by the University of York ethics committee. Data was mostly collected in an uncontrolled environment, as participants were encouraged to play the game wherever they wanted to. Although this meant we could not control the environment as in a laboratory study, by doing this we were able to collect a large number of data sets. Previous studies suggest that using a smartphone game, provides useful data even though the environment cannot be controlled (Brown et al., 2015). However, some data was also collected in schools in a controlled environment. Data from 490 participants who provided their age and completed at least one block of the game were considered. Data from 18 participants who failed at the lowest level in at least one condition (WM load of two) or who had more than 10 practice trials before completing a block were excluded, leaving data from 472 participants (age range: 5-77 years, ages 5-9 years: N=66 , 10-14 years: N=168, 15-19 years: N=59, 20-24 years: N=25, 25-29 years: N=24, 30-39 years: N=43, 40-49 years: N=36, 50-59 years: N=32, 60-69 years: N=14, 70-77 years: N=5). In a separate analysis, 111 further participants were excluded who were successful at the maximum level in any condition (WM load of 12) leaving 343 participants (age range: 5-77, ages 5-9 N=65 , 10-14 N=130, 15-19 N=40, 20-24 N=8, 25-29 N=12, 30-39 N=25, 40-49 N=20, 50-59 N=24, 60-69 N=14, 70-77 N=5). Of the data sets, 106 were collected in two school visits (ages 12-19, mean= 13.87, SD=1.99). In a separate analysis of the data collected in schools, participants who got 12 in any conditions were excluded, leaving 70 data sets (ages 12-18, mean =13.86, SD=2.01).

Experimental design and task

Participants were presented with a 5x4 grid and asked to remember the positions of red circles in that grid and ignore the yellow circles (see figure 1). There were three conditions: No distraction (ND), ED, and DD. In the ND condition, red circles were presented for 1s without any overt distraction, followed by an empty grid presented for 1s, during the ‘delay’ period. In the ED condition, red circles and yellow circles were presented simultaneously for 1s, again followed by an empty grid presented for 1s, during the ‘delay’ period. In the DD condition, red circles were presented for 1s and then yellow circles were presented for 1s, during the ‘delay’ period. Red and yellow circles were presented in pseudo-random positions, and in the ED and DD condition, yellow circles were always in different positions to red circles. Irrespective of condition, at the response period, each position in the grid lit up and participants were asked to ‘touch the lights that glowed red’.

In the first trial of each condition, participants were presented with three red circles to remember. If participants were unsuccessful at this load (i.e. did not tap in the correct positions), they were presented with two red circles to remember on the next trial of that condition. Participants were given two attempts at this load, if they were unsuccessful on both attempts, that condition would end. If participants were successful (i.e. tapped in the correct positions), the number of circles increased back up to three. Each time a participant succeeded at a load, the load increased by one in the next trial of that condition, up to a maximum of 12 circles. From load four, if participants were unsuccessful at two attempts at a load, that condition would end. Once each condition was completed (either through being unsuccessful at a load, or reaching the maximum of 12), the game would end.

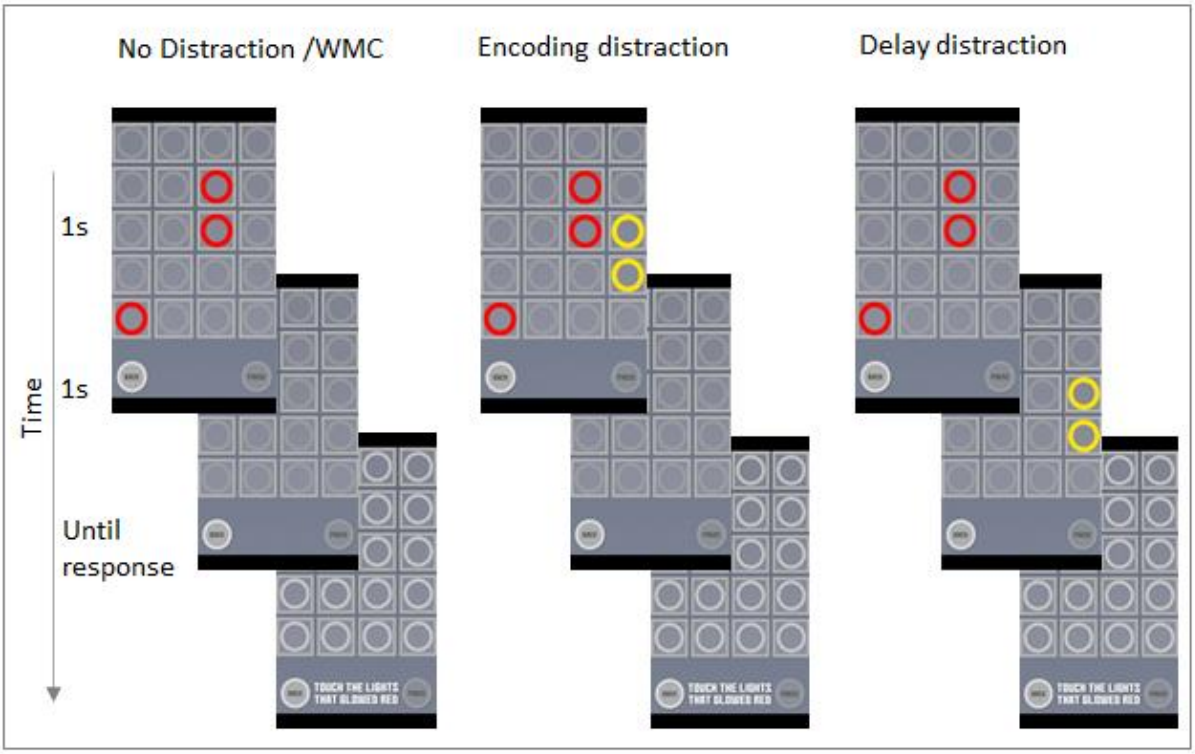

Figure 1; Example trials from no distraction (ND), encoding distraction (ED), and delay distraction (DD) conditions. Participants were asked to remember red circles and ignore yellow circles, at the response screen they were asked to 'touch the lights that glowed red' and they had to press on the screen the positions where red circles had been presented. In ND, participants were not presented with any overt distraction. In ED participants were presented with two yellow circles during the encoding period (at the same time as red circles), to ignore. In DD participants were presented with two yellow circles during the delay period (after red circles were no longer on screen), to ignore.

Data analysis

Participants could have multiple attempts at the game, however only data from the first complete attempt was selected. The highest load at which a participant successfully completed a trial, was used as a measure of 'performance' in each condition. For example, if a participant were successful at load 6, and then unsuccessful at load 7, their performance score in that condition would be 6. Performance in the ND condition was used as a measure of VWMC. Separate analyses were run without data from participants who got the maximum score (12) in any condition, in order to take out any ceiling effects. The data often did not meet the assumption of normality for the ANOVA's (exact data that fails assumption of normality are reported in the results section). However, as ANOVAs are fairly robust to violations of normality we continued to run the ANOVA in these cases (Schmider, Ziegler, Danay, Beyer & Bühner, 2010; Blanca, Alarcón, Arnau, Bono & Bendayan, 2017). All analysis was performed with IBM SPSS version 25. The analysis follows the approach taken in McNab et al (2015).

Firstly, the performance scores were first separated into age bins: 5-9, 10-14, 15-19, 20-24, 25-29, 30-39, 40-49, 50-59, 60-69 and 70-77 years, these were based on similar age bins used in McNab et al (2015). A two-way ANOVA was run with the factors age group (9 levels) and distraction condition (ND, ED, and DD), in order to investigate differences in the distraction effects, and age, and whether distraction effects differentially change during ageing. The same two-way ANOVA was then run separately for children (using the age bins, 5-9, 10-14, and 15-19) and adults (using the age bins 25-29, 30-39, 40-49, 50-59, and 60-69).

Next, we wanted to investigate age-related changes in filtering ability. In McNab et al. (2015), distraction cost was used as a measure of filtering ability, however for consistency with other chapters, the residuals from the regression models $ED= \alpha + \beta DD$ and $DD= \alpha + \beta ED$ were used, for ED and DD filtering ability respectively. Using this method, variance associated with storage and instructions relating to remembering/ignoring stimuli, which would be shared by both ED and DD, was accounted for, leaving the unique variance in performance for ED and DD. The standardised residuals from these regressions were then used for correlation analyses. The regression analysis was carried out separately for ages 5-19 and 25-77. The peak scoring age group was not included, as it is unclear whether participants in this group would be more representative of the younger or older groups. Correlation analysis was then carried out separately for ages 5-19 years and 25-77 years, and for ED and DD filtering ability.

As in McNab et al. (2015), to investigate the unique contribution of ED and DD to VWMC, regression analysis was performed using the model $VWMC = \alpha + \beta_1 ED + \beta_2 DD + \beta_3 age$. Again, this was performed separately for ages 5-19 years and 25-77 years. To further investigate how the contribution of ED and DD to VWMC change over development and healthy ageing, the interaction terms were added to the model ($VWMC = \alpha + \beta_1 ED + \beta_2 DD + \beta_3 age + \beta_4 (ED \times age) + \beta_5 (DD \times age) + \beta_6 (ED \times DD x age)$), and this regression model was run separately for ages 5-19 years and 25-77 years.

Next, correlation coefficients for partial correlations between performance in ND and ED, and ND and DD, controlling for performance in the other distraction condition were calculated (i.e. ND and ED controlling for DD), for each of the 10 age bins described previously, in order to investigate the relationship between individual differences in ED or DD filtering and VWMC. The correlation coefficients for ED and DD at different ages are compared, however ED and DD were not directly compared. This approach replicates previous analysis in McNab et al (2015) where they found that ED becomes more correlated with VWMC during healthy ageing and allowed us to investigate whether this is also the case during development.

Finally, separate analyses were run on the data collected in schools, in order to provide results from a controlled setting, although with fewer participants. On this data a one-way ANOVA was run with the factor distraction condition (ND, ED, and DD), in order to investigate whether there were any distraction effects. Similar regression analyses were run as above, using the model $VWMC=\alpha + \beta_1 ED + \beta_2 DD$, to investigate the unique contribution of ED and DD to VWMC. Finally, as above, partial correlations between performance in ND and ED, and ND and DD, controlling for performance in the other distraction condition were calculated, in order to investigate whether ED or DD was more similar to VWMC in children, however ED and DD were not directly compared.

Results

WM performance

To investigate differences in performance associated with age, and distraction condition, a two-way ANOVA was run with the factors age group (9 levels) and distraction condition (ND, ED, and DD). See figure 2 for mean scores for each age-group. As there were only 5 participants in the age bin 70-77 years, these were not included in the ANOVA. The data did not meet the assumption of homogeneity in any of the distraction conditions (Levene's $p<.05$), and was only normally distributed for age group 50-59 years in ED and DD conditions, age group 60-69 years, in ND, ED, and DD conditions and in age group 70-77 years, in ND and ED conditions (Shapiro-Wilk $p>.05$). There was a main effect of distraction condition ($F(2, 916)=29.42$, $p<.001$), and paired t-tests revealed that scores for ND were greater than for ED ($t=4.30$, $p<.001$) and DD ($t=10.56$, $p<.001$), and scores for ED were greater than for DD ($t=5.59$, $p<.001$). There was also a main effect of age group (F(8, 458)=21.03, p<.001). Individual t-tests were not run across ages, as this would result in many comparisons. There was no interaction between age and distraction F(16,916)=0.99, p=.464), suggesting that ND, ED and DD, do not differentially change with age. The same analysis was run without participants who scored 12 (the maximum), in any condition. Data did not meet the assumption of homogeneity for DD (Levene's p<.05) and was not normally distributed for ages 5-9 , 10-14 and 15-19 years, in all conditions and ages 20-24 and 30-39 years in ND and ED conditions (Shapiro-Wilk p<.05). Similar to the results with all participants, a two-way ANOVA revealed a main effect of age group (F(8,329)=10.43, p<.001) and distraction condition (F(2,658)= 15.55, p<.001), and no interaction (F(16,658)=0.81, p=.672).

To investigate performance during development and ageing during adulthood separately, two two-way ANOVA's were run again with the factor's distraction condition and age, however only including the age bins, 5-9, 10-14, and 15-19 in the first ANOVA, and age bins 25-29, 30-39, 40-49, 50-59, and 60-69 in the second ANOVA. For the first ANOVA, including ages 5-9, 10-14, and 15-19, the data did not meet the assumption of homogeneity for ED or DD (Levene's p<.05), and did not meet the assumption of normality in any condition (Shapiro-Wilk p<.05). There was a main effect of distraction condition (F(2,580)=25.050, p<.001), and age (F(2,290)=42.679, p<.001), however there was no interaction (F(4,580)=0.681, p=.677), suggesting that performance on ND, ED, and DD, did not differentially change over development. Without participants who got 12 in any condition, data again did not meet the assumption of normality (Shapiro-Wilk p<.01) and did not meet the assumption of homogeneity for DD (Levene's p<.05). Similarly, there was a main effect of distraction condition (F(2,464)= 18.938, p<.001), age (2,232)=27.142, p<.001). Paired t-tests showed that performance in ND was significantly higher than in ED (t=3.57, p<.001) and in DD (t=8.75, p<.001), and performance in ED was significantly higher than in DD (t=4.55, p<.001). Finally, similar to the findings with participants who got 12 in any condition, there was no interaction between distraction condition and age (F(4,464)=0.201, p=.938)).

For the second ANOVA, including age bins 25-29, 30-39, 40-49, 50-59 and 60-69, data was not normally distributed for ND, ED, and DD (Shapiro-Wilk p<.05), and failed the assumption of homogeneity for ND and ED (Levene's p<.05). There was a main effect of age (F(4,144)=7.45, p<.001), reflecting lower performance in older adults. There was also a main effect of distraction (F(2,288)=15.29, p<.001) and paired t-tests revealed that performance in ND was significantly higher than in ED (t=3.16, p=.002) and DD (t=6.35, p<.001), and ED was significantly higher than DD (t=3.14, p=.002). However, the interaction between distraction condition and age was not significant (F(8, 288)=0.79, p=.605), suggesting performance in ND, ED, and DD did not differentially change during healthy ageing. Without participants who got 12 in any condition, similarly the data was not normally distributed for ND, ED, and DD (Shapiro-Wilk p<.05), there was a main effect of age (F(4,90)=5.43, p<.001), and distraction condition (F(2, 180)=8.37, p<.001). Paired t-tests showed that performance in ND, was significantly higher than in ED (t=3.06, p=.003) and in DD (t=4.96, p<.001), but DD was not significantly lower than ED (t=1.765, p=.081).

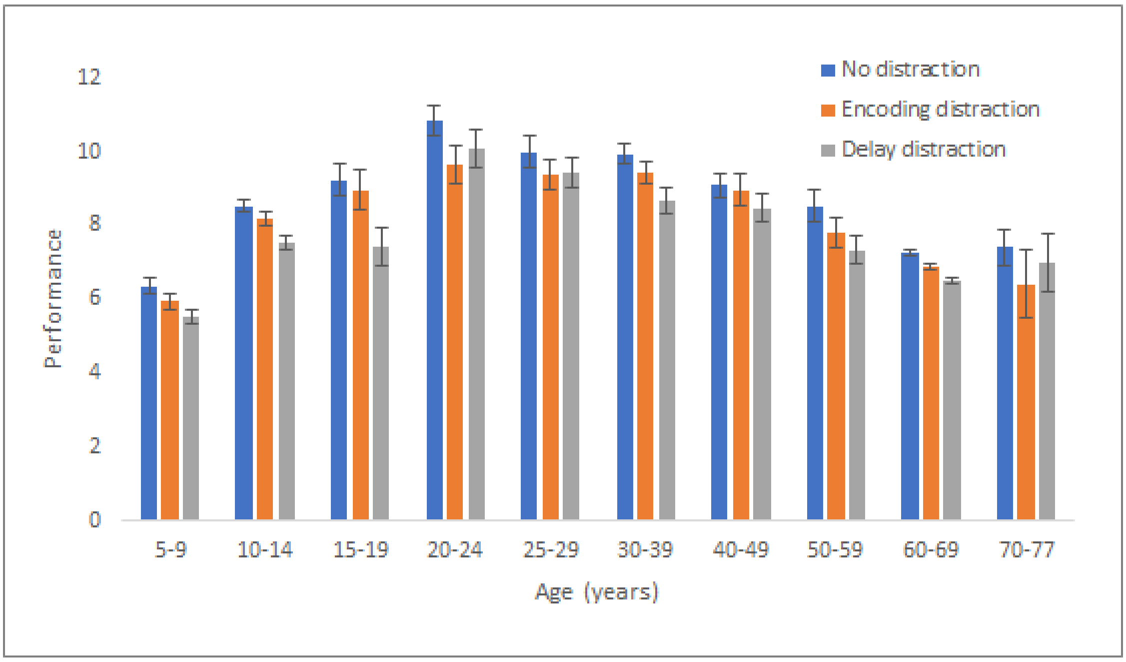

Figure 2; mean score in each condition for each age group (all participants). Blue bars represent 'no distraction', orange bars represent 'encoding distraction', and grey bars represent 'delay distraction'. Error bars represent +/- 1 SEM.

Age-related changes in filtering ability

Next, in order to understand whether filtering ability increases during development, ED and DD filtering ability was correlated with age. In order to get a measure of filtering ability for ED and DD, the residuals from the regression models ED= $\alpha + \beta$DD and DD= $\alpha + \beta$ED were used, respectively (full description in the data analysis section of the methods). For ED filtering, in ages 5-19 years, as expected there was a positive correlation between age and filtering ability (see figure 3a), suggesting that as children develop, ED filtering ability improves. This was still significant when corrected for multiple comparisons (Bonferroni-corrected p=.004). For ages 25-77 years, there was a negative correlation between age and ED filtering ability (see figure 3b), suggesting that during healthy ageing in adults, ED filtering ability decreases. This was still significant when corrected for multiple comparisons (Bonferroni-corrected p=.032). For DD filtering, in ages 5-19 years, there was no significant correlation between DD filtering and age (see figure 3c). For ages 25-77 years, there was a negative association between age and DD filtering ability, however this did not reach significant (see figure 3d). Without participants who scored 12 in any condition, similar to results with all participants, for ED, in ages 5-19 years, there was a positive correlation between age and filtering ability (r=.207, p=.001, Bonferroni-corrected p=.004), and for adults ages 25-77 years, there was a negative correlation (r=-.210, p=.036, Bonferroni-corrected p=.144). For DD, in ages 5-19 years there was no significant correlation between DD filtering ability and age (r=-.037, p=.712) and similarly for ages 25-77 years, there was no significant correlation between age and DD filtering ability (r=-.037, p=.712).

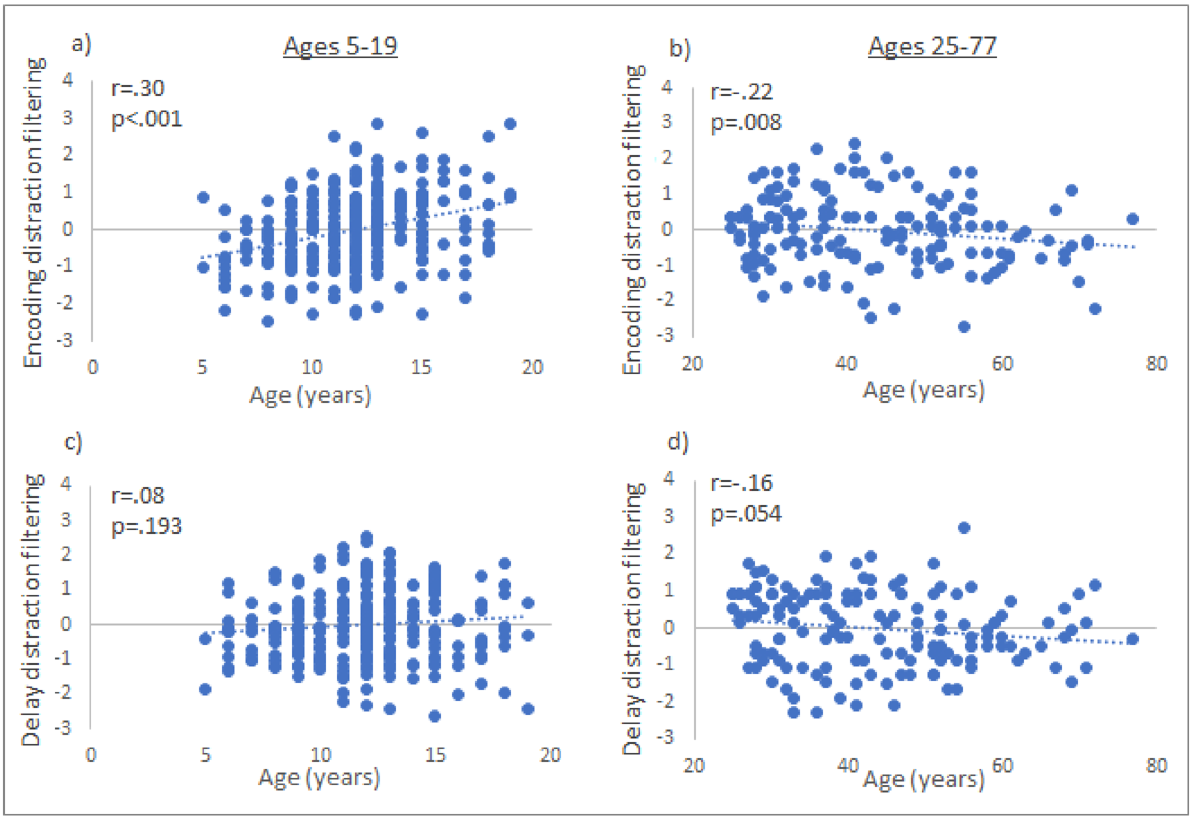

Figure 3; Correlations between age and encoding distraction (ED: a and b) and delay distraction (DD: c and d) filtering ability (all participants). Data from ages 5-19 years are presented in graphs a and c, and data from ages 25-77 years are presented in graphs b and d.

Contribution of ED and DD to VWMC

To investigate whether performance in ED, DD, and age uniquely contribute to VWMC, replicating the approach in McNab et al (2015), regression analysis was carried out using the model VWMC=$\alpha + \beta_1$ ED + β_2 DD+ β_3 age, for ages 5-19 years and ages 25-77 years. The results of the regression model for ages 5-19 are reported first. Although there are significant correlations between predictor variables (ED and DD $r=.61$, $p<.001$; ED and age $r=.487$,$p<.001$; DD and age $r=.383$, $p<.001$), the Variance Inflation Factors (VIF) are less than 5 (ED VIF=1.81; DD VIF=1.62; age VIF=1.33), suggesting we can proceed with the regression, as a VIF of 5-10 is generally considered problematic, and a VIF of over 10 is often considered the threshold where regression analysis is not appropriate (Chatterjee & Price, 1991; Midi & Baheri, 2010). The model accounted for a significant amount of variance in VWMC (R square=.508, $F(3,292)=101.363$, $p<.001$), and ED, DD, and age significantly predicted VWMC (see table 1). Next, interaction terms were added to the regression model: $VWMC=\alpha + \beta_1 ED + \beta_2 DD+ \beta_3 age + \beta_4 (ED \times age) +\beta_5 (DD \times age) + \beta_6 (ED \times DD x age)$. Again, the model accounted for a significant amount of variance in VWMC (R square =.523, $F(6,292)=52.196$, $p<.001$), and the only interaction to significantly predict VWMC was between DD and age (see table 1). These results suggest that over development performance in DD becomes less predictive of VWMC, however there is also a trend towards ED becoming more predictive of VWMC during development, although this was not significant (illustrated in figure 4). Similarly, without participants who got 12 in any condition, there were significant correlations between predictor variables (ED and DD $r=47$, $p<.001$; ED and age $r=.39$, $p<.001$; DD and age $r=.31$, $p<.001$), however the VIFs were less than 5 (ED VIF=1.39; DD VIF=1.31, age VIF=1.21). The model $VWMC=\alpha + \beta_1 ED + \beta_2 DD+ \beta_3 age$, accounted for a significant amount of variance in VWMC (R square=.333, $F(3,324)=38.409$, $p<.001$) and all three variables significantly predicted VWMC (see table 1). However, when the interaction terms were added ($VWMC=\alpha + \beta_1 ED + \beta_2 DD+ \beta_3 age + \beta_4 (ED \times age) +\beta_5 (DD \times age) + \beta_6 (ED \times DD x age)$), whilst the model still accounted for a significant amount of variance in VWMC (R square= .341, $F(6,228)=19.677$, $p<.001$), none of the interaction terms significantly predicted VWMC (see table 1)

Table 1; standardised beta values and p values for the regression models VWMC=α + β_1 encoding distraction (ED) + β_2 delay distraction (DD) + β_3 age and VWMC=α + β_1 ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age), for ages 5-19. Values reported from all participants, and after excluding those who scored 12 in any condition.

Participants included	Regression model	Predictor	Standardised beta	p value
All	VWMC=α + β_1 ED + β_2 DD+ β_3 age	ED	0.29	<.001
		DD	0.45	<.001
		Age	0.10	.046
	VWMC=α + β_1 ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age)	ED	0.00	.999
		DD	1.05	<.001
		Age	0.34	.079
		ED x age	0.27	.461
		DD x age	-1.05	.024
		ED x DD x age	0.32	.321
Excluding participants who scored 12 in any condition	VWMC=α + β_1 ED + β_2 DD+ β_3 age	ED	0.19	.003
		DD	0.40	<.001
		Age	0.13	.034

$VWMC=\alpha + \beta_1$ ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age)	ED	0.22	.382
	DD	0.80	.008
	Age	0.53	.053
	ED x age	0.23	.601
	DD x age	0.79	.165
	ED x DD x age	0.32	.434

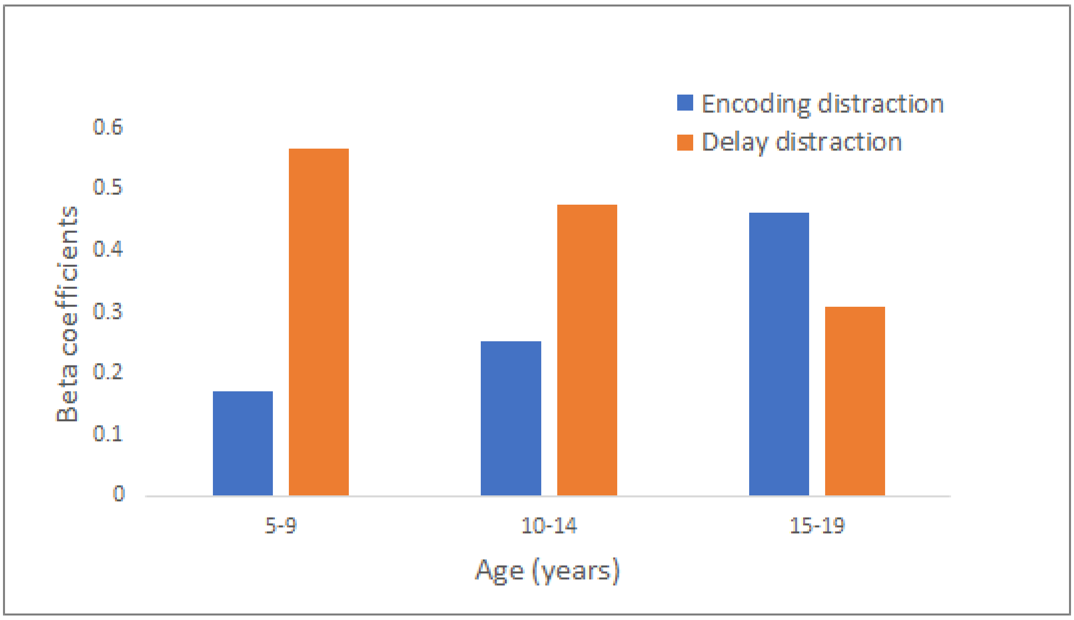

Figure 4; Beta coefficients for encoding distraction (ED; blue) and delay distraction (DD; orange) from the regression model VWMC= $\alpha + B_1$ ED + B_2 DD, calculated for each age group (all participants). Beta coefficients represent the unique contribution of ED and DD to VWMC.

For ages 25-77 years, there were significant correlations between predictor variables (ED and DD $r=.69$ $p<.001$; ED and age $r=-.40$, $p<.001$,; DD and age $r=-.39$, $p<.001$), however the VIFs were less than 5 (ED VIF=1.99; DD VIF=1.98, age VIF=1.23). The model $VWMC=\alpha + \beta_1$ ED + β_2 DD+ β_3 age, accounted for a significant amount of variance in VWMC (R square =.559, $F(3,153)=63.41$, $p<.001$), and ED, DD and age significantly predicted VWMC (see table 2). When including the interaction terms in the model ($VWMC=\alpha + \beta_1$ ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age)), the model accounted for a significant amount of variance in VWMC (R square= .562, $F(6,147)=31.47$, $p<.001$), however none of the predictor variables, significantly predicted VWMC (see table 2). Without participants who got 12 in any condition, similarly, there were significant correlations between predictor variables (ED and DD $r=.44$ $p<.001$; ED and age $r=-.39$, $p<.001$,; DD and age $r=-.29$, $p=.003$), however the VIFs were less than 5 (ED VIF=1.36; DD VIF=1.26, age VIF=1.20). The model $VWMC=\alpha + \beta_1$ ED + β_2 DD+ β_3 age, accounted for a significant amount of variance in VWMC (R square =.398, $F(3,99)=21.18$, $p<.001$) and ED and DD predicted VWMC, however age did not (see table 2). When the interaction terms were added to the model ($VWMC=\alpha + \beta_1$ ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age)), similar to with all participants in the model, the model accounted for a significant amount of the variance in VWMC (R square = .400, $F(6,93)= 10.32$, $p<.001$), and the interaction terms did not significantly predict VWMC (see table 2).

Table 2 standardised beta values and p values for the regression models VWMC=α + β_1 encoding distraction (ED) + β_2 delay distraction (DD) + β_3 age and VWMC=α + β_1 ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age), for ages 25-77 . Values reported from all participants, and after excluding participants who scored 12 (the maximum) in any condition.

Participants included	Regression model	Predictor	Standardised beta	p value
All	VWMC=α + β_1 ED + β_2 DD+ β_3 age	ED	0.38	<.001
		DD	0.35	<.001
		Age	-0.14	.023
	VWMC=α + β_1 ED + β_2 DD+ β_3 age + β_4 (ED × age) +β_5 (DD × age) + β_6 (ED × DD x age)	ED	0.13	.672
		DD	0.49	.121
		Age	0.34	.203
		ED x age	0.37	.356
		DD x age	-0.06	.878
		ED x DD x age	-0.14	.734
Excluding participants who scored 12	VWMC=α + β_1 ED + β_2 DD+ β_3 age	ED	0.37	<.001
		DD	0.33	<.001
		Age	-0.10	.269

in any condition				
	$VWMC=\alpha + \beta_1 ED + \beta_2 DD+ \beta_3 age + \beta_4 (ED \times age) +\beta_5 (DD \times age) + \beta_6 (ED \times DD \times age)$	ED	0.30	.376
		DD	0.41	.298
		Age	0.05	.916
		ED x age	-0.05	.935
		DD x age	-0.26	.637
		ED x DD x age	0.19	.779

Next, to further understand how the correlations between ED and DD and VWMC change over development and healthy ageing, partial correlations between performance in ND and ED, and ND and DD, controlling for performance in the other distraction condition were calculated, for each of the 10 age bins described previously (see figure 5a). As can be seen in figure 5a, for the youngest two groups, there was a higher partial correlation between DD and ND (when controlling for ED) than ED and ND (when controlling for DD), however for the oldest two groups this is the opposite i.e. there was a higher partial correlation between ED and ND (controlling for DD), than DD and ND (controlling for ED). In order to investigate this further, we collapsed across the two youngest (ages 5-14) and two oldest (ages 60-77) age bins and compared across ages using Fishers z test (see figure 5b). This revealed a significant difference in the correlation coefficient for ND and DD (controlling for ED) between children and older adults (z=2.80, p=.003), however there was no significant difference in the correlation coefficients for ND and ED (controlling for DD), between children and older adults (z=-0.59, p=.279). These results suggest that DD is more correlated with VWMC (when controlling for performance in ED), in children than older adults. Without participants who got 12 in any condition, similarly DD was significantly more correlated with ND (when controlling for ED) in children than older adults (z=2.45, p=.007), and for the correlation between ED and ND (controlling for DD), there was not a significant difference between age groups (z=-0.88, p=.191).

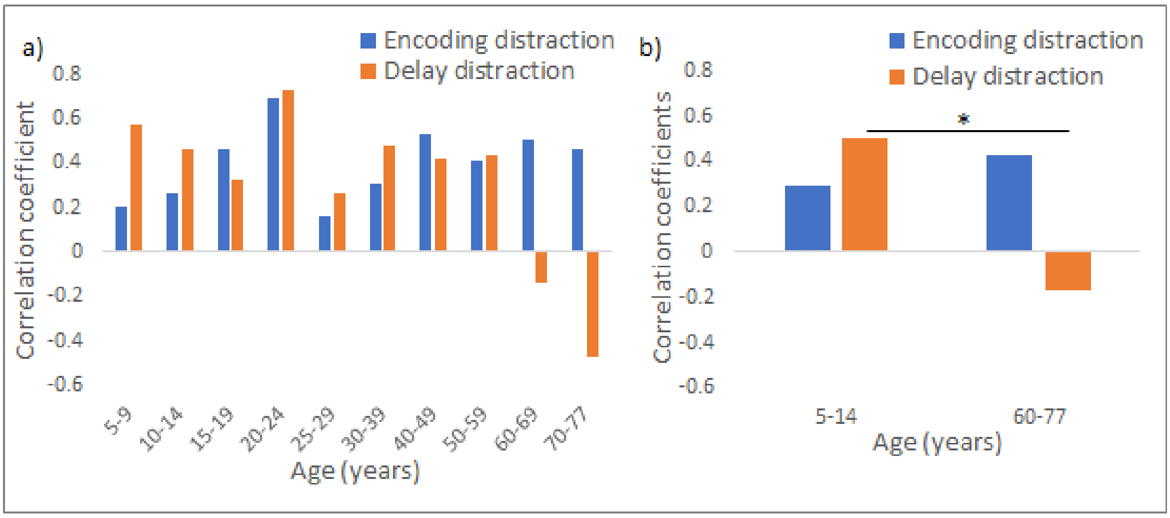

*Figure 5; Blue bars represent correlation coefficients for partial correlations between performance in no distraction (ND) and encoding distraction (ED), controlling for delay distraction (DD) and orange bars represent correlation coefficients for participant correlations between performance in ND and ED, controlling for DD. a) Correlation coefficients for each age group. b) Correlation coefficients for the youngest two age groups and oldest two age groups. *P<.05 (Fisher's z test).*

Data collected in schools

Finally, data collected in schools, in a controlled environment, was analysed separately (see figure 6). Data in all three distraction conditions failed the assumption of normality (Shapiro-Wilk p<.05). A one-way ANOVA revealed a main effect of distraction condition (F(2,210)=8.21, p<.001). Paired t-tests revealed performance in ND was significantly higher than DD (t=3.836, p<.001), and performance in ED was significantly higher than in DD (t=3.22, p=.002), as seen when the data from all the participants was analysed. However, ND was not significantly higher than ED (t=.59, p=.558). Regression analysis was carried out using the model $VWMC=\alpha + \beta_1 ED + \beta_2 DD$. Whilst the predictor variables, ED and DD, were significantly correlated (r=.61, p<.001), the VIF was less than 5 (VIF=1.59). The model significantly accounted for the variance in VWMC (R square = .43, F(2,105)=38.92, p<.001), and both ED and DD significantly predicted VWMC (ED β =.20, p=.006; DD β =.46, p<.001), similar to the analysis above using the full data set. Partial correlation analysis revealed a significant correlation between ND and ED, controlling for DD (r=.27, p=.006) and between ND and DD, controlling for ED (r=.44, p<.001). As previously found (with the full data set), the correlation coefficient between ND and DD (controlling for ED), is higher than the correlation coefficient between ND and ED (controlling for DD) in children.

Without participants who got 12 in any condition, data in all three distraction conditions failed the assumption of normality (Shapiro-Wilk p<.05). A one-way ANOVA revealed a main effect of distraction condition (F(2,138)=6.80, p=.002), and paired t-tests showed performance in ND (mean=7.79, SD=2.16) was significantly higher than in DD (mean=6.87, SD=2.01; t=3.49, p=.001), however not significantly different than ED (mean= 7.61, SD=1.97; t=0.59,p=.554), and performance in ED was significantly higher than in DD (t=3.12, p=.003). Next, regression analysis using the model VWMC=$\alpha + \beta_1$ ED + β_2 DD was performed. Again, whilst the predictor variables, ED and DD, were significantly correlated (r=, p<.001) the VIF was less than 5 (VIF=1.33). The model significantly accounted for the variance in VWMC (R square=.21, F(2,69)=9.09, p<.001), and performance in DD predicted VWMC (β=.38, p=.003), however performance in ED did not (β=.13, p=.308). Partial correlation analysis revealed a positive correlation between ND and DD, controlling for ED (r=.35, p=.003), and there was a positive association between ND and ED, when controlling for DD, however this was not significant (r=.12, p=.308).

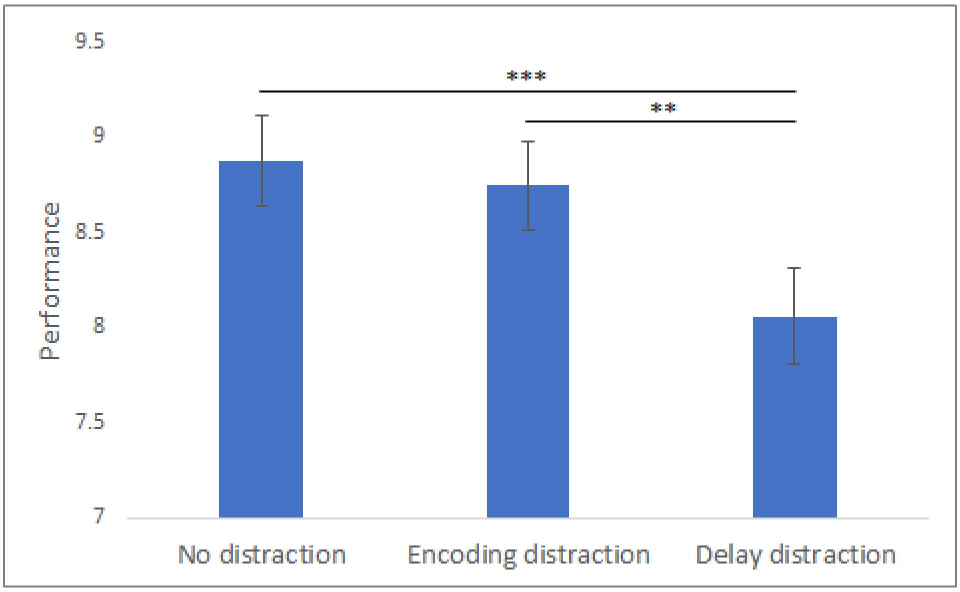

*Figure 6; Scores in no distraction, encoding distraction and delay distraction (all participants). Error bars represent +/- 1 SEM. **P<.01, ***P<.001*

Discussion

The aim of this study was to investigate whether ED and DD filtering make a unique contribution to VWMC in children, and how their contribution changes over development. We found that performance in ED and DD (across all ages) was significantly lower than ND, suggesting that conditions with distraction are harder than conditions with no distraction. We also found that performance in DD was significantly lower than ED, suggesting it is harder to ignore distraction presented during the delay than during encoding. In children, performance (averaged across conditions) increased with development, as expected. However, there was no interaction between age and distraction condition, suggesting that performance on ND, ED, and DD did not differentially change over development. This was not expected, as previous research suggests children are more affected by distraction than adults (Oleson, Macoveanu, Tegner & Klingberg, 2007). However, when using a measure of filtering ability, we find ED filtering ability significantly correlated with age, suggesting that during development children get better at ignoring distraction presented during encoding. As predicted, we found that performance in ED and DD significantly and uniquely predicted VWMC in children. However, performance in DD was more predictive of VWMC in younger children and became less predictive over development. There was also a trend towards ED becoming more predictive over development, however this was not significant.

This is the opposite to what has been seen in older adults, as previous research finds that ED and DD uniquely predict VWMC and ED becomes more predictive of VWMC in healthy ageing (McNab et al 2015). Another aim of this study was to replicate these findings in older adults. We found performance (averaged across distraction conditions) declined with age. However, unexpectedly, there was no interaction between age and distraction condition, suggesting that performance on ND, ED, and DD did not differentially change over healthy ageing. However, when using a measure of filtering ability, we found that ED filtering ability negatively correlated with age, and a trend towards a negative correlation between DD filtering ability and age, suggesting ability to ignore ED and DD filtering declines during healthy ageing. We also found that ED and DD significantly and uniquely predicted VWMC. However, unlike what we had predicted we did not find that performance in ED was more predictive in older adults, or that performance in DD declined more rapidly than ED during healthy ageing.

WM Performance

One-hundred-and-eleven participants reached the maximum score of 12, suggesting that there may have be some ceiling effects. It’s also possible that these participants may also have been using strategies such as chunking to aid in memory for the positions of red circles, as seen in previous VWM studies, which highlight the importance of considering and trying to dissociate item-level WM from ensemble-level WM (e.g. Schurgin & Brady, 2019; Nassar, Helmers, & Frank, 2018). In order to take into account ceiling effects, and possible chunking effects, all of the analysis in this study, was performed with and without participants who scored 12 in any condition. When excluding participants who scored 12 in any condition, the findings were often similar to those obtained when those participants were included and the differences that were observed are discussed below.

When considering the data from all ages, we found there was a main effect of age; figure 1 shows that performance (across conditions) increases until age group 20-24 years and then decreases during healthy ageing. We also found a main effect of distraction condition, finding that performance (across ages) on ED and DD was lower than ND, and performance on DD was lower than ED. However, we did not find any interaction between age and distraction condition. This suggests that performance on ND, ED, and DD does not differentially change during development or healthy ageing. Using separate ANOVA's, we investigated performance during development and during healthy ageing. The analysis of the adult data revealed that there was no interaction between age and distraction condition. This is not in line with previous research which finds that older adults are more effected by distraction than younger adults (Brown et al., 2015) or that performance in DD declines more rapidly than performance in ED (McNab et al, 2015). However, sample sizes in the adult age groups, and particularly for older adults are low in the current study, and so these findings (or lack of) may be due to low numbers of older adults. In McNab et al (2015), for example, they had 29,631 participants in total (ages 18-69), and 1020 participants in the age bin 60-69, whereas in the current study for ages 20-77 there were 179 participants and in the age bin 60-69, there were only 14 participants. Particularly as this is a smartphone study, and therefore test environments cannot be controlled, it is likely that we would need a larger sample size to see these effects. Additionally, when investigating individual differences in filtering ability, we did find a significant negative correlation between ED filtering and age, and a negative association between DD filtering and age (although this did not reach significant), which suggests that the ability to ignore distraction does decline during healthy ageing. It is possible that correlation analysis had more sensitivity to detect this effect, than the ANOVA, where participants were grouped into age bins.

During development we found that performance (across conditions) increased, this is in line with previous research that finds measures of WM increase over development (Gathercole, 1999; Westerberg et al, 2004; Conklin, Luciana, Hooper & Yarger, 2007).

However, we do not find that distractions have more of an effect on performance in children, as we found no interaction between condition and age. This is not in line with previous findings, as Oleson, Macoveanu, Tegner & Klingberg (2007) found that distractions have more of an effect on children than adults. In that study participants took part in a visuo-spatial WM task, where distraction could be presented during a 12s delay period, and distance from the target was recorded at the response. There were a few differences in the paradigm that could have led to the differences in findings. For example, in Olesen et al (2007) they recorded distance from the target however in the current study performance scores were calculated based on a correct/incorrect decision. This could lead to differences in results, as previous research has shown that measures of precision and VWMC are modified by different factors, for example learning and experience can affect precision, but not VWMC (K values) (Lorenc, Pratte, Angeloni & Tong, 2014). Also, when using reaction time measures, in Oleson et al (2007), the interaction between age group and distraction condition was no longer significant, therefore this distraction effect might only be seen using measures of precision. Additionally, in Oleson et al (2007) there was a 12s delay period, whereas in the current study the delay period was only 1s and so children might be more prone to distraction when they are presented over a longer time period. This is found to be the case in older adults; Cashdollar et al (2013) found that greater distraction effects seen in older adults were due to the length of time processing distraction (rather than due to the initial attentional capture of distractors), and so this might be the case in children as well. Additionally, similar to in older adults, when investigating individual differences in filtering ability, we did find a significant positive correlation between ED filtering and age, which suggests that the ability to ignore ED distraction does improve over development. Again, it is possible that correlation analysis had more sensitivity to detect this affect, than the ANOVA, where participants were grouped into age bins.

Individual differences in ED and DD

In line with previous findings that performance in ED and DD significantly and uniquely predict VWMC in adults (McNab & Dolan, 2014) and as predicted, we find for the first time, that in children performance in ED and DD significantly and uniquely predicts VWMC. This suggests that there might be separate mechanisms for ED and DD filtering in children as well as in adults. We found that performance in DD was more predictive of VWMC in young children and becomes less predictive over development and there is a trend suggesting that performance in ED might become more predictive over development (see figure 4), however this was not significant. In our results we see that whilst ED filtering ability is significantly positively correlated with age during development i.e. as children develop, they get better at ignoring ED, DD filtering ability does not reach significance. Therefore, it may be that DD becomes less predictive of VWMC over development partly because as VWMC increases, DD filtering ability does not increase (as much). It might be that there is less of a need to rely on DD filtering mechanisms as ED filtering ability becomes more predictive of VWMC during development (as there is a trend towards this). These changes in the contribution to VWMC might be in line with the development of the basal ganglia, as McNab and Dolan (2014) suggest that the basal ganglia might be involved in ED, but not DD filtering (although this needs to be directly tested) and Ullman, Almeida and Klingberg (2014) found that activity in the basal ganglia predicted future VWMC in children.

However, it is also possible that the finding that DD filtering becomes less predictive over development is due to noisy data, as in the age group 15-19, there was greater variance in performance in this group compared with ages 5-9 and 10-14 (see figure 2), and in particular in DD, this is also where it appears performance has not increased with age (although there was no significant interaction to suggest that DD differentially changes over age). Additionally, when participants who scored 12 in any condition were taken out, DD was no longer significantly more predictive of VWMC in younger children than older children. Therefore, the results provide tentative evidence that DD is most predictive in younger children and becomes less predictive over development, and that ED might become more predictive over development.

Previous research finds that the opposite is true in older adults – during healthy ageing ED becomes more predictive of VWMC (McNab et al, 2015). In the current study we find that ED filtering negatively correlated with age, and there was a trend towards a negative association between DD filtering and age, as expected and ED, DD, and age significantly and uniquely predicted VWMC, in line with previous research (McNab & Dolan, 2014; McNab et al, 2015). However, we did not find that ED becomes more predictive of VWMC during healthy ageing. This is inconsistent with findings from McNab et al (2015), where they found that ED becomes more predictive of VWMC. However, as mentioned previously sample sizes in the adult age groups and particularly in the older adult categories are much lower than in McNab et al (2015), and so the findings (or lack of) may be due to this. Additionally, when looking at the data we do see a trend towards similar findings as seen in McNab et al (2015). For example, when considering correlation coefficients between ED and VWMC (controlling for DD), and DD and VWMC (controlling for ED), we see that in the oldest two age categories, the coefficients for ED are positive, whereas for DD they are negative (see figure 5), and this is in line with previous findings, that during ageing ED is more similar to VWMC in healthy ageing and delay distraction is less similar (McNab et al 2015). We also find that in children the correlation coefficient for DD and ND (controlling for ED) is significantly higher than in older adults, suggesting that DD is more similar to VWMC in children, than it is in older adults.

When participants who scored 12 were taken out of this analysis ED and DD still uniquely predicted VWMC, however age was no longer significant. It is likely that this is because there were a lot of participants in the younger adults age-groups who were taken out due to this exclusion criteria. For example, in ages 25-29, 50% of participants had to be taken out of the analysis. However, in the older two age groups (ages 60-69 and ages 70-77), no participants were excluded. Therefore, it is likely that taking out these participants from the younger adult groups has 'flattened' the slope when looking at the correlations between age and performance, and this is why we no longer see that age predicts VWMC. Therefore, we conclude that ED, DD and age do predict VWMC, and that ED and DD filtering ability declines with healthy ageing, and whilst we did not find that ED filtering becomes more predictive of VWMC over healthy ageing, it is possible that this is due to issues with sample size.

Data collected in schools

As mentioned previously, whilst using a smartphone game allows us to collect large amounts of data, a limitation of this method is that the data is not collected in a controlled environment. However, data from 106 participants was collected in a school setting in a controlled environment. The findings from this data also show that ED and DD significantly and uniquely predict VWMC, giving further evidence that these separate mechanisms for ED and DD filtering ability are present during childhood. Partial correlations suggest that both DD (controlling for ED) and ED (controlling for DD) positively correlate with VWMC. Additionally, the correlation coefficient for DD is higher than that for ED and when participants who scored 12 in any condition were excluded from the analysis, performance in DD still predicted VWMC, however performance in ED did not, further supporting the theory that DD is more predictive of VWMC in children than ED.

Conclusions

From this research and previous research, we see that ED and DD filtering mechanisms are present throughout the lifespan, however, differentially predict VWMC at different times during development and healthy ageing. The findings from this study could have implications for understanding the basis for low VWMC in children, which has been linked to, for example math ability and academic progress (Bull, Epsy & Wiebe, 2008; Friso-van den Bos, van der Ven, Kroesberg & van Luit, 2013; Gathercole & Pickering, 2000). It could also have implications for understanding VWMC impairments found in developmental disorders such as ADHD (Barkley, 1997; Martinussen, Hayden, Hogg-Johnson, & Tannock, 2005). When considering cognitive training, previous work has found that training can improve WM in individuals with ADHD (Klingberg, Forssberg & Westerberg, 2002). By identifying the type of distraction-filtering mechanism impaired in particular groups or in individuals, it is possible that training could be tailored to the individual.

Future research might also consider using more sensitive measures of estimating VWMC, such as distance from target. Previous research has identified changes in memory precision of object identity and location associated with healthy ageing (Pertzof, Heider, Liang & Husain, 2015) that were previously not seen using a binary response (same or different) (Mitchell, Johnson, Raye, Mather, & D'Esposito, 2000). Similarly, Sarigiannidis, Crickmore and Astle (2016), investigated differences in precision and guess-rate in children aged 7-12 using a visuo-spatial WM task, and found that whilst younger children were less likely to remember the target, when they did remember the target, there was no difference in precision, compared with older children. The results from these studies suggest that using more sensitive measures for estimating WM performance can offer further insight into WM changes over development and healthy ageing, and would allow for further comparisons of the effects of ED and DD on VWMC, particularly on the precision of object location. In the current study, data on the distance from the target was not collected, as we aimed to replicate the approach taken in McNab et al. (2015), which previously established differences between ED and DD performance in healthy ageing using a binary measure (correct or incorrect). However, using more sensitive measures of WMC should be considered in future research.

In summary, as found previously in adults, performance in ED and DD, as well as age uniquely predict VWMC. We did not find interactions between ED and DD and age to significantly predict VWMC, however this could be due to issues with sample sizes in the older adult age groups. For the first time, we show that during development, performance in ED and DD, as well as age uniquely predict VWMC. This suggests that separate ED and DD filtering mechanisms are already present in children. Finally, we found that in early childhood DD is more predictive of VWMC and becomes less predictive over development and that there is a trend towards ED filtering becoming more predictive of VWMC. This might be in line with the development of the basal ganglia. These findings in children, are the opposite to previous findings in older adults, which find that as we get older ED becomes more predictive of VWMC. These findings could have important implications when considering cognitive training, as it could allow us to focus training at particular distraction mechanisms tailored to the individual. Currently research has focussed on ED and DD in visuo-spatial WM tasks, and so future research should investigate if this generalises to other forms of WM. In the next chapter findings for ED and DD in a faces and scenes WM task will be discussed and compared with findings from a visuo-spatial WM task.

Chapter 3: ED and DD filtering compared across visual-spatial and visual-object WM tasks.

Introduction

Research into Encoding Distraction (ED) and Delay Distraction (DD) filtering has focussed on visual-spatial Working Memory (WM) tasks (McNab & Dolan, 2014; McNab et al 2015). However, there are many sub-types of WM e.g. visual-spatial, visual-object and verbal WM. A popular model of WM proposes that WM consists of four components: the central executive for attentional control, the phonological loop to store and manipulate speech information, the visuo-spatial sketch pad to store and manipulate visual and spatial information, and the episodic buffer to temporarily store and bind information together (Baddeley, 2003). The visuo-spatial sketchpad can be split into a further two components: visual and spatial, and research suggests there might be a dissociation between these two types of WM (Logie & Marchetti, 1991; Logie, 1995; Della Sala, Gray, Baddeley, Allamano & Wilson, 1999).

In Della Sala et al. (1999) participants completed a Corsi block task (spatial task) and a visual pattern task (non-spatial task) and performance on these tasks was compared. In the Corsi block task, participants were presented with an array of nine blocks, the experimenter tapped a sequence of blocks, and participants were asked to repeat the sequence. In the visual pattern task, participants were presented with a matrix, where half of the squares were filled, and asked to remember the patterns. They found that there was a positive association between the Corsi block task and visual pattern task, however that correlations were significantly stronger between performance on different versions of the visual pattern task, than between the Corsi block and visual pattern task, suggesting there might be some differences in the mechanisms underlying processing these tasks. Additionally, when they introduced either visual or spatial interference during the delay period of the tasks, they found that the visual interference affected the visual task more than the spatial task, and the spatial interference affected the spatial task more than the visual task. Additionally, research has also found that over development there is a more rapid improvement in performance on visual patterns than spatial tasks (Pickering et al., 2001; Logie & Pearson, 1997). These results suggest that there is a dissociation between the visual-spatial and visual-pattern WM tasks.

However, there is also some evidence of similarities in performance across visual and spatial WM. In Della Sala et al. (1999) whilst the correlation between visual-pattern and visual-spatial tasks, was lower than between different visual-spatial tasks, there was still a positive association between performance on the visual-spatial and visual-pattern tasks, and performance is similarly affected by the relevant distraction, this might suggest some similarities in more general WM mechanisms. Similarly, Gathercole, Pickering, Ambridge and Wearing (2004) found a moderate correlation between a visual-pattern and a visual-spatial WM task, suggesting some similarities in the underlying mechanisms needed to perform both tasks. They also did not find that performance on visual-pattern tasks increased more rapidly than on spatial tasks, as was found in previous studies (Pickering et al., 2001; Logie & Pearson, 1997). They suggested this discrepancy in findings was due to previous differences in improvement rates reflecting differences in the scales, as performance on visual pattern tasks is associated with higher performance scores. In Gathercole et al., (2004) scores were standardised and so they suggest that these scaling differences are eliminated in their study. Together, these findings suggest that whilst there are some differences in visual and spatial WM processes, there also appears to be some similarities in more general WM mechanisms.

Similarly, findings from neuroimaging studies support some dissociation of neural pathways, but also some overlap. A popular theory was that the dorsolateral pathway is associated with spatial WM, whilst the ventrolateral pathway is associated with object WM (Wilson et al., 1993; Courtney, Ungerleider, Kiel & Haxby, 1996; Courtney, Petit, Maisog, Ungerleider & Haxby, 1998; Ren, Zhang, He, Feng, Bi & Qiu, 2019). For example, in Courtney, Petit, Maisog, Underleider and Haxby (1998), participants were presented with three faces in different locations on the screen, followed by a single test face. In the spatial task they were asked to indicate whether the face was at one of the three locations regardless of the identity of the face, whereas in the object WM task they were asked to identify whether the face was one of the three faces they had been presented with, regardless of location. Using fMRI, they found that the object WM task activated regions in the inferior frontal cortex, whilst the spatial WM task activated more superior frontal areas. Additionally, activity associated with ignoring visual-spatial distraction in visual-spatial tasks is also often in the middle frontal gyrus/ dorsolateral prefrontal cortex (DLPFC) (McNab & Klingberg, 2008; Toepper et al, 2010; Sakai, Rowe & Passingham, 2002), whilst in visual-object tasks it is often in the inferior frontal gyrus/ ventrolateral prefrontal cortex (VLPFC) (Minamoto et al, 2010; Dolcos, Miller, Kragel, Jha & McCarthy, 2007; Jha, Fabien & Aguirre, 2004).

However, Postle and D'esposito (2000), reanalysed data from early fMRI studies supporting a ventral/ dorsal divide, which had used a blocked design method of analysing the neuroimaging data, averaging over long periods. The development of event-related fMRI analysis meant that the data could be analysed with greater sensitivity, and Postle and D'esposito(2000) found that generally activity for both spatial and non-spatial WM tasks was distributed across the PFC. Additionally, many other studies have since shown that spatial and object WM tasks are not processed solely in the dorsolateral or ventrolateral stream (e.g.

Baker et al, 1996; Nystrom et al, 2000, Oliveri et al, 2001; Levy & Goldman-Rakic, 2000; Wager & Smith, 2003, Postle & D'esposito, 2000). For example, Oliveri et al (2001) found that TMS applied to the DLPFC interfered with both spatial and object working memory tasks, not just the spatial task. Similarly lesions in the ventrolateral prefrontal cortex (VLPFC) can impair both spatial and object WM, not just object WM (Levy & Goldman-Rakic, 2000). Additionally, distractor filtering studies also suggest that spatial and object WM might not be independently processed in either the dorsal or ventral pathway, respectively. For example, in an object WM task, Feredoes, Heinen, Weiskopf, Ruff and Driver (2011), found the DLPFC to play a role in enhancing relevant information in the presence of distraction. These recent findings suggest that it is likely both regions play a role in WM processes, regardless of stimulus type.

Whilst activity in the PFC has been extensively studied in relation to WM processes, a popular theory termed 'sensory recruitment theory' suggests that the sensory regions that are involved in the perceptual processing of information, are also involved in WM storage (Postle et al., 2006). Evidence for this comes from research finding persistent neural activity, during the delay period, in these sensory regions (e.g. Super, Spekreijse, & Lamme, 2001; Harrison & Tong, 2009; Serences, Ester, Vogel & Awh, 2009). For example, using MVPA, Serences et al (2009) found that sustained patterns of activation were present during the delay period in early visual regions representing the relevant features of objects in WM. This would suggest that different features of WM items are stored in different sensory regions in the brain, which might suggest differences in performance across different WM tasks. Given the similarities and differences in the findings from studies comparing visual spatial and visual object WM tasks, and the differences in how relevant items might be maintained in these tasks, it is not known whether there would be similar ED and DD mechanisms in visual object WM, as seen in visual spatial WM.

In this study, we investigated whether individual differences in VWMC for visual-object WM, are similar to visual-spatial WM, and whether ED and DD filtering mechanisms identified previously using visual-spatial WM tasks correspond to those found in visual-object WM. In order to do this performance on a visual spatial working memory task, where participants had to remember positions of red circles on a grid, and ignore yellow circles, and two visual-object WM tasks, where participants had to either remember faces and ignore scenes, or remember scenes and ignore faces, was investigated. Two visual-object tasks were included in order be able to compare ED and DD mechanisms between visual-object tasks, as well as between visual-object and visual-spatial VWM tasks, as in Della Sala et al. (1999). Whilst there is some behavioural dissociation and neural differences in how visual-spatial and visual-object WM are processed, there are also similarities, as studies have found performance on visual spatial and pattern WM are positively associated, and there is overlap in the neural mechanisms associated with both types of WM, suggesting more general WM mechanisms might support both stimulus types. Therefore we predicted that for all stimulus types (red circles, remember faces, and remember scenes), VWMC for one stimulus type will correlate with VWMC for other stimulus types and ED filtering ability or DD filtering ability for one stimulus type will correlate with ED filtering ability or DD filtering ability for other stimulus types, respectively. This would suggest that common visual WM filtering mechanisms are involved in both visual-spatial and visual-object WM. Lastly, we predict that ED and DD will uniquely contribute to VWMC measured in both the visual-spatial task (as previously found in McNab & Dolan, 2014) and in the visual-object WM tasks (within domains). This would suggest that ED and DD filtering mechanisms are common to both types of WM.

A second aim of the study was to identify whether participants close their eyes when distractors are presented during the delay period. A possible limitation of tasks comparing ED and DD performance, is that participants could shut their eyes when distractions are presented during the delay period, as there is no relevant information on the screen at this point. Therefore, differences in performance on these tasks could be associated with this, rather than being associated with different underlying filtering mechanisms. To address this, eye-tracking has been included in this study, to check whether participants close their eyes during the presentation of delay distractions.

Methods

Participants

Data from 45 volunteers who were right-handed, with normal or corrected-to-normal vision were collected. Three datasets were excluded due to a low VWMC score (K-value <1) in the 'red circles' task (described below), leaving 42 participants (8 males, mean=19,74, range = 18-26, SD=2.14). Eye-tracking data were collected for the first 25 participants, however one data set was lost due to a technical error, leaving 24 participants in each condition, and for the 'red circles' task (described below), a second data set was lost due to a technical error, leaving data from 23 participants in this task. All participants gave informed consent and ethical approval was granted by York Neuroimaging Centre's ethics committee.

Experimental design

In this study, there were three stimulus conditions: remember the scenes (and ignore faces), remember the faces (and ignore scenes) and remember the positions of the red circles (and ignore the positions of the yellow circles). For each of these there was a VWMC task, and three distraction conditions: No Distraction (ND), Encoding Distraction (ED) and Delay Distraction (DD). This made a total of 12 conditions, which were organised into a separate block per condition and these were split over two sessions. Each participant completed all blocks. In the first session participants completed the four blocks of the ‘red circle’ task, and either the four blocks of the ‘remember scenes’ task, or the four blocks of the ‘remember faces’ task (this was counterbalanced). The four conditions of the remaining task were carried out in the second session. The order of the blocks for each task was counterbalanced. For the first 25 participants, eye-movements were monitored during each block using EYELINK 1000, to check that participants were not consistently closing their eyes whilst the distractions were on the screen. At the end of the second session a forward and backward digit span task was also completed, however the results are not reported here.

Red circles task

In the ‘red circles’ task, participants were presented with red circles (targets) and, in the distractor-filtering conditions, yellow circles (distractors) at pseudo-random positions of a circular grid (see figure 7). The grid had 16 positions and subtended a visual angle of approximately 20° both horizontally and vertically. In the VWMC task, participants were simultaneously presented with 3, 4 or 5 red circles and no yellow circles. There was a total of 42 trials, 14 for each WM load. In the ND task participants were presented with 4 red circles and no yellow circles. In the ED task participants were simultaneously presented with 4 red circles and 2 yellow circles and in the DD task participants were first presented with 4 red circles and then during the delay period, 2 yellow circles. There were 30 trials in each of the ND, ED, and DD blocks. At the end of each trial, irrespective of condition, participants were presented with a question mark in one position of the grid and asked to respond with a button press ‘yes’ or ‘no’, whether there had been a red circle at the position. For half of the trials the correct response was “yes”. No more than two red circles could be positioned next to each other in the grid. In the distraction filtering conditions, one yellow circle was always adjacent to a red circle and at the response, the question mark was always placed either in the position of a red circle, or in an adjacent position.

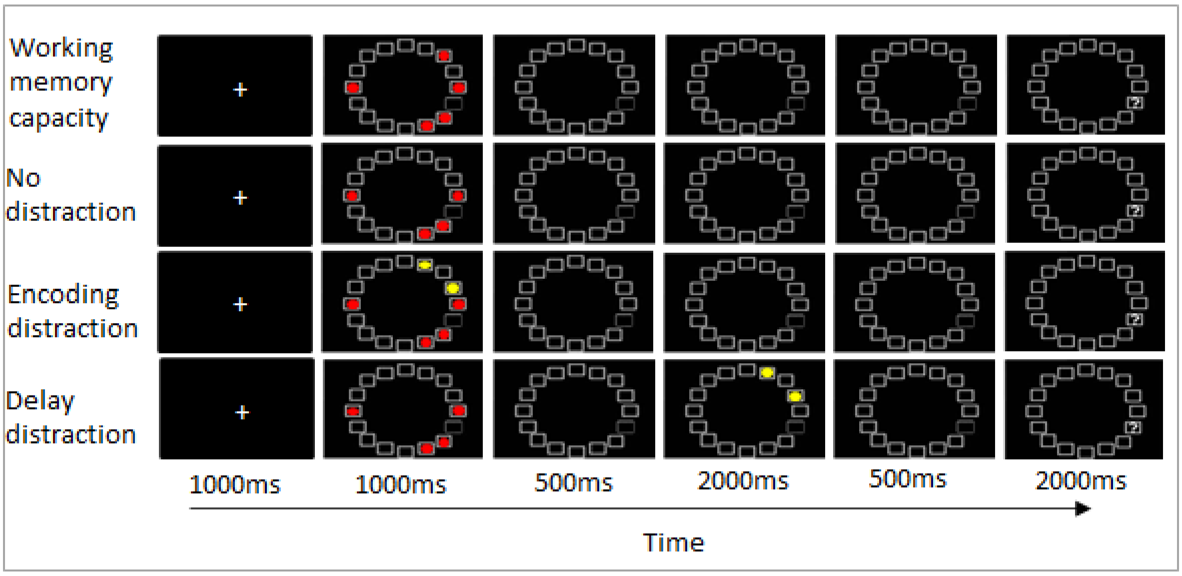

Figure 7; Example trials from the ‘red circle’ task. In the VWMC condition, participants were asked to remember the positions of 3, 4, or 5 red circles, which were presented for 1 second. At the response stage, they were presented with a question mark in one square and asked to respond with a button press (yes or no) to indicate whether there had been a red circle in that *position. In No Distraction (ND), Encoding Distraction (ED) and Delay Distraction (DD) conditions, participants were asked to remember the positions of 4 red circles, which were presented for 1 second and at the response stage, they were presented with a question mark at one position and asked to respond (yes or no) to indicate whether there had been a red circle at that position. In the ND condition, participants were presented with red circles, without overt distraction. In the ED condition, participants were also presented with 2 yellow circles during the encoding period, which were to be ignored and in the DD condition participants were presented with 2 yellow circles during the delay period, which were to be ignored.*

Faces and scenes tasks

In the 'remember scenes' task, participants were presented with scenes (targets) to be remembered and faces (distractors) to be ignored and in the 'remember faces' task, participants were presented with faces (targets) to be remembered and scenes (distractors) to be ignored (see figure 8). The images were presented in a 2x2 grid and subtended a horizontal visual angle of approximately 6.92° and a vertical visual angle of approximately 6.46°. 168 Greyscale images of natural scenes (84 images) and faces (84 images) with neutral expressions were used. These were taken from the database of images used in Gazzaley et al (2005). Within each block, each face and each scene were presented only once, and the same faces and scenes were presented in each block. In the VWMC task, participants were presented with either 1, 2 or 3 targets simultaneously and no distractions. There was a total of 42 trials: 14 of each load. In the ND task participants were simultaneously presented with 2 targets and no distractions. In the ED task participants were simultaneously presented with 2 targets and 2 distractions and in the DD task participants were simultaneously presented with 2 targets, and then during the delay, after the targets had disappeared, 2 distractions were simultaneously presented. There were 30 trials in each of the ND, ED, and DD blocks. At the response screen participants were presented with one face, in the remember faces task or one scene in the remember scenes task and asked to respond with a button press ‘same’ or ‘different’, to indicate whether the probe image was the same as one of the target images. For half of the trials the probe image was the same as one of the target images.

Figure 8; Example trials from each condition of the 'remember faces' and 'remember scenes' tasks. For each stimulus type, there were 4 blocks: VWMC, No Distraction (ND), Encoding Distraction (ED) and Delay Distraction (DD). In each task participants were asked to remember the target stimuli and ignore the distraction stimuli. At the response they were presented with a probe image and asked to indicate whether the probe image was the same or different to *the target image. In the VWMC task, participants were presented with either 1,2 or 3 targets, and no distractions. The targets were presented at pseudo-random positions in the grid. In the ND, ED, and DD conditions, 2 targets were always presented at pseudo-random positions in the grid. In the ED and DD conditions, distractions were presented either at the same time as targets (ED) or during the delay period (DD), and these images were always presented in different grid positions to the targets.*

Data analysis

VWMC was estimated for each participant for each of the twelve conditions by calculating K values, as reported in previous studies (Cowan, 2001; Vogel et al., 2005; McNab & Dolan,2014); K= S(H-F), where K is an estimate of VWMC, S refers to set size, H to Hit rate and F to false alarm rate. The false alarm rate is used as an estimate of how much a participant is guessing, and so by taking this into account when estimating the capacity, calculating K values allows us to correct for guessing. For the VWMC condition for each task, K values from the 2 highest loads were averaged together, to estimate VWMC (as in McNab & Klingberg, 2008). Three participants were excluded based on K values of less than 1 in the 'red circles' VWMC task, as this indicates participants were likely to be guessing on a large number of trials, as a K value of 0 is 'chance'. All statistical analysis was performed in IBM SPSS version 25, and two-tailed tests are reported. Eye-tracking data was processed in MATLAB R2018b.

To assess the difficulty of each condition and compare performance across stimulus types, a 3x3 ANOVA was run using the accuracy data for stimulus type (circles, remember faces and remember scenes) and distraction condition (ND, ED, and DD). K-values could not be used to compare across stimulus types, as different stimuli had different set sizes. Subsequent 2x2 ANOVAs and t-tests were then performed to investigate the interaction found in the 3x3 ANOVA. Separate 1-way ANOVA's comparing ND, ED, and DD for each stimulus type (circles, remember faces and remember scenes) were then performed using K values, to check that we saw similar results with K-values as with accuracy. All analysis after this was performed using K values, as this allowed us to account for guessing.

To investigate the relationship between performance for each of the three stimulus types (circles, remember faces, remember scenes), correlations between performance on the VWMC tasks were run. We also wanted to investigate the relationship between filtering ability for each of the three stimulus types for ED and DD. In order to get a measure of filtering ability for ED and DD, the residuals from the regression models $ED = \alpha + \beta DD$ and $DD = \alpha + \beta ED$ were used, respectively, where α represents the intercept and β represents the regression coefficient. Using this method, variance associated with storage and instructions relating to remembering/ignoring stimuli, which would be shared by both ED and DD, was accounted for, leaving the unique variance in performance for ED and DD, which will be referred to as ED and DD filtering ability respectively. The standardised residuals from these regressions were then used for correlation analyses.

Finally, to investigate the contribution of ED and DD to VWMC, regression analyses were performed, as in previous studies (McNab & Dolan, 2014; McNab et al, 2015). In the regression, performance in ED and DD conditions was used to predict VWMC, and this was performed for each of the three stimulus types (circles, remember faces and remember scenes).

Results

Eye-tracking results

The number of blinks during the 'encoding' period and 'delay' period in each of the three stimulus types was calculated (see figure 9). As the encoding period was 1s, and the delay period 2s, number of blinks in the delay period were divided by two, to ensure the number of blinks is proportionate to the encoding period. For each stimulus type a 2x3 ANOVA was run, which considered the factors time period (encoding and delay) and distraction condition (ND, ED, and DD). For 'remember faces' and 'remember scenes' there was a main effect of time period (remember faces: F(1,23)= 85.50, p<.001; remember scenes: F(1,23)= 92.52 , p<.001), indicating that there were more blinks during the delay period than the encoding period. However, there was no main effect of time in the 'red circles' condition (F(1,22)=2.35, p=.140).There was no main effect of distraction condition for any stimulus type (red circles: F(2,44)=0.45 p=.639; remember faces: F(1.06,24.35)= 1.31, p=.266, Greenhouse-Geisser corrected; remember scenes: F(1.38,31.84)= 0.61, p=.880) and no interaction (red circles: F(2,44)=1.91 p=.160; remember faces: F(2,46)=1.48 , p=.266; remember scenes: F(2,46)= 1.30, p=.281). As we were particularly interested in the delay period, a one-way ANOVA was run on the data at the delay period for each stimulus type, and again there was no main effect of distraction condition (red circles: F(2,44)=1.15, p=.325; remember faces: F(1.18, 27.12)= 1.088, p=.346, Greenhouse-Geisser corrected; remember scenes: F(2,46)=0.34,p=.714). These results indicate that whilst there were significantly more blinks during the delay period than at the encoding period, for 'remember faces' and 'remember scenes', there was no significant difference between the number of blinks in each distraction condition.

Next, the average duration of blinks during the ‘encoding’ and ‘delay’ period were calculated for each distraction condition, if the participant blinked during this time period. As many participants did not blink at all during the encoding period, in at least one block (19 out of 23), the average duration could not be calculated for these participants, and so only data from the delay period is considered. All participants blinked at least once during the delay period, in the faces and scenes tasks and so all 24 participants are included in the analysis. However, in the red circles task eight participants did not blink during the delay period, leaving 15 participants in the analysis. A one-way ANOVA, considering distraction condition (ND, ED, and DD) found that there was no main effect of distraction on the average duration of blinks during the delay period for any of the stimulus types (red circles: F(1,22)=8.02 p=.010; remember faces: F(1,23)= 118.684, p<.001; remember scenes: F(1,23)= 90.362, p<.001)). This suggests that the duration of eye-blinks does not differentially change dependent on distraction condition. This suggests that there was no significant difference between the average duration of blinks in each distraction condition.

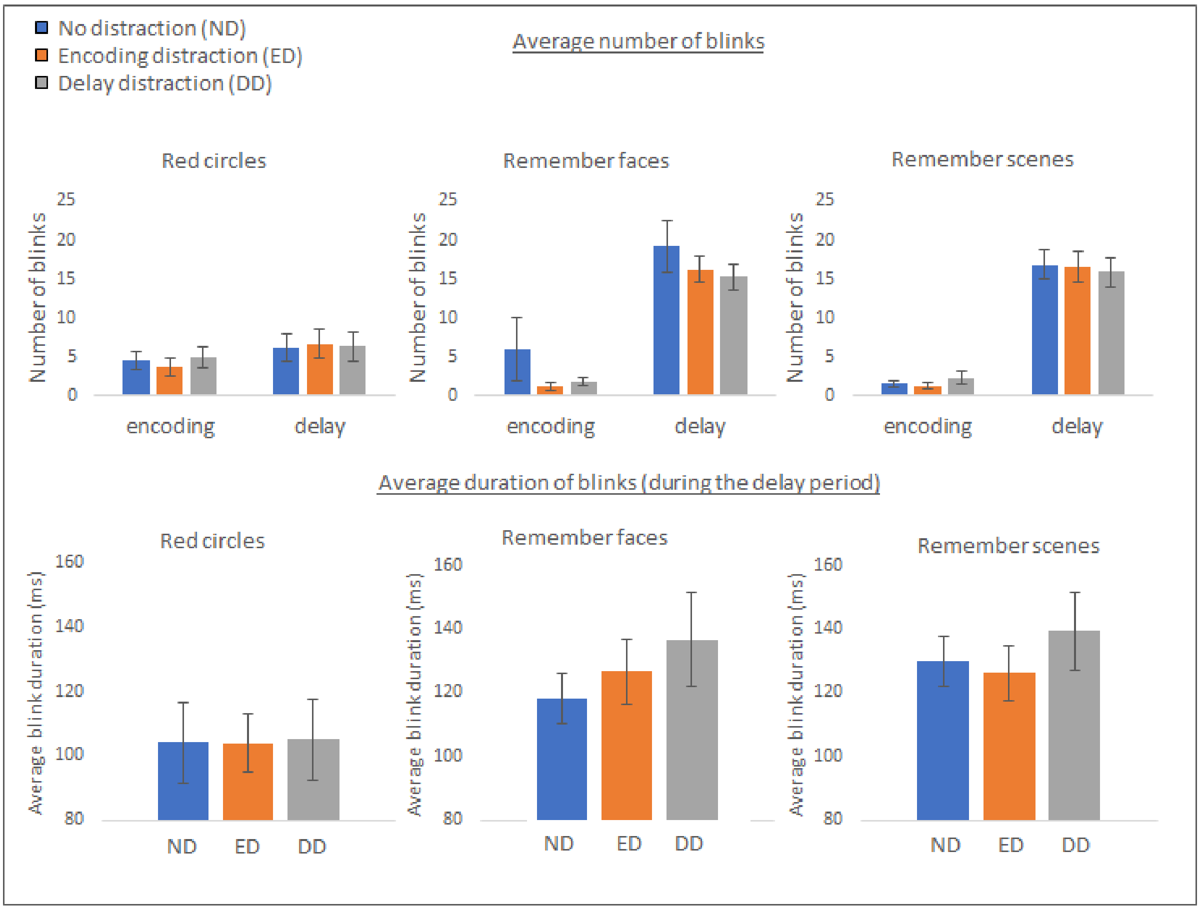

Figure 9; Average number of blinks in the encoding period and delay period, in each distraction condition, for each of the three stimulus types. Average duration of blinks during the delay period, in each condition, for each of the three stimulus types. Blue bars represent 'no distraction', orange bars represent 'encoding distraction', and grey bars represent 'delay distraction'. Error bars represented +/- 1 SEM.

Accuracy

A 3x3 ANOVA, examining the effects of stimulus type (red circles, remember scenes, remember faces) and distraction condition (ND, ED, and DD) on accuracy was performed. The data failed the assumption of normality for all distraction conditions in the red circles task, and for ND and ED conditions in the remember faces task, however as ANOVA's are fairly robust to violations of normality we continued with the ANOVA (Schmider, Ziegler, Danay, Beyer & Bühner, 2010; Blanca, Alarcón, Arnau, Bono & Bendayan, 2017). There was a significant main effect of stimulus type (F(2,82)=109.87, p<.001), where 'remember scenes' had the lowest accuracy, followed by 'remember faces' and the 'red circles' task had the highest accuracy, as can be seen in figure 10. There was a main effect of distraction condition (F(2,82)=3.18, p=.047) and there was a significant interaction between stimulus type and distraction condition (F(4,164)=2.979, p=.021).

Three subsequent ANOVA's, comparing two stimulus types at a time were performed to determine what was driving this interaction. The first 3x2 ANOVA including the factors distraction conditions (ND, ED, and DD) and stimulus type (only including 'remember scenes' and 'red circles'), revealed a significant interaction between stimulus type and distraction condition (F(2,82)=5.52, p=.034)). The second 3x2 ANOVA, this time only including the stimulus types 'remember scenes' and 'remember faces', also revealed a significant interaction between stimulus type and distraction condition (F(2,82)=4.23, p=.018). However, the third 3x2 ANOVA, which included the stimulus types 'remember faces' and 'red circles', did not reveal a significant interaction between stimulus type and distraction condition (F(2,82)=0.512, p=.601). This suggests the above interaction, was driven by differences in performance in the distraction conditions between the 'remember scenes' task and the other two stimulus types.

Subsequent ANOVA's were performed in order to determine which distraction conditions were driving the interactions between 'remember scenes' and 'red circles', and between 'remember scenes' and 'remember faces'. To determine what was driving the interaction between the ‘remember scenes’ and ‘red circles’, three 2x2 ANOVA’s were performed, comparing two distraction conditions at a time. The first 2x2 ANOVA, including distraction conditions ND and DD revealed a significant interaction between stimulus type and distraction condition (F(1,41)=5.61,p=.023). The second 2x2 ANOVA, including distraction conditions ED and DD, also revealed a significant interaction between stimulus type and distraction condition (F(1,41)=4.44, p=.041). However, the third ANOVA, including distraction conditions ND and ED, revealed no interaction between two stimulus types (F(1,41)=0.02, p=.876). This suggests that the interaction between stimulus type and distraction condition for ‘remember scenes’ and ‘red circles’, when all distraction conditions are included in the ANOVA, was driven by differences in the DD condition, compared with ED and ND.

Similarly, to determine what was driving the interaction between the ‘remember scenes’ and ‘remember faces’, three 2x2 ANOVA’s were performed, comparing two distraction conditions at a time. The first 2x2 ANOVA, including ND and DD distraction conditions, revealed a significant interaction between stimulus type and distraction condition (F(1,41) =6.51,p=.015). The second 2x2 ANOVA, including ED and DD distraction conditions, also revealed a significant interaction between stimulus type and distraction condition (F (1,41)=5.12,p=.029). However, for the 2x2 ANOVA including ND and ED distraction conditions, there was no significant interaction between stimulus type and distraction conditions (F(1,41)=0.41, p=.536). This suggests that the interaction between stimulus type and distraction condition for ‘remember scenes’ and ‘remember faces’, when all distraction conditions are included in the ANOVA, was driven by differences in the DD condition, compared with ED and ND.

Paired t-tests showed that in the ‘remember scenes’ task, there was a significant difference in performance in the DD condition compared with the ED condition (t=2.64, p=.012) and the ND conditions (t=3.35, p=.002), however there were no significant distraction effects for the ‘remember faces’ task or the ‘red circles’ task (p>.05). These findings indicate that in the ‘remember scenes’ task, participants had a significantly lower accuracy for DD than ND and ED, and that this was significantly different from the ‘remember faces’ and ‘red circles’ task, where these distraction effects were not found.

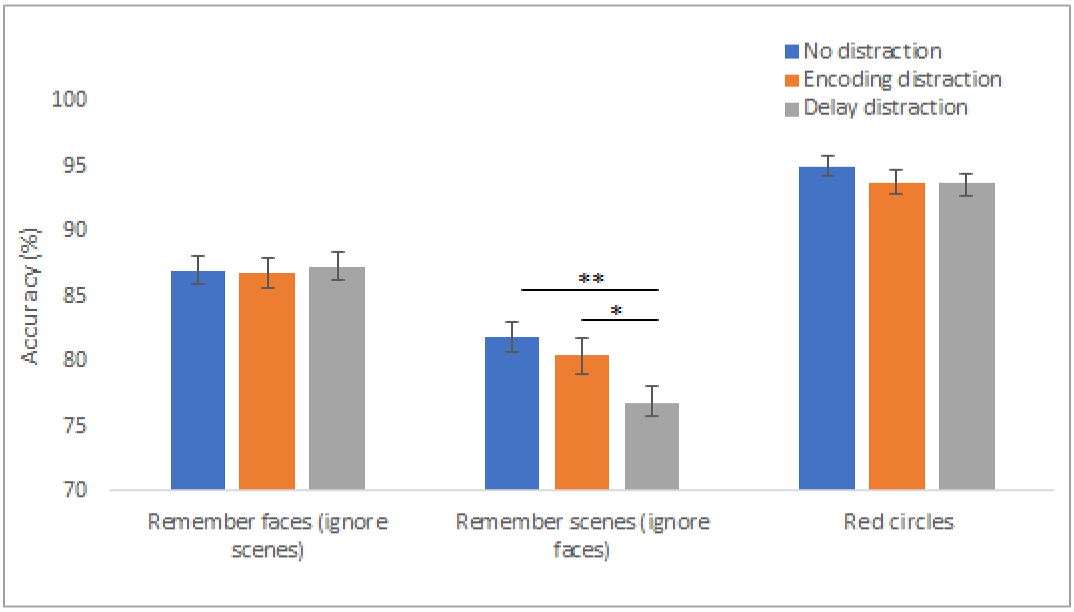

*Figure 10; Accuracy across all three stimulus types for each distraction condition. Blue bars represent ‘no distraction’, orange bars represent ‘encoding distraction’, and grey bars represent ‘delay distraction’. Error bars represent +/- 1 SEM. **p<.01, *p<.05.*

K values

Three, one-way ANOVA's were performed using K values, to investigate distraction effects for each stimulus type (red circles, remember faces, remember scenes). Similar to the accuracy data, the K value data did not meet the assumption of normality for any of the distraction conditions in the red circles task or in the ND and ED conditions in the remember faces task, however we continued with the ANOVA. There was no main effect of distraction condition in the 'red circles' task (F(1.752,71.822)=1.037, p=.359; Greenhouse-Geisser scores reported as data failed the assumption of sphericity- see figure 11a) or the 'remember faces' task (F(2,82)=0.080, p=.923- see figure 11b). However, in the 'remember scenes' task there was a main effect of distraction condition (F(2,82)=6.883, p=.002) and paired t-tests revealed that performance in DD was significantly lower than in ND (t=3.292, p=.002) and in ED (t=2.894, p=.006), as can be seen in figure 11c.

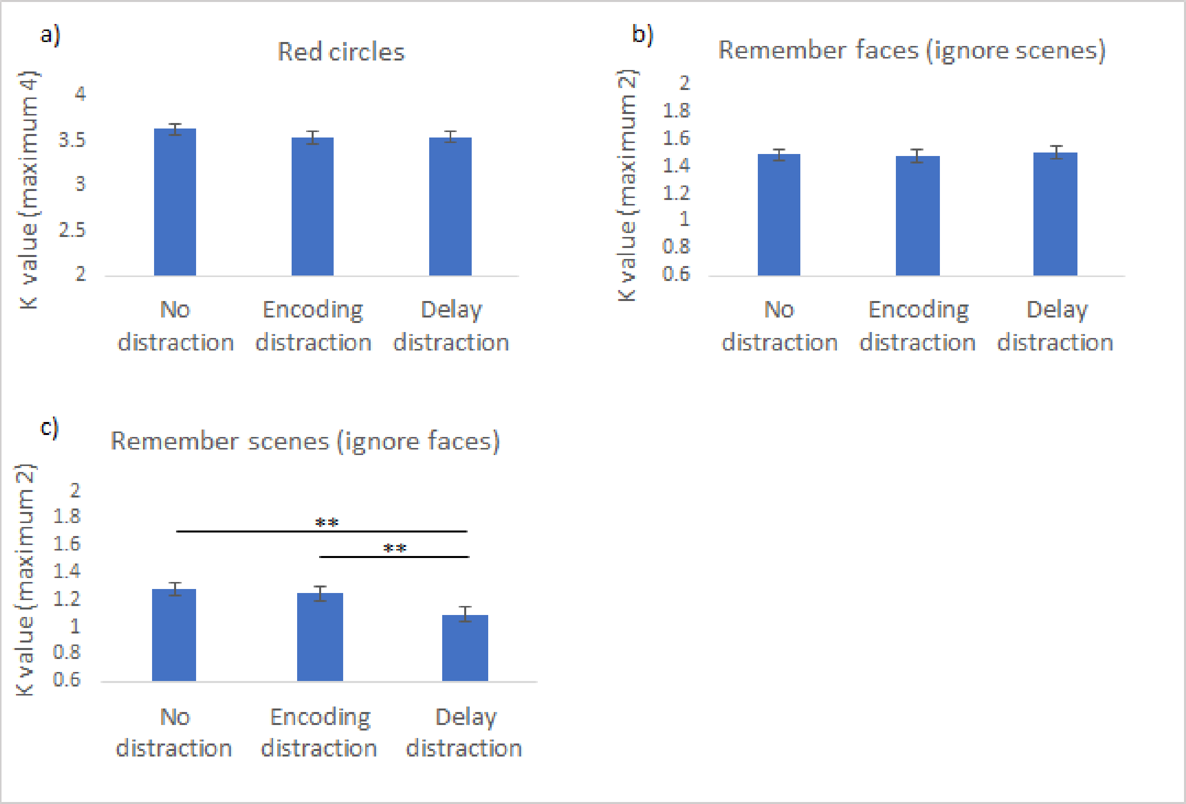

*Figure 11; K values for all three stimulus types (a-c) and for each distraction condition. For the 'red circles' task, the maximum possible K value is 4, as this task had a working memory load of 4 items. Whereas, for 'remember faces' and 'remember scenes', the maximum possible K value is 2, as in these tasks the working memory load was 2 items. Error bars represent +/- 1 SEM. **p<.01*

Correlation analysis revealed a significant correlation between VWMC scores in the 'remember faces' and 'remember scenes' task (figure 12a), and between the 'remember faces' and 'red circles' task (figure 12b), however not between the 'remember scenes' and 'red circles' task (figure 12c). This indicates that VWMC in one stimulus type was positively associated with VWMC in another stimulus type, however this was not significant when comparing 'remember scenes' and 'red circles'. Additionally, when corrected for multiple comparisons only the correlation between ‘remember scenes’ and ‘remember faces’ was still significant (Bonferroni-corrected p=.021), as the correlation between ‘remember faces’ and ‘red circles’ was no longer significant (Bonferroni-corrected p=.069). Spearman’s Rho values are reported as the data did not meet the assumption of normality in the faces or circles task.

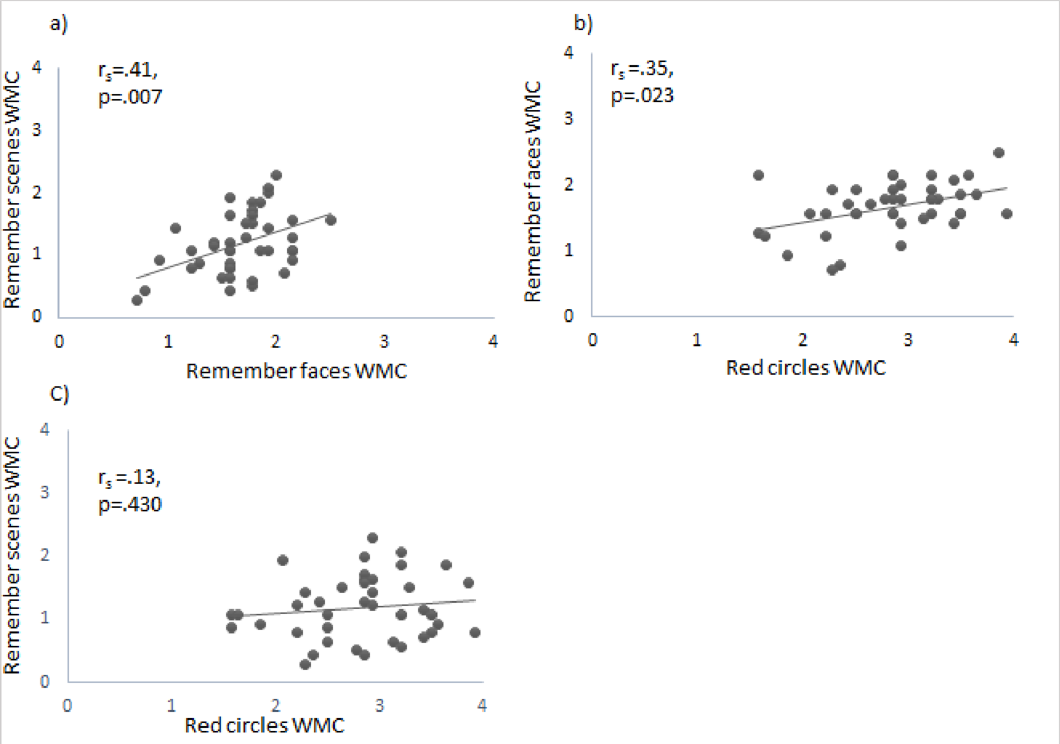

Figure 12; Correlations between VWMC for ‘remember scenes’ and VWMC for ‘remember faces’ (a), between VWMC for ‘remember faces’ and VWMC for ‘red circles’ (b) and between VWMC for ‘remember scenes’ and VWMC for ‘red circles’ (c). Positive associations indicate that a higher VWMC in one stimulus type is associated with a higher WMC in the other stimulus type. VWMC is estimated by calculating K-values for each task (K= S(H-F), where K is an estimate of VWMC, S refers to set size, H to Hit rate and F to false alarm rate). For ‘remember faces’ and ‘remember scenes’ the maximum this could be was 2.5 and for the ‘red circles’ the maximum this could be was 4.5.

Next, the relationship between filtering ability for each of the three stimulus types (red circles, remember scenes, and remember faces) for ED and DD was investigated. Standardised residuals from the regression equation $ED= \alpha + \beta_1 DD$, and $DD= \alpha + \beta_1 ED$, were used as a measure of filtering ability for ED and DD respectively (full explanation in data analysis section of methods). As can be seen in figure 13a-c, there were no significant correlations between ED filtering ability for the different stimulus types. However, as can be seen in figure 13d-f, there were significant positive correlations between DD filtering ability for all stimulus types. This indicates that higher filtering ability in DD for one stimulus type was associated with higher filtering ability in DD for the other stimulus types. However, when corrected for multiple comparisons only the correlation between ‘remember scenes’ and ‘red circles was still significant (Bonferroni-corrected $p= .006$), as the correlation between ‘remember faces’ and ‘red circles’ was no longer significant (Bonferroni-corrected $p=.096$), and the correlation between ‘remember faces’ and ‘remember scenes’ was no longer significant (Bonferroni-corrected $p=.204$). Spearman’s Rho values are reported as the data did not meet the normality assumption for ED and DD filtering ability in the ‘red circles’ or ‘remember faces’ tasks.

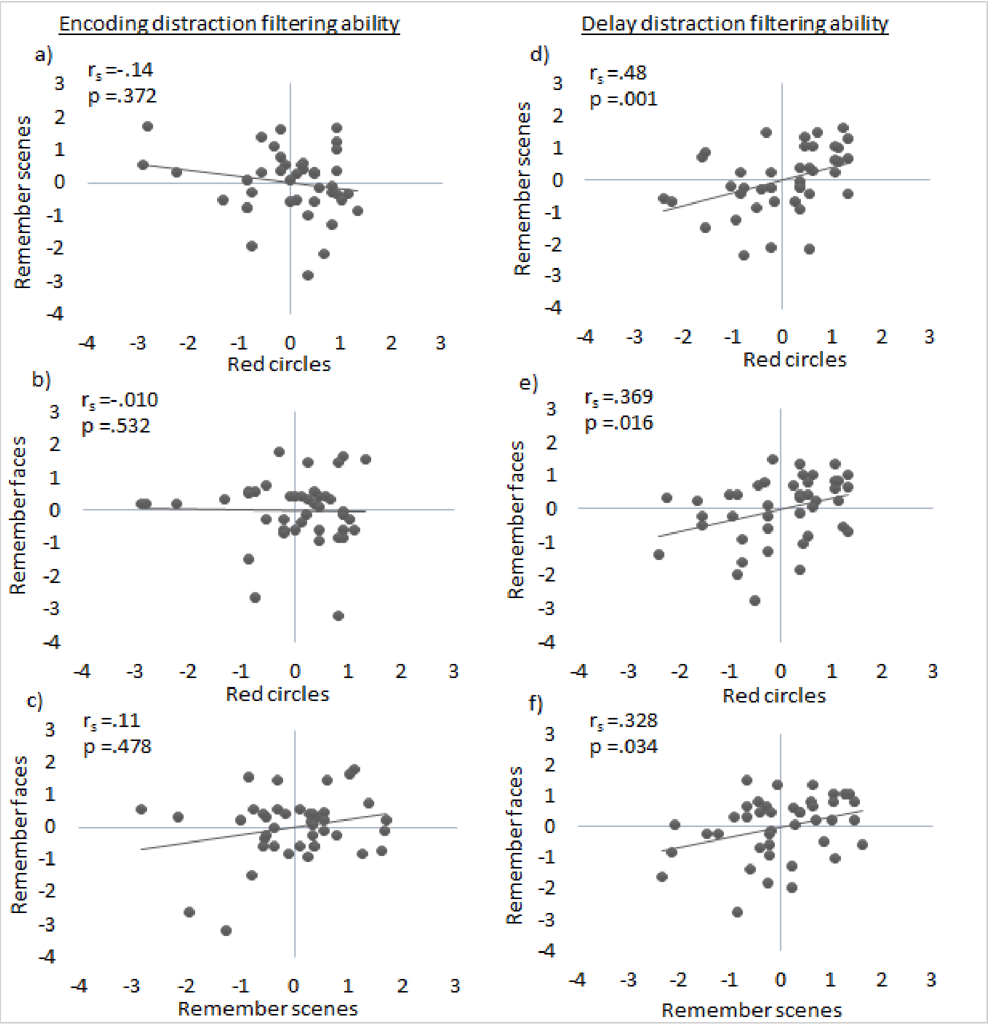

Figure 13; a-c correlations between filtering ability in ED after accounting for performance in DD for 'remember scenes' and 'red circles' (a), 'remember faces' and 'red circles' (b) and 'remember faces' and 'remember scenes'. d-f, correlations between filtering ability in performance in DD after accounting for performance in ED for 'remember scenes' and 'red circles' (d), 'remember faces' and 'red circles' (e) and 'remember faces' and 'remember scenes' (f).

Finally, regression analysis was performed to investigate whether performance in ED and DD predicts VWMC. For each of the three stimulus types, the regression model VWMC= $\alpha + \beta_1$ ED + β_2 DD was used. For 'red circles' and 'remember faces', predictor variables (ED and DD) were not correlated (red circles: r=.15, p=.343; remember faces: r=.24, p=.128), however for 'remember scenes' the predictor variables were significantly correlated (r=.50, p=.001). However, the VIFs are less than 5 for all stimulus types (red circles: VIF=1.02; remember faces: VIF=1.06; remember scenes: VIF=1.33), suggesting it is still appropriate to use a regression model (Chatterjee & Price, 1991; Midi & Baheri, 2010). The model did not significantly account for the variance in VWMC for any of the stimulus types (red circles: F(2,39)=2.41, p=.103; remember faces: F(2,39)=1.36, p=.268; remember scenes: F(2,39)=2.53, p=.093).

Discussion

The first aim of this study was to understand whether there are similar distraction-filtering mechanisms underlying visual-spatial and visual-object WM. To do this we investigated individual differences in performance across visual-spatial and visual-object WM tasks, assuming that similarities in performance reflect some common mechanisms underlying performance in both tasks. We found that performance (averaged across all distraction conditions), is lower in the 'remember scenes' conditions, than 'remember faces' or in the 'red circles' task. However, we also found that ignoring faces whilst remembering scenes has a greater effect on performance (relative to the no distraction condition), than ignoring scenes whilst remember faces, or ignoring the positions of yellow circles, whilst trying to remember red circles, suggesting that faces are harder to ignore than scenes, or yellow circles. As predicted, we find that there was a positive correlation between VWMC for remember faces and remember scenes, and remember faces and red circles, suggesting individual differences in WM are similar across these tasks. However, whilst there was a positive association between VWMC for remember scenes and red circles, this was not significant. When considering filtering ability, we find positive correlations between all three stimulus types for DD filtering ability, suggesting similar individual differences in DD filtering ability regardless of stimuli. However, we do not see this for ED. Finally, contrary to our predictions, we did not find that performance in ED and DD filtering significantly and uniquely predict VWMC in the 'red circles' task, which has been found in previous studies (results reported in chapter 2; McNab & Dolan, 2014; McNab et al 2015), and we did not find this for the 'remember scenes' or 'remember faces' tasks either.

Performance (averaged across distraction conditions) was lower in the 'remember scenes' task than in the 'remember faces' and 'red circles' task. Many studies find no difference in accuracy rates for remembering faces compared with remembering scenes (Lepsien & Nobre, 2007; Ranganath, DeGutis & D'esposito, 2004; Rutman, Clapp, Chadick & Gazzaley, 2010). However, a key difference between these studies and the current study is that they all used sequential presentation of targets, whereas in the current study targets were presented simultaneously. Previous research shows there are differences in performance between presenting targets either sequentially or simultaneously, finding that performance is higher for sequential than simultaneous presentation (Ihssen, Linden, & Shapiro, 2010). They suggest that this might be because separating the stimuli overcomes limitations of resources for visual attention and WM that are seen when multiple items have to encoded simultaneously (Mayer et al, 2007). It is possible that differences in encoding scenes and faces, make it more difficult to encode scenes when presented simultaneously. For example, research finds that there is a peripheral-field bias for scene processing and a centre-field bias for face processing (Levy, Hasson, Avidan, Hendler & Malach, 2001), and as the stimuli in our study were presented centrally, this could lead to better performance in the remember face task. Additionally, we find that faces were more distracting (when remembering scenes) than scenes (when remembering faces) or yellow circles (when remembering red circles). This could be due to faces being a more salient distraction, as research finds that relevant distractions have more of an effect on performance than irrelevant distractions (e.g. Yoon, Curtis & D'esposito, 2006; Bonnefond & Jensen, 2012), and in particular that images of faces are more distracting than other stimuli (Jenkins, Lavie & Driver, 2003; Lavie, Ro & Russell, 2003; Carmel, Fairnie & Lavie, 2012).

When considering individual differences in WM performance without distraction, we found that VWMC for faces and scenes correlate. This was predicted as both are types of object WM tasks, and so we would expect individual differences in performance to be similar and this is in line with previous research (Della Sala, Gray, Baddeley, Allamano & Wilson (1999). VWMC for faces and the positions of red circles also correlate, as predicted, this suggests that there are similar individual differences in performance in visual-spatial and visual-object WM. Also in line with previous research (Della Sala, Gray, Baddeley, Allamano & Wilson, 1999), the correlation between VWMC for faces and the positions of red circles is not as strong as the correlation between remember faces and remember scenes, although these have not been directly compared in the current study. This might suggest that whilst there are some similar WM mechanisms underlying visual-object and visual-spatial WM, there might also be some dissociations. Contrary to our predictions, VWMC for scenes and VWMC for the positions of red circles were not significantly correlated. This could be due to task difficulty, as performance on the 'remember scenes' task was significantly lower than in the red circles task, and the data suggests some ceiling effects for the red circle task, therefore it may not have been very sensitive to individual differences. However, overall, the findings suggest similarities in VWMC across visual-object and visual-spatial tasks, indicating some similar mechanisms underlying performance for both types of WM.

When considering individual differences in distraction filtering, we found that ED filtering ability does not correlate between stimulus types, for example ED filtering ability for remember faces/ ignore scenes, does not correlate with remember scenes/ ignore faces. However, there is a significant positive correlation in DD filtering between all three stimulus types. It is possible that ED requires a more task-selective mechanism, as when distraction is presented during encoding participants must selectively remember the relevant stimuli and ignore the irrelevant stimuli, whereas DD filtering might require a less selective mechanism as when distraction is presented during the delay, the task-instructions about which stimuli to ignore are irrelevant, and participants can ignore anything on screen, regardless of stimuli type. Neuroimaging studies show some support for this theory as studies which use ED often find the basal ganglia to be involved (McNab & Klingberg, 2008; Baier et al., 2010; Haeger, Lee, Fell & Axmacher, 2015), which is thought to be involved with the selective gating of items into WM (Frank, Loughry and O'Reilly, 2001). However, studies using DD do not support a role of the basal ganglia in distraction filtering (Cools, Miyakawa, Sheridan & D'esposito, 2010; Mehta et al., 2004). Therefore, if ED requires a more task-selective mechanism, this could explain the finding that ED filtering ability does not correlate across stimulus types, as some people might be better at selectively ignoring certain types of distraction. Whereas, if DD requires a less selective mechanism, this might explain the finding that filtering ability does correlate across stimulus types, as more general suppression mechanism might be responsible for filtering distraction during the delay regardless of stimulus type. Findings discussed in the next chapter provide some support for this theory. However, it is still speculative, and should be investigated further in the future.

Previous research using a visual-spatial task finds that ED and DD significantly and uniquely predict VWMC (results presented in chapter 2; McNab & Dolan, 2014; McNab et al 2015). However, we did not replicate this in the current study. We had also predicted that ED and DD would significantly and uniquely predict VWMC in the 'remember faces' and 'remember scenes' tasks, however we did not find this. One key difference between this study and previous studies is that this study used a blocked design, whereas in previous studies distraction conditions have been intermixed (e.g. McNab & Dolan, 2014; McNab et al 2015). In a blocked design it is predictable when the distractions are going to be presented, and previous research suggests that there are larger distraction effects for unpredictable compared with predictable distraction and predictable distraction is less likely to be affected by working memory load (Carlson, Hasher, Zachs & Connelly, 1995; Sussman, Winkler & Schröger, 2003; Macdonald & Lavie, 2008). Neuroimaging studies using VWMC tasks, also show that brain activity can be modulated by predictability of distractions (Hakim, Feldmann-Wüstefeld, Awh & Vogel, 2019; Bettencourt & Xu, 2016). For example, in Hakim et al., (2019) they varied the percentage of trials were distractors were presented, from 25% (low predictability) to 75% (high predictability). They found that in the high predictability condition, CDA activity was higher than in the low predictability condition, suggesting that when distractions are more predictable participants are better able to protect WM from distraction. Additionally, Bonnefond & Jensen (2012) suggest that 'the doors to perception close when a distractor is expected'. These theories would fit in with our findings, as we did not find any distraction effects for the 'remember faces' or 'red circles' tasks and only found distraction effects for DD in the 'remember scenes' task. Therefore, a blocked design might not be as sensitive to picking up distraction effects or filtering mechanisms as a mixed design, and this might be why we did not find that ED and DD significantly predict VWMC for any of the stimuli types. Future research could directly compare distraction effects in a blocked compared with mixed design and investigate further whether ED and DD significantly and uniquely predict WM in visual-object WM tasks.

It should be noted that there is debate over the ability to dissociate between visual-object and visual-spatial working memory tasks, as regardless of what the task is, spatial information will be available e.g. position of the item on screen. Many studies support the idea that spatial location is somewhat automatically encoded in WM regardless of whether it is task-relevant, and that this can be used to guide decision making in WM tasks (e.g. Treisman & Zhang, 2006, Hollingworth, 2007; Boduroglu & Shah, 2009; Lin & He, 2012, Udale, Farrel & Kent, 2017). For example, in a visual-object change-detection task, Hollingworth (2007), found an advantage of the test image being in the same spatial location as the initial image, suggesting that spatial information was encoded as well as the features of the image, even though location was irrelevant to the task. However, studies also find that when a single probe is presented, any effects of changing location are no longer present (Treisman & Zhang, 2006; Udale, Farrel & Kent, 2017), and this was also the case when the probe was presented with a task-irrelevant background (which provides a spatial reference to the probe to encode) (Udale, Farrel, & Kent, 2017). Udale, Farrel & Kent (2017) argue that this suggests that spatial information does not always influence decision making in change detection tasks, and may not always be automatically encoded. In the current study, in the object WM tasks, faces and scenes are presented in four locations on the screen, in arrays of either one, two, or three items. Therefore, it is likely that, at least in the trials with two or three objects, that spatial information is integrated into WM. Nevertheless, studies do find a behavioural dissociation between visual-spatial and visual-object WM tasks, similar to those used in the current study, (e.g. Pickering et al., 2001; Logie & Pearson, 1997; Della Sala et al. 1999), and in the current study we see that correlations between visual-object tasks are stronger than correlations between visual-object and visual-spatial WM tasks, as seen previously (Della Sala et al., 1999), suggesting that there are some differences in the underlying WM processes used to complete these tasks. The findings from this study suggest some similarities in the underlying mechanisms between visual-object and visual-spatial WM, and similarities in DD filtering performance, but not ED filtering performance. This helps us understand further whether findings from visual-spatial WM tasks can be generalised to visual-object WM tasks and vice versa. Additionally, the finding that DD filtering, but not ED filtering performance is similar across visual-object and visual-spatial WM, might have implications for cognitive training, as one issue with cognitive training is that whilst participants improve at the task they are trained on, the improvements often do not generalise to other tasks or skills (Melby-Lervåg & Hulme, 2013). However, as we observed that DD filtering ability correlates across stimuli types, focussing on improving DD filtering might lead to transfer of training effects to other tasks.

The second aim of the study was to identify whether participants close their eyes when distractors are presented during the delay period. The analysis of the eye-tracking data revealed that there were more blinks during the delay period than during the encoding period in the ‘remember faces’ and ‘remember scenes’ conditions. This is possibly due to concentrating when the relevant information is on screen and then blinking when it has gone off screen. Given this, it is possible that less information is taken in during the delay period. However, the average duration of blinks during the delay period spans 100-150ms of a 2000ms delay period and so it is only a small percentage of the delay period that is taken up.

Additionally, there were no significant differences in the number of blinks between distraction conditions at either the encoding period or delay period. Therefore, it does not appear that participants were intentionally blinking during the delay period in the DD condition, as a strategy to ignore distraction. From this we can assume that any differences between ED and DD are unlikely to be due to participants closing their eyes in the DD condition.

In summary, we found that there were correlations in performance between visual-object WM and visual-spatial WM, suggesting there are some similar mechanisms underlying performance for both types of WM. For the first time we observed positive correlations between DD filtering across all stimulus types. This suggests a general filtering mechanism that underlies DD filtering regardless of stimulus type. However, we did not find correlations for ED filtering between stimulus types, which suggests that ED filtering requires a more task-selective filtering mechanism, and participants can be better at ignoring certain types of distraction. This theory is investigated further in the next chapter, in a study investigating the neural correlates of ED and DD filtering ability. Finally, we did not replicate previous findings that ED and DD significantly and uniquely predict VWMC in a visuo-spatial task or find that ED and DD significantly predict VWMC in either of the visual-object WM tasks. Overall, we provide evidence of commonalities in the underlying WM mechanisms associated with visual-object and visual-spatial WM.

Chapter 4: Suppression and enhancement in task-specific visual regions associated with ED and DD filtering.

Introduction

In chapters 2 and 3, the behavioural mechanisms of ED and DD filtering have been discussed. In particular in Chapter 2, finding that the contribution of ED and DD to VWMC differentially change over development and healthy ageing. Additionally, results from Chapter 3 provide evidence of similar mechanisms underlying performance in visual-object and visual-spatial WM tasks. However, the neural mechanisms associated with ED and DD have not been directly compared.

Neuroimaging studies investigating the top-down activity associated with distraction to WM presented during encoding, find that the basal ganglia and prefrontal regions are associated with the process of preparing for distraction (McNab & Klingberg, 2008; Toepper et al., 2010; Dolcos, Miller, Kragel, Jha, McCarthey, 2007). However, studies which present distractions during the delay period, suggest that the basal ganglia may not be involved in distraction filtering. For example, Cools, Miyakawa, Sheridan, and D'esposito (2010) used a delay distraction paradigm and found that patients with Parkinson's disease (off-medication), with impaired basal ganglia functioning, showed enhanced distractor filtering, which is inconsistent with a role of the basal ganglia in distraction filtering. Similarly, Mehta et al. (2004) also used a delay distraction paradigm and found that after participants ingested Sulpiride, which is a dopamine antagonist and negatively affects the striatum in the basal ganglia, distractor-filtering improved rather than declined. Based on this apparent inconsistency in the literature for the role of the basal ganglia in distraction filtering, McNab and Dolan (2014) speculated that the basal ganglia is involved in distractor filtering at encoding, but not when distractors are presented during the delay period. As discussed in previous chapters, this might be because the basal ganglia has been associated with selective gating of items into WM (Frank, Loughry & O'Reilly, 2001; Gruber, Dayan, Gutkin, & Solla, 2006; McNab & Klingberg, 2008) and ED filtering might require a more task-selective mechanism than DD filtering, as ED requires participants to selectively attend to certain stimuli and ignore other stimuli, whilst during DD filtering participants can ignore anything on screen, regardless of stimulus type. Together with the behavioural findings that ED and DD significantly and uniquely predict VWMC (results presented in Chapter 2; McNab & Dolan, 2014; McNab et al 2015), this supports the theory that there are separate neural mechanisms underlying ED and DD distraction filtering. Within this study we use activity in visual processing regions, specific to the task (I.e. activity in the para-hippocampal place area when participants are asked to remember scenes), to investigate modulations in attention associated with distractions presented during encoding and during the delay.

fMRI and EEG studies investigating activity in task-specific visual regions during WM tasks, have found that when trying to remember or ignore stimuli, enhancement or suppression relative to a passive task is observed respectively (Gazzaley, Cooney, McEvoy, Knight & D'Esposito, 2005a; Gazzaley, Cooney, Rissman, & D'Esposito, 2005b; Clapp & Gazzaley, 2012). In Gazzaley et al (2005b), they presented participants with two images of scenes and two images of faces, sequentially and in a random order. Participants were asked to either remember the scenes/ ignore the faces or remember the faces/ ignore the scenes or to passively view the stimuli. They found an enhancement of activity in the left para-hippocampal place area (LPPA - a scene processing region) when participants were instructed to remember scenes and a suppression of activity in the LPPA when they were asked to ignore scenes, relative to the passive view condition. This suggests top-down modulation to sensory cortices plays an important role in effectively ignoring distractions and remembering relevant information. As targets and distractions were presented sequentially in Gazzaley et al (2005b), it is not clear whether the same distractor-suppression would be seen for ED and DD filtering. However, as participants did not know the order of the target and distraction stimuli, they would have to attend to what the stimuli was in order to decide whether to remember or ignore it, and so it is possible that the distraction filtering mechanisms in this study are similar to ED filtering mechanisms, as in both paradigms, participants must selectively attend to or ignore task-specific stimuli. Whereas in DD filtering, participants do not need to selectively ignore a particular stimulus, as they can ignore anything on screen regardless of stimuli type. Therefore, it is possible that we will see similar suppression effects, as seen in Gazzaley et al (2005b), for ED filtering, but not DD filtering.

There is also evidence that suppression and enhancement in these task-specific sensory regions might relate to performance. Using EEG, Clapp and Gazzaley (2012) found that 'suppression' of distractors, relative to a passive view condition, correlated with WM performance on the task, in both younger and older adults. Additionally, using fMRI Gazzaley et al. (2005b) found a suppression deficit in older adults compared with younger adults, however this was only significant for the low performing older adults, suggesting that this suppression deficit might be related to WM performance. Similarly, studies find an association between enhancement activity and WM performance (Gazzaley et al, 2005a; Padgaonkar, Zanto, Bollinger & Gazzaley, 2017). For example, Padgaonkar, Zanto, Bollinger, and Gazzaley (2017) investigated enhancement in visual regions in a WM task, relative to a passive view task, using EEG. A median split of the group based on 'enhancement' activity (active – passive) showed that greater enhancement was associated with higher accuracy and faster reaction times. This suggests that greater enhancement is associated with better performance, although this was only found in older adults. However, it is not known whether individual differences in suppression and enhancement correlate with VWMC and distraction-filtering ability, or how this might differ when using ED and DD paradigms, which differ from paradigms previously used, which presented targets and distractions sequentially. These questions will be addressed in the current study.

In order to investigate whether enhancement and suppression are observed in ED and DD tasks, and whether this activity relates to performance, this study used an approach similar to Gazzaley et al. (2005). In the current study, participants were asked to remember faces/ ignore scenes, remember scenes / ignore faces, or passively view the stimuli. However, targets were presented simultaneously rather than sequentially, in order to be in line with previous research using ED and DD paradigms (Experiments in chapters 2 & 3; McNab & Dolan, 2014; McNab et al, 2015). When asked to remember / ignore faces or scenes, participants were presented with either no distraction (ND), distractions presented at the encoding period (ED), or distractions presented during the delay period (DD), and there was a passive view task which matched the stimuli arrangements in each of these active distraction conditions. To replicate the approach in Gazzaley et al. (2005a and b), the passive conditions were compared to active conditions (remember /ignore conditions), to calculate enhancement and suppression indexes. However, the passive view condition may not give us a good measure of 'distraction' activity alone, as it does not consider that in the distraction conditions, participants are also remembering stimuli, therefore activity in the distraction conditions was also compared to activity in the ND conditions.

Firstly, it is hypothesised that in the ED condition, enhancement and suppression will be observed in task-specific visual regions. This is in line with previous findings (Gazzaley et al, 2005a and b), as it is possible that the distraction filtering mechanisms in that study, were similar to ED filtering mechanisms. Secondly, it is hypothesised that in the DD condition, we will still see enhancement of activity in task-specific regions to the relevant stimuli however, we may not see selective suppression in task-specific visual regions. This is because it is thought that DD is a less selective mechanism, than ED, and so there may be no need for selective suppression in task-specific visual regions. This is supported by studies finding that the basal ganglia, which is involved in selective gating of items into WM (Frank, Loughry & O'Reilly, 2001; Gruber, Dayan, Gutkin, & Solla, 2006; McNab & Klingberg, 2008) may not play an important role in DD filtering (Cools, Miyakawa, Sheridan and D'esposito,2010; Mehta et al, 2004; McNab & Dolan, 2014). It is also indicated from findings in chapter 3, that DD filtering ability correlates across stimulus types, which suggests a general filtering mechanism regardless of stimuli, whereas ED filtering ability does not correlate across stimulus types, which might suggest that ED filtering requires task-specific mechanisms to ignore distraction, which do not necessarily correlate across stimulus types, as participants could be better at remembering / ignoring certain stimuli. Therefore, it is hypothesised that suppression will be observed in task-specific sensory regions for ED, but not DD filtering.

A second aim of the study was to understand how suppression and enhancement (if observed), relate to performance. In particular we focussed on VWMC and filtering ability (calculated as in previous chapters, using the residuals from the regression models $ED= \alpha + \beta DD$ and $DD= \alpha + \beta ED$ for ED and DD filtering, respectively). As 'suppression' of activity has been associated with WM performance (Gazzaley et al, 2005b; Clapp & Gazzaley, 2012), it was predicted that suppression in ED will correlate with VWMC, and ED filtering ability (we do not predict suppression will be observed in DD). Similarly, as previous studies have indicated that there is an association between 'enhancement' in the visual cortex and WM performance (Gazzaley et al, 2005a; Padgaonkar, Zanto, Bollinger & Gazzaley, 2017), it is hypothesised that ‘enhancement’, in all three distraction conditions (ND, ED, and DD), will correlate with VWMC for both ED and DD. However, it is less clear whether ‘enhancement’ activity will correlate with distraction-filtering.

Methods

Participants

Thirty-two volunteers who were right-handed, had normal or corrected-to-normal vision and no previous neurological illness were recruited and gave informed consent, which was approved by York Neuroimaging Centre’s ethics committee. Data from seven participants were excluded due to performance being at or below chance (50%) for any block. After 21 participants were scanned, practice trials (prior to scanning), and feedback on performance at the end of each block (during scanning) were added to the procedure. Two further participants were excluded due to a technical error displaying the stimuli, and excessive movement (>4mm mean displacement). Data from the remaining 23 participants (14 females, ages 18-29 years, mean= 21.52, SD=2.56) were analysed. In the out-of-scanner task, data from one additional participant were lost due to a technical error, leaving data from 22 participants for these tasks.

Experimental design and task

For the in-scanner task, participants were either asked to remember the faces (and ignore any scenes that were presented) or remember the scenes (and ignore any faces that were presented). This will be referred to as stimulus type. For each stimulus type there were three distraction conditions: ND, ED, and DD. There were also five ‘passive-view’ blocks which matched each of the above ‘active’ conditions. This made a total of 11 conditions, which were presented in 11 separate blocks (See Figure 14 for paradigm):

1. Remember faces, no distraction (active task)
2. Remember faces, encoding distraction (active task)
3. Remember faces, delay distraction (active task)
4. Remember scenes, no distraction (active task)
5. Remember scenes, encoding distraction (active task)
6. Remember scenes, delay distraction (active task)
7. Passively view stimuli in remember faces, no distraction
8. Passively view stimuli in remember faces and remember scenes, encoding distraction (the stimuli arrangement is the same for both remember faces and remember scenes conditions).
9. Passively view stimuli in remember faces, delay distraction
10. Passively view stimuli in remember scenes, no distraction
11. Passively view stimuli in remember scenes, delay distraction

Each participant completed two scanning sessions. The first included the two ND blocks and two matching ‘passive-view’ blocks (order counterbalanced), and a functional localiser scan. The second session included the seven remaining ED, DD, and matching ‘passive-view’ blocks (order counterbalanced).

Greyscale images of natural scenes and faces with neutral expressions were used. These were taken from the database of images used in Gazzaley et al (2005a and b). For each of the 11 blocks, the same set of face and scene images were used, and each face and scene was only presented once in each block. Images were presented in a 2x2 grid and subtended an approximate horizontal visual angle of 6.92° and vertical visual angle of 6.46°. For each of the 'active' blocks, the two images to be remembered were presented simultaneously, in pseudo-randomly selected positions of the grid. In the ND blocks, this was all that was presented without any overt distraction. In the ED blocks two stimuli to-be-ignored were presented at the same time as the to-be-remembered stimuli in the remaining positions of the grid. In the DD blocks two stimuli to-be-ignored were presented during the delay period, in the remaining positions of the grid. At the response period a single, centrally presented face or scene was presented in the remember faces or remember scenes task, respectively. Participants were asked to indicate, with a button press, whether it was the 'same' or 'different' to one of the to-be-remembered stimuli. For half of the trials the correct answer was 'same'. For each 'passive-view' block, participants were presented with stimuli matching the 'active' block for that condition, however they were asked to passively view the stimuli, and at the response period they were presented with a centrally presented arrow, and asked to indicate with a button press whether it was pointing left or right (for half of the trials a left arrow was presented). There were 30 trials in each block. Of these trials, 24 were as described above, however in 6 trials a white fixation cross was presented at the response period, which participants did not need to respond to. This was to help de-correlate the regressors representing the response screen from those representing the other stages of the trial.

For the functional localiser scan, 16 centrally presented images of faces or scenes were presented sequentially for 1.4s each. 14 blocks of faces and scenes (7 face blocks and 7 scene blocks) were presented in pairs, with 22.4s between each pair. The order of face and scene blocks were pseudo-random. During these blocks, participants were asked to do a 1-back task, where they were asked to press a button if the image presented was the same as the previous image (which was true for 28 images).

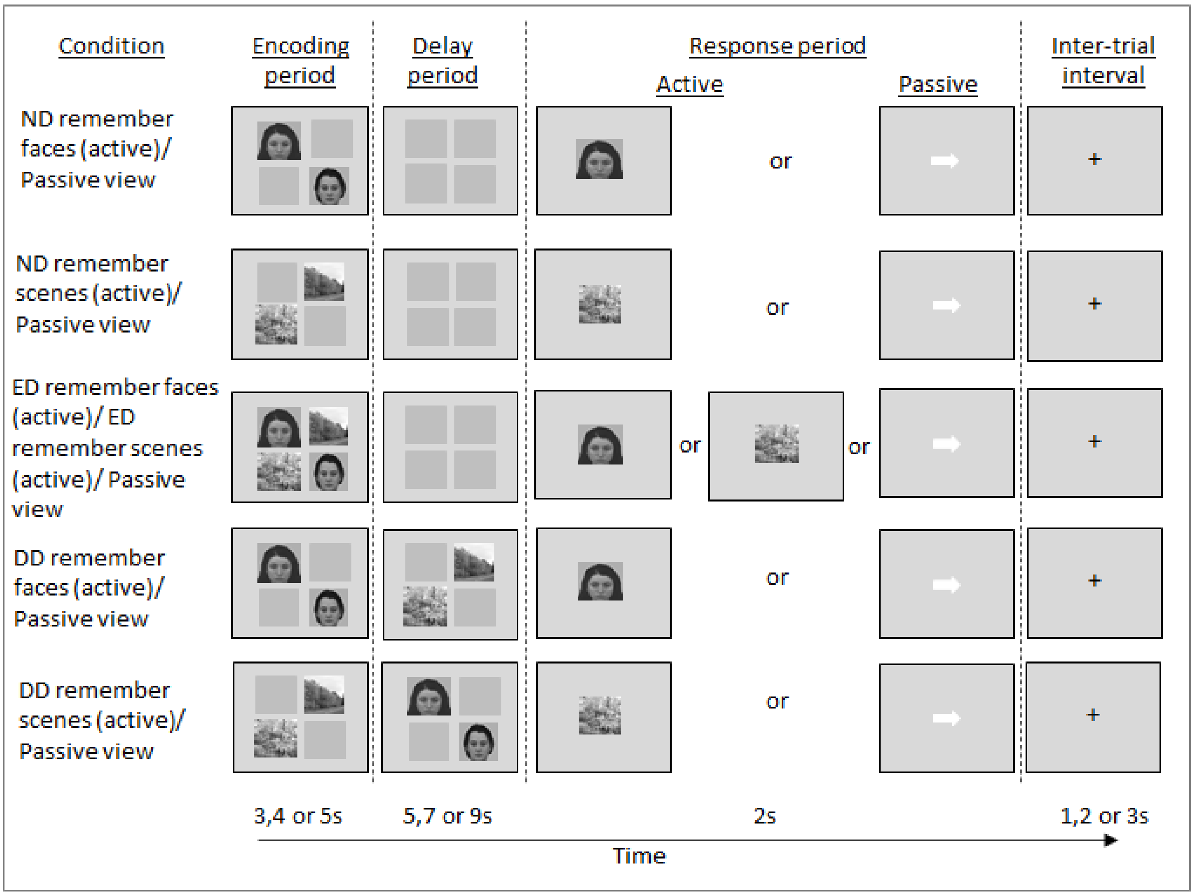

Figure 14; Example trials of each distraction condition (No Distraction: ND, Encoding Distraction: ED and Delay Distraction: DD) for each stimulus type (remember scenes/ignore faces and remember faces/ignore scenes) and each task (actively remember/ignore and passively view). In the active task, participants were asked to remember two target stimuli. In *the ND condition this is all participants were presented with, with no overt distraction. In the ED condition participants were also presented with two distraction stimuli at the encoding period and in the DD conditions participants were presented with two distraction stimuli at the delay period. At the response they were presented with either a face or scene, in the remember faces and remember scenes task, respectively, and asked to indicate whether the image was the same or different to one of the target images. In the passive tasks, participants were presented with the same stimuli, as in the active conditions, however at the response period they were presented with an arrow and asked to indicate whether it was pointing left or right. The targets were presented in two pseudo-randomly selected quadrants of the screen and the distractions were presented in the remaining two quadrants.*

Outside of the scanner, participants completed a visuo-spatial VWMC task and distractor-filtering task. In the VWMC task, participants were asked to remember the positions of 4 (15 trials) or 5 (25 trials) red circles presented simultaneously, for 1s on a circular grid made up of 16 squares (see figure 15). In the distractor-filtering task, participants were asked to remember the positions of 3 red circles presented on a circular grid for 1s, with or without distraction. In the ND trials, there was no overt distraction. In the ED trials, two yellow circles, to-be-ignored, were presented together with the red circles. In the DD trials, two yellow circles, to-be-ignored, were presented during the delay period, for 2s (after the red circles had disappeared). There were 30 trials of each condition in total, which were presented over 2 blocks (15 trials of each condition in each block). Irrespective of task and condition, at the response period participants were presented with a question mark at one position of the grid and asked to respond whether there was a red circle at this position. For half of the trials, the correct answer was ‘yes’. No more than two red circles could be positioned next to each other in the grid. In the distraction filtering conditions, one yellow circle was always adjacent to a red circle and at the response, the question mark was always placed either in the position of a red circle, or in an adjacent position.

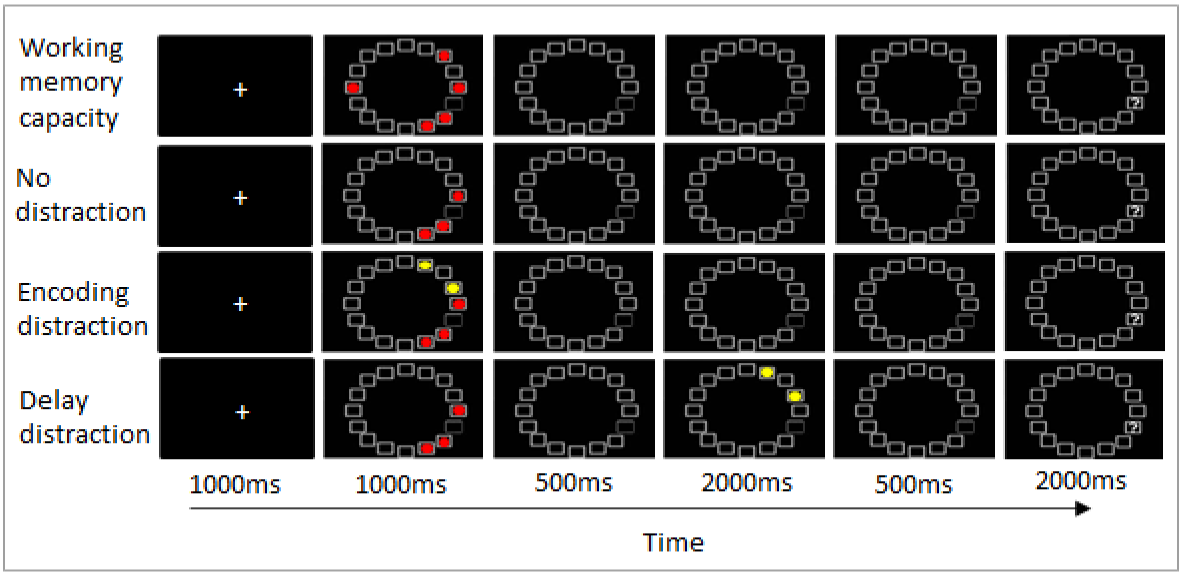

Figure 15; Example trials from the out-of-scanner task. In the Working Memory Capacity (VWMC) condition, participants were asked to remember the positions of 4 or 5 red circles, which were presented for 1 second. At the response stage, they were presented with a question mark in one square and asked to respond with a button press (yes or no) to indicate whether there had been a red circle in that position. In No Distraction (ND), Encoding Distraction (ED) and Delay Distraction (DD) conditions, participants were asked to remember the positions of 3 red circles, which were presented for 1 second and at the response stage, they were presented with a question mark at one position and asked to respond (yes or no) to indicate whether there had been a red circle at that position. In the ND condition, participants were presented with red circles, without overt distraction. In the ED condition, participants *were also presented with 2 yellow circles during the encoding period, which were to be ignored and in the DD condition participants were presented with 2 yellow circles during the delay period, which were to be ignored.*

MRI acquisition

Imaging data was collected using a 3.0 Tesla MRI scanner (Siemens). A 20-channel phased-array head coil was used to acquire the data. The experimental and functional localiser scan data were collected using a bottom up interleaved echo planar imaging (EPI) sequence. The experimental scan was acquired with the following parameters; TR=2.1s, TE= 30ms, flip angle= 80 degrees, FOV= 192x92x108mm, matrix size= 64x64, number of volumes=213, voxel size= 3x3mm, slice thickness=3mm with no inter-slice gap and 36 slices were acquired. Three volumes were acquired at the beginning of the scan, to allow for T1 equilibrium; these were discarded during analysis. The functional localiser scan was acquired with the following parameters; TR=2s, TE= 30ms, flip angle=80 degrees, FOV=192x192x108mm, matrix size=64x64, number of volumes=227, voxel size= 3x3mm, slice thickness=3mm with no inter-slice gap and 36 slices were acquired. A T1-weighted structural image was obtained for each participant (TR= 2.3s, TE=2.26ms, flip angle= 8 degrees, FOV= 256x256, voxel size= 1x1, slice thickness=1mm, number of slices=176) and a T1-weighted FLAIR image (TR=3s, TE=8.6ms, flip angle = 150 , FOV=192x192mm, matrix size = 256 x 256, voxel size= 0.75x0.75mm, slice thickness = 3.0mm, number of slices=36) was also taken in the same plane as the EPI data, for co-registration of the functional data to the structural image.

Data analysis

For data processing FEAT (fMRI expert analysis tool) version 6.0 part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) was used. The data was skull stripped using BET (Brain extraction tool) (Smith, 2002). Pre-processing included removing the first 3 volumes (6.3s) of each scan, motion correction using MCFLIRT (Jenkinson, Bannister, Brady & Smith, 2002), slice timing correction using Fourier-space-time-series phase-shifting and non-brain removal using BET (Smith, 2002). Spatial smoothing using a Gaussian Kernel of FWHM (full width at half maximum) 8mm and high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma=100s) were applied. Registration of the fMRI data to the structural data and standard brain (MNI152 2mm) was carried out using FLIRT (Jenkinson & Smith, 2001; Jenkinson, Bannister, Brady & Smith, 2002). Registration from structural data to the standard brain was further refined using FNIRT (Andersson 2007a, 2007b). A time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich, Ripley, Brady & Smith, 2001). The regressors included in the general linear model were the encoding period, delay period, and the response period. Only correct trials were analysed and so there was an additional regressor for incorrect trials. The regressors were convolved with a single gamma hemodynamic response function (HRF).

The regions of interest (ROI) for scene-selective and face-selective regions were defined from the functional localiser scan, using the contrasts: scenes>faces and faces>scenes. From the scenes>faces contrast, the left and right para-hippocampal place area (PPA) were selected and from the face>scene contrast, the left and right fusiform face areas (FFA) were selected. The maximally active voxel for each anatomical region, in each participant's native brain space was selected. Two voxels were added to the peak voxel in the x, y, and z direction, making the ROI 7 contiguous voxels. See figure 16 for an example of ROIs created for one participant. The parameter estimates from the first-level analysis were extracted, for the encoding period, delay period and response period for each stimulus type and distraction condition for each participant and these were converted to percent signal change. This data was then analysed using IBM SPSS version 25 and p-values were determined using a two-tailed test. For some of the analysis, the data did not meet the assumption of normality (these instances are reported in the results section). However, as ANOVAs are fairly robust to violations of the assumption of normality, we continued with the ANOVAs (Schmider, Ziegler, Danay, Beyer & Bühner, 2010; Blanca, Alarcón, Arnau, Bono & Bendayan, 2017).

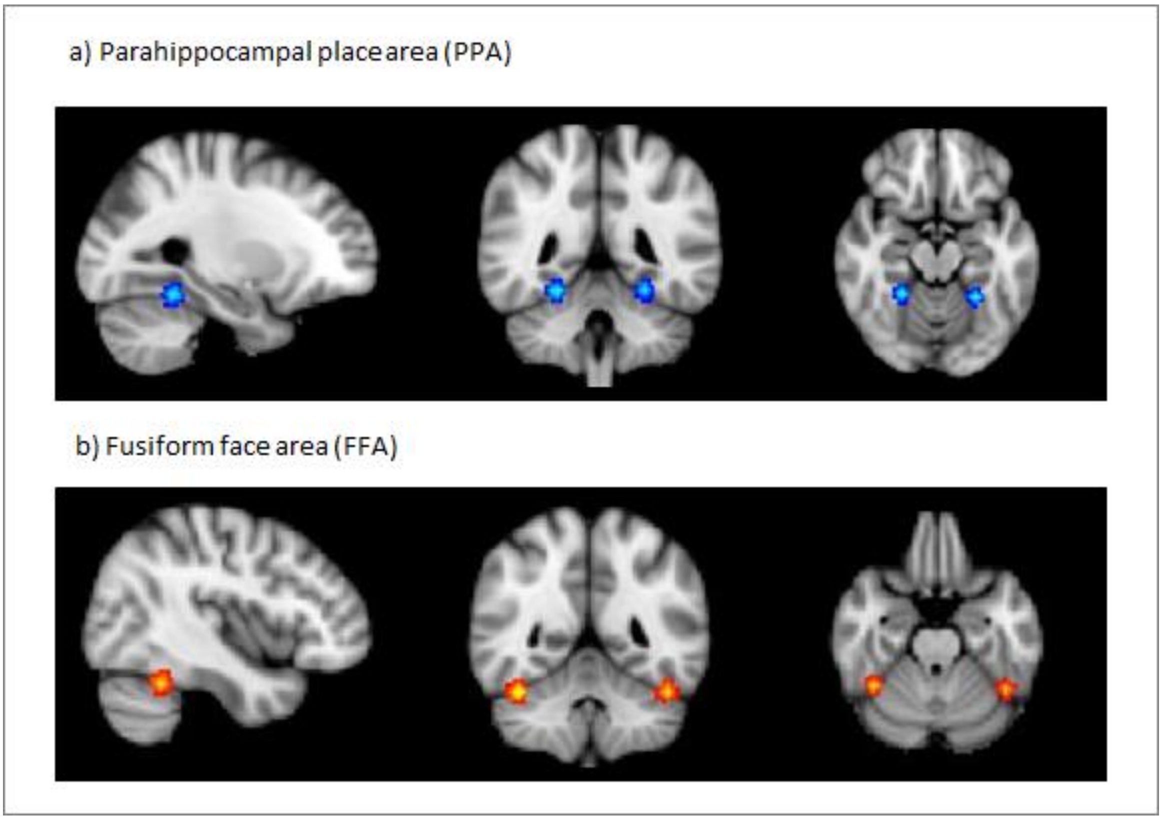

Figure 16; Example of ROIs created for one participant transformed into MNI standard space. Figure 16a illustrates the left and right parahippocampal place area (PPA), and figure 16b illustrates the left and right fusiform face area (FFA).

Results

Behavioural results

To investigate performance and distraction effects, A 3x2 ANOVA was performed on the behavioural data from the in-scanner task, including the factors distraction condition (ND, ED, and DD) and stimulus type (remember faces / ignore scenes and remember scenes / ignore faces). See figure 17 for mean accuracy scores. The data did not meet the assumption of normality for remember faces /ignore scenes in the ND and ED conditions (Shapiro-Wilk p<.05). There was a main effect of distraction condition (F(2,44)= 11.89, p<.001) and stimulus type (F(1,22)= 41.06, p<.001) and a significant interaction (F(2,44)= 4.52, p=.016). In order to understand what was driving this interaction separate one-way ANOVA's were performed for each stimulus type. For the stimulus type 'remember scenes/ ignore faces', there was a main effect of distraction condition (F(2,44)=14.236, p<.001). Paired t-tests revealed accuracy in DD was significantly lower than in ND (t=3.52, p=.002) and in ED (t=4.57, p<.001), however there was no significant difference between accuracy in ND and ED (t=-1.817, p=.083). This suggests that for stimulus type 'remember scenes/ ignore faces' there were distraction effects for DD, but not ED. For the stimulus type 'remember faces / ignore scenes' there was no main effect of distraction condition (F(2,44)=1.92, p=.158). These findings suggest there were distraction effects for the stimulus type remember scenes /ignore faces, with performance on DD being significantly lower than ND and ED, but not for remember faces /ignore scenes. As distraction effects were only seen for the stimulus type 'remember scenes / ignore faces', the fMRI analysis will focus on findings from this stimulus type.

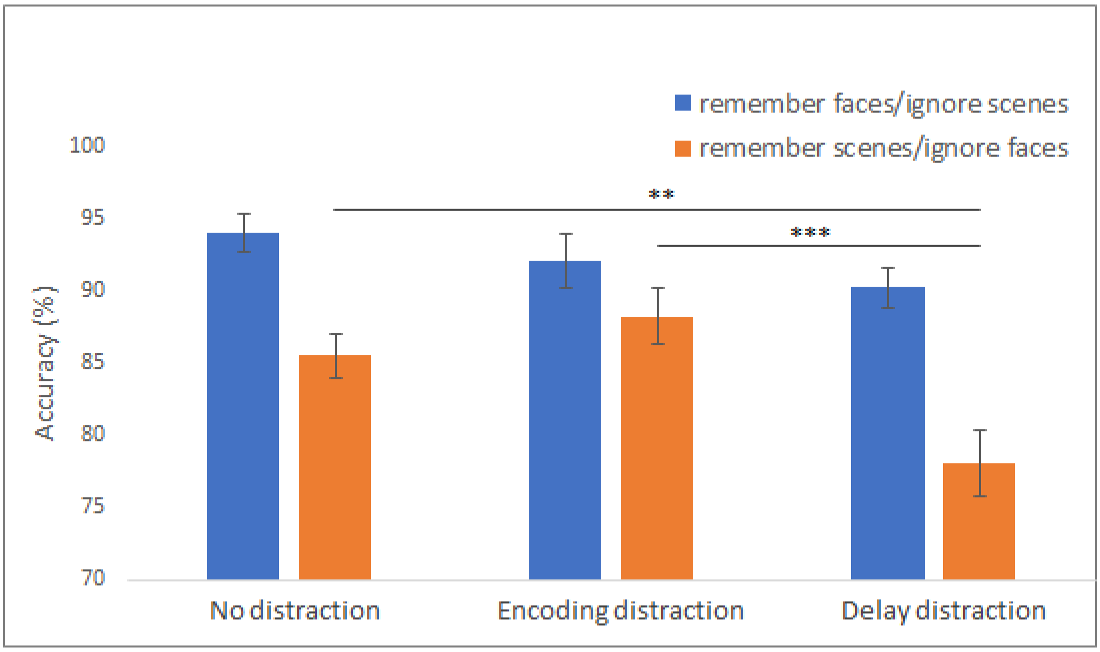

*Figure 17; Mean accuracy (%) scores for both stimulus types, in each distraction condition. Blue bars represent 'remember faces/ ignore scenes' and orange bars represent 'remember scenes / ignore faces'. Error bars represent +/- 1 SEM. ***p<.001, **p<.01.*

PPA activity

Firstly, activity in the PPA (a scene-selective region) was investigated, associated with the stimulus type remember scenes / ignore faces. Data was averaged over the left and right PPA. To investigate this, a 3x2x2 ANOVA was run, including the factors distraction condition (ND, ED, and DD), time period (encoding period and delay period), and task (active/passive). See figure 18 for mean % signal change in each of these conditions. ROI data from the passive ED condition at the encoding period and the passive ND condition during the delay period were not normally distributed. There was no main effect of distraction condition (F(2,44)=0.71, p=.500), suggesting activity in the PPA was similar across ND, ED, and DD conditions. As expected, there was a main effect of time period (F1,22) =180.23, p<.001), which reflects greater activity in the PPA during the encoding period, when images of scenes were on screen, compared with the delay period, when there were no images of scenes on screen. There was also a main effect of task (F(1,22)=7.83, p=.010), which reflects greater activity in the active conditions (when participants were actively remembering scenes/ ignoring faces), compared with the passive conditions when participants were passively viewing the stimuli. However, there was a significant interaction between the time period and task (F(1,22)=45.404, p<.001), and paired t-tests show that activity was significantly higher in the active task compared with the passive task for all three distraction conditions at the encoding period (ND: t=4.926, p<.001; ED: t=3.233, p=.004; DD: t=2.752, p=.012), but not at the delay period (p>.05). This suggests that there was an enhancement of activity in the active task, compared with the passive task, but only at the encoding period, when the stimuli to-be-remembered were on screen. There were no significant interactions between distraction condition and time period (F(2,44)=0.19, p=.830), distraction condition and task (F(2,44)= 2.836, p=.069) or between distraction condition, time period and task (F(2,44)=0.729, p=.488). This suggests that when comparing activity in different distraction conditions (ND, ED, and DD), activity in each distraction condition was similar, and this was the case regardless of task or time period.

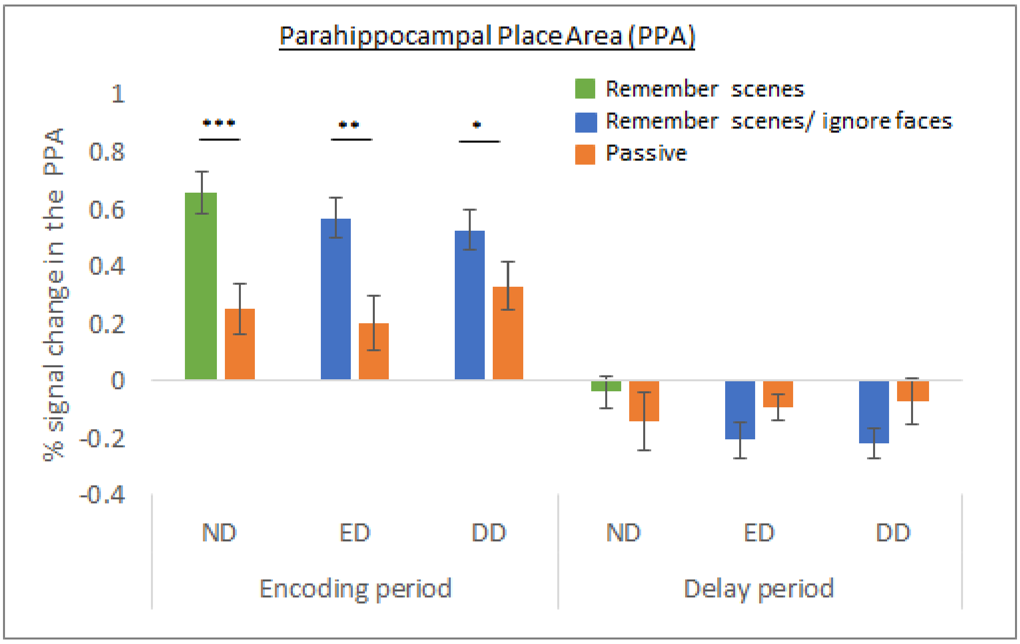

*Figure 18; Mean % signal change in the PPA in the remember scenes / ignore faces and passive view tasks, for the ND, ED, and DD blocks at the encoding period and the delay period. Green bars represent the active remember scenes condition, blue bars represent the active remember scenes and ignore faces task, and orange bars represent the matching passive task. Error bars represent +/- 1 SEM. ***p<.001, **p<.01,*p<.05.*

Next, activity in the PPA associated with the stimulus type remember faces/ ignore scenes was analysed. A 2x2x2 ANOVA was performed, including the factors distraction condition (distraction and no distraction), time period (encoding period and delay period), and task (active and passive). See Figure 19 for the mean % signal change in these conditions. ROI data from the active ND condition, and ED condition at the encoding period and the passive ED condition during the encoding period were not normally distributed. There was no main effect of time period (F(1,22)=0.24, p=.626), or task (F(1,22)=0.25, p=.621). However, there was a main effect of distraction condition (F(1,22)=19.972, p<.001), which suggests there was greater activity in the distraction condition, than the no distraction in the PPA, which was expected as scenes are on screen in the distraction condition, whereas in the no distraction condition no scenes are on screen. There was no significant interaction between time period and distraction condition (F(1,22)=0.25, p=.621), or between time period, distraction condition, and task (F(1,22)=0.144, p=.739). However, there was a significant interaction between distraction condition and task (F(1,22)=5.64, p=.027). This reflects an increase in activity in the remember condition, compared with the passive condition, in the no distraction condition, that is not present in the distraction condition. However, when the ANOVA's were run separately for each time period, there was no interaction between distraction condition and task at the encoding period (F(1,22)=2.75, p=.111), or at the delay period (F(1,22)=3.42, p=.078).

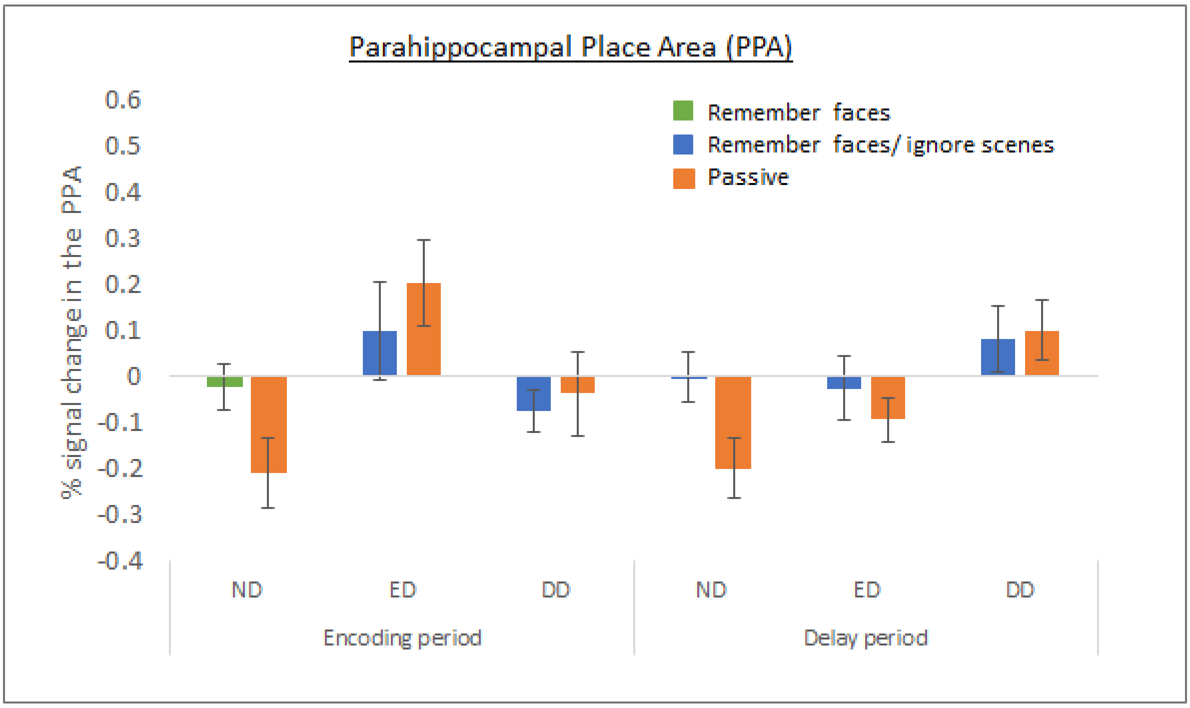

Figure 19; Mean % signal change in the PPA in the remember faces / ignore scenes and passive view tasks, for the ND, ED, and DD blocks at the encoding period and the delay period. The green bar represents the active remember faces condition, blue bars represent the active *remember faces and ignore scenes task, and orange bars represent the matching passive task. Error bars represent +/- 1 SEM.*

FFA activity

Next, activity in the FFA (a face-selective region) was investigated associated with the stimulus type remember scenes / ignore faces. To investigate this a 2x2x2 ANOVA was performed, including the factors distraction condition (distraction and no distraction), time period (encoding period and delay period) and task (active and passive). See figure 20 for mean % signal change in these conditions. ROI data from the active ED condition at the encoding period, and passive ND condition at the delay period were not normally distributed. There was a main effect of distraction condition (F(1,22)=37.865, p<.001), reflecting greater activity in the distraction compared with no distraction conditions, as expected as faces were on screen in the distraction conditions, but not in the no distraction condition. There was also a main effect of time period (F(1,22)=12.05, p=.002), reflecting more activity at the encoding period, than during the delay period. However, there was no main effect of task (F(1,22)=1.329, p=.261). There were also no significant interactions between distraction condition and time period (F(1,22)=0.904, p=.352) , distraction condition and task (F(1,22)=2.899, p=.103) or time period and task (F(1,22)=0.137, p=.715). However, interestingly, there was a significant three-way interaction between distraction condition, time period and task (F(2,44)= 4.741, p=.040). To understand what was driving this interaction, separate ANOVAs were run for each time period. At the encoding period there was a significant interaction between distraction condition and task (F(1,22)= 8.098, p=.009), which reflects a greater difference in activity between the active and passive tasks in the ND condition compared with the ED condition. In the ND condition participants were presented with only scenes (to either remember or passively view), however in the ED conditions, participants were presented with scenes and faces (to either remember/ignore or passively view), therefore we would expect greater activity in the ED conditions than in the ND conditions in both the active and passive tasks, as a face was on screen in the ED condition. However, there was only an increase in activity from ND to ED in the passive condition, not in the active ED condition (when a face was on screen but needed to be ignored). This lack of an increase could be considered a form of 'suppression' in the FFA, when participants need to actively ignore faces in the ED condition. However, for the delay period there was not a significant interaction between distraction condition and task (F(1,22)=0.152, p=.700). This suggests that the 'suppression' effect that is seen when participants are asked to ignore faces in the ED condition, is not seen in the DD condition.

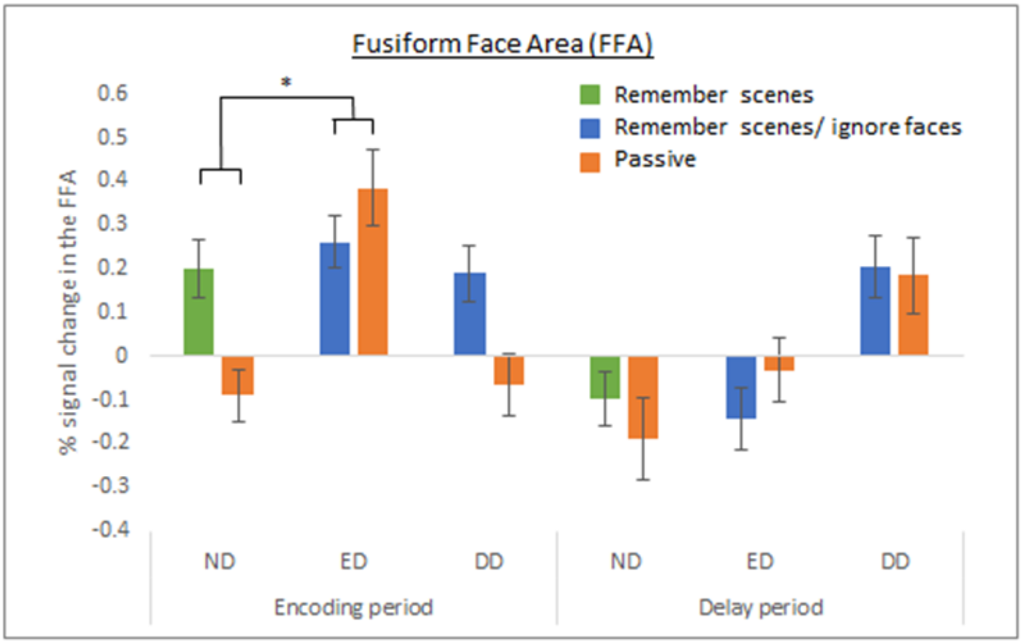

*Figure 20; Mean % signal change in the FFA in the remember scenes / ignore faces and passive view tasks for ND, ED, and DD blocks at the encoding period and the delay period.. Green bars represent the active remember scenes task, blue bars represent the active remember scenes/ ignore faces task, and orange bars represent the matching passive task. Error bars represent +/- 1 SEM. **p<.01*

Next, activity in the FFA associated with the stimulus type remember faces/ ignore scenes was analysed. A 3x2x2 ANOVA was performed, including the factors distraction condition (ND, ED, and DD), time period (encoding period and delay period), and task (active and passive). See Figure 21 for the mean % signal change in these conditions. ROI data from the passive ND, ED, and DD condition at the delay period were not normally distributed. There was no main effect of distraction condition (F(2,44)=1.07, p=.351), or task (F(1,22)=0.62, p=.441). However, there was a main effect of time period (F(1,22)=70.041, p<.001), reflecting greater activity in the FFA during the encoding period compared with the delay period; this was expected as faces were on screen during the encoding period, and not during the delay period. There was no interaction between distraction condition and task (F(2,44)=0.28, p=.761), or between distraction condition, time period and task (F(2,44)=0.15, p=.858). However, there was a significant interaction between time period and task (F(1,22)=7.89, p=.010), reflecting greater activity in the remember condition compared with the passive condition at the encoding period, that is not present during the delay period. However, t-tests show that the difference between activity in the remember condition compared with the passive condition at the encoding period, was only significant for ND (t=2.26, p=.034), but not for ED (t=0.69, p=.500), or DD (t=1.01, p=.325). There was also a significant interaction between distraction condition and time (F(2,44)=5.45, p=.008). To investigate what this interaction reflects three 2x2x2 ANOVA's were run, with the factors distraction condition (ND and ED, ND and DD, or ED and DD), time period (encoding period and delay period), and task (active passive). There was no significant interaction between distraction condition and time when comparing the distraction conditions ND and ED (F(1,22)=2.62, p=.120), or the when comparing the distraction conditions ED and DD (F(1,22)=2.38, p=.137). However, there was a significant interaction between distraction condition and time when comparing the distraction conditions ND and DD (F(1,22)=13.72, p=.001). This suggests the interaction in the initial ANOVA reflects differences in activity during the delay period between the ND and DD condition, that are not seen during the encoding period.

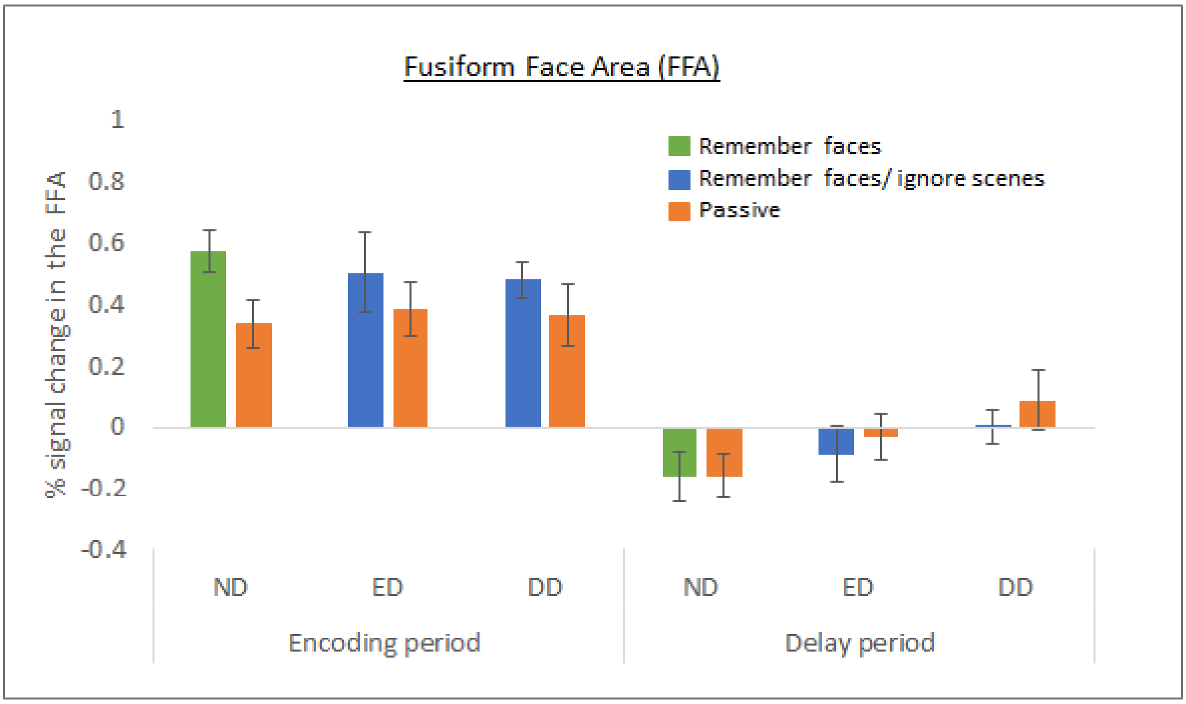

Figure 21; Mean % signal change in the FFA in the remember faces / ignore scenes and passive view tasks, for ND, ED, and DD blocks at the encoding period and the delay period. Green bars represent the active remember scenes task, blue bars represent the active remember scenes/ ignore faces task, and orange bars represent the matching passive task. Error bars represent +/- 1 SEM.

Enhancement of activity and performance

Next, we investigated whether the 'enhancement' effects seen at the encoding period for all three distraction conditions in the remember scenes/ ignore faces condition was related to performance in the out-of-scanner task (see Appendix 1 for mean accuracy and k-values for each condition). To do this, an enhancement index was calculated by subtracting activity in the PPA in the passive conditions from activity in the active conditions (active – passive), as in Gazzaley et al. (2005a and b), for each of the ND, ED, and DD conditions. The first performance measure investigated was VWMC calculated from the out-of-scanner red circles task. To get a measure of VWMC, K values were calculated (as described in chapter two). The VWMC data was not normally distributed and so Spearman's Rho values are reported. As can be seen in figure 22 a-c, there was a trend towards a positive correlation between enhancement and VWMC for all three distraction conditions, suggesting that greater enhancement in the PPA when trying to remember scenes, is associated with a higher VWMC, regardless of whether participants also had to ignore distraction. However, this was not significant. A power analysis revealed that with a small effect size (r=.25) and an alpha of .05, a sample of 64 participants would be required to achieve a power of .80. As can be seen in figure 22a-c one participant who got a VWMC score 1.55 could be considered an outlier, and so the correlation analysis was also run without this participant. Similarly, there was a trend towards a positive correlation for each distraction condition, however this was not significant (ND: r_s =.14, p=.553; ED: r_s =.22 p=.350; DD: r_s =.16 p=.497).

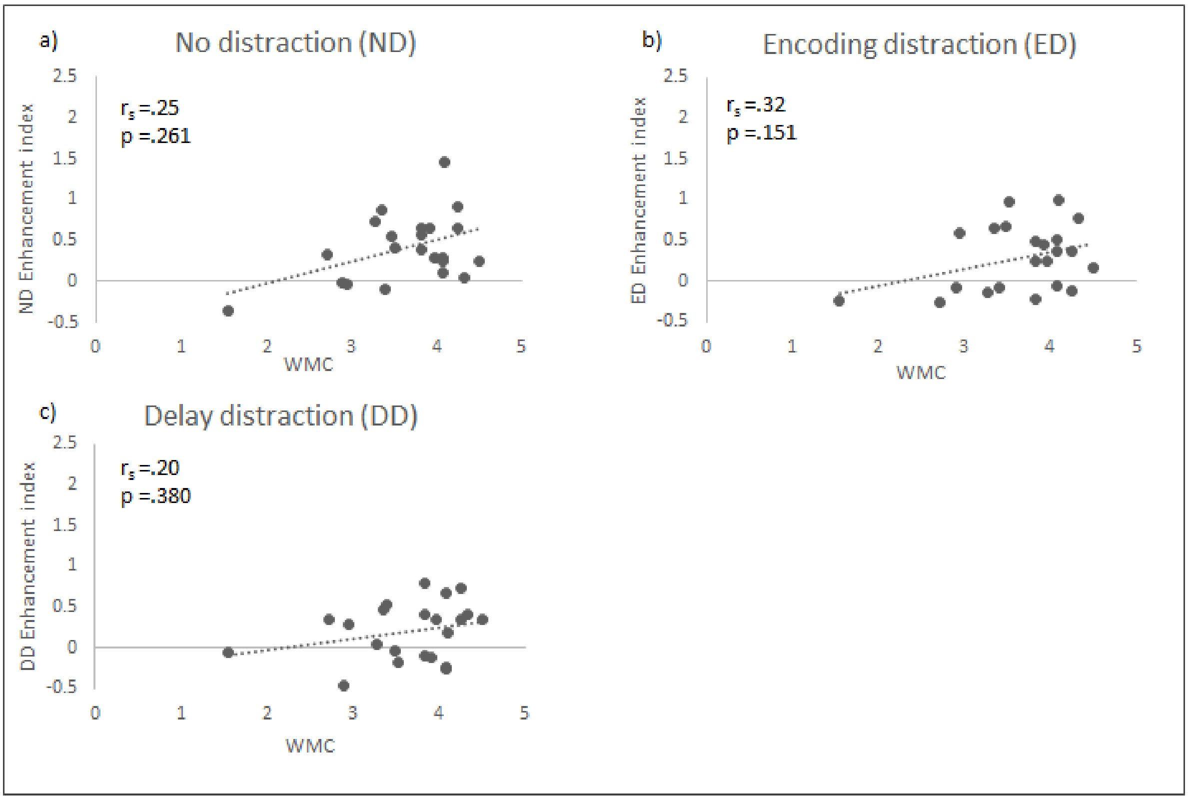

Figure 22; Correlations between VWMC (K values), calculated from the the out-of-scaanner task, and 'enhancement' (encoding period activity in the PPA in the active minus passive task). Figure a shows 'enhancement' calculated from the ND condition, Figure b shows 'enhancement' calculated from the ED condition and Figure c shows 'enhancement' calculated from the DD condition. Spearman's Rho correlation values are reported.

A second measure of performance investigated was 'filtering ability'. As described in chapters two and three, the residuals from regression models ED= α + βDD and DD= α + βED were used as a measure of ED and DD 'filtering ability', respectively. ED 'filtering ability' and DD 'filtering ability' scores were not normally distributed, and so Spearman's Rho values are reported. As can be seen in figure 23a-c, there was a trend towards a positive correlation for enhancement in all three distraction conditions and ED filtering ability i.e. greater enhancement was associated with higher ED filtering ability, however this was only significant for enhancement in the DD condition. However, if the p-value is corrected for multiple comparisons, this is no longer significant (Bonferroni-corrected p=.120) As can be seen in figure 23, one participant who had an ED filtering ability score of -3.5, could be considered an outlier, and so the correlation analysis was also run without this participant. Similarly, there was a trend towards a positive correlation for all the distraction conditions, and this was still only significant for enhancement in the DD condition (ND: r_s=.22, p=.338; ED: r_s=.17, p=.464; DD: r_s=.55, p=.011). Again, if the p-value is corrected for multiple comparisons, this is no longer significant (Bonferroni-corrected p=.066) The same correlation analysis was then repeated for DD filtering ability and enhancement in ND, ED, and DD. As can be seen in Figure 23d-f, there were no significant correlations between enhancement in any of the distraction conditions and DD filtering ability, and there was not a trend towards a positive association, as seen with ED filtering ability.

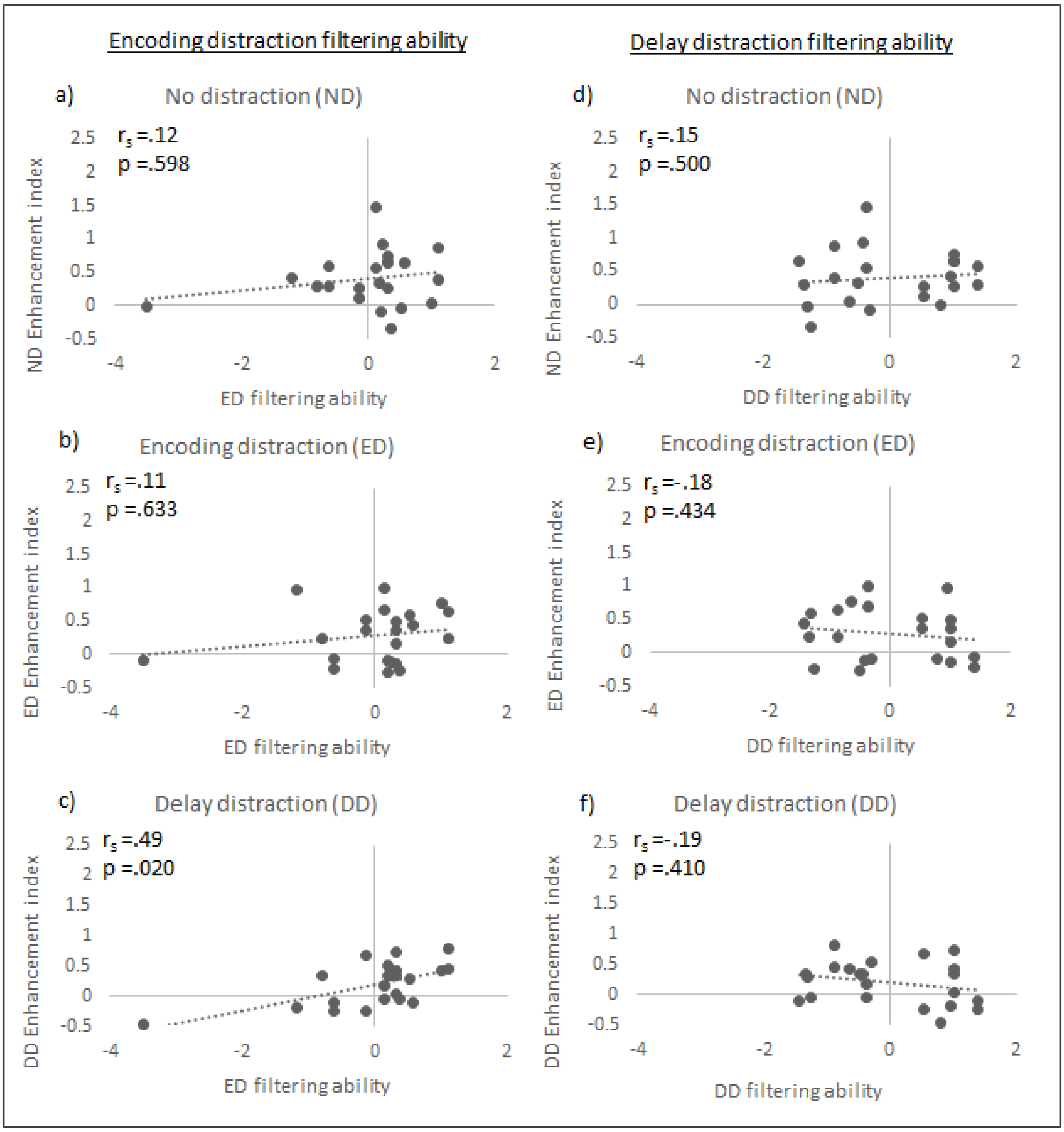

Figure 23; Correlations between 'filtering ability' calculated from the the out-of-scanner task, and 'enhancement' (encoding period activity in the PPA in the active minus passive task). Figures a-c, show correlations between ED filtering ability and enhancement calculated from the ND condition (a), ED condition (b), and DD condition (c). Figures d-f, show correlations between DD filtering ability and enhancement calculated from the ND condition (d), ED condition (e), and DD condition (f). Spearman's Rho correlation values are reported.

Suppression of activity and performance

Finally, we investigated whether the suppression effects seen for ED, in the remember scenes/ ignore faces task, relate to performance in the out-of-scanner task (see Appendix 1 for mean accuracy and K-values for each condition). To do this a ‘suppression index’ was calculated. In Gazzaley et al. (2005a and b), the suppression index used was activity in the passive condition minus activity in the active condition (passive-active), however as we found that ND was important for the suppression effect, the ‘suppression index’ was modified to account for activity in both the ND and the passive conditions. Therefore, the suppression index used was: (ED passive-ND passive) - (ED remember- ND remember), in which higher values reflect higher levels of suppression. As with enhancement, the relationship between suppression and VWMC and ED and DD filtering ability, calculated from a separate out-of-scanner task, was investigated. However, only ED suppression was investigated, as there were no suppression effects for DD. As can be seen in figure 24a, there was no significant correlation between ED suppression and VWMC. Without the participant who had a VWMC score of 1.55, who might be considered an outlier, there was still no significant correlation (r=.178, p=.441). Figure 24b and c show that there was also no significant correlation between ED suppression and ED filtering ability or DD filtering ability. Without the participant with an ED filtering score of -3.5, who might be considered an outlier, there was still no significant correlation between ED filtering ability and ED suppression (r=-.20, p=392). However, a post-hoc power analysis revealed that with a medium effect size (r=.5; as reported in Clapp & Gazzaley, 2012) and an alpha of .05, a sample of 31 participants would be required to achieve a power of .80.

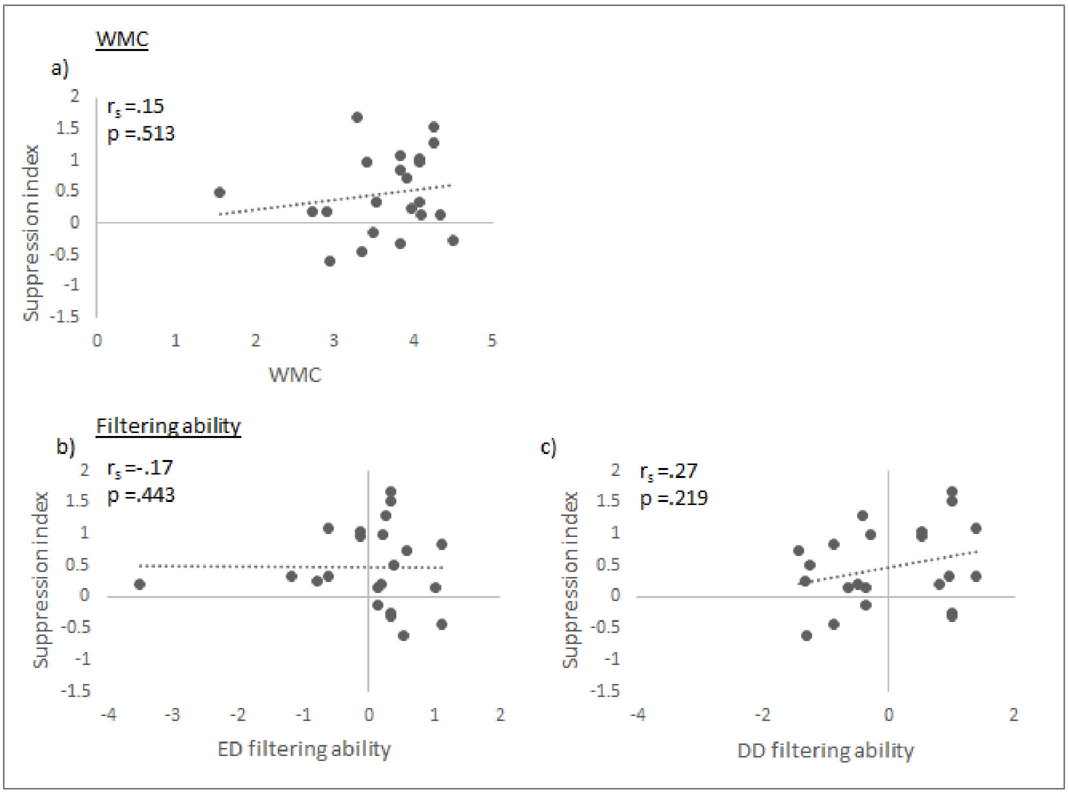

Figure 24; Correlations between 'suppression' (calculated from encoding period activity in the FFA, using the formula:(ED passive-ND passive) - (ED remember- ND remember), and VWMC (K values) and filtering ability, calculated from the out-of-scanner task. Figure a shows the correlation between suppression in the FFA in the ED condition and VWMC. Figure b shows the correlation between suppression in the FFA in the ED conditions and ED filtering ability, and Figure c shows the correlation between suppression in the FFA in the ED condition and DD filtering ability. Spearman's Rho correlation values reported.

Discussion

The aim of this study was to investigate modulations in attention in task-specific visual regions associated with ED and DD filtering, and how this relates to performance. Firstly, enhancement, relative to a passive view task, was observed during the encoding period in the PPA when scenes were to be remembered and in the FFA when faces were to be remembered, when compared to the respective delay period. For the remember scenes/ignore faces condition there was significant enhancement between the remember and passive conditions at the encoding period in all three conditions. However, in the remember faces/ignore scenes condition, there was only significant enhancement in the ND condition. Next, suppression was investigated. Previous research has identified a suppression mechanism for distraction filtering relative to a passive view task (Gazzaley et al, 2005a and b). However, in the current study a suppression effect was observed in the ED condition, relative to a passive view task *and* a no distraction condition, in the remember scenes/ ignore faces task, which has not been previously reported. However, this suppression effect was not observed for DD. In the remember faces/ignore scenes task, there was no significant interaction between task and distraction condition, which would indicate a suppression mechanism, for either ED or DD. Next, individual differences in enhancement and VWMC were investigated. For the remember scenes/ignore faces task. For all three distraction conditions, there was a positive association between enhancement and VWMC, however this was not significant. Similarly, there was a trend towards a positive correlation between enhancement in all three distraction conditions and ED filtering ability. There was no trend towards a significant correlation between enhancement in any distraction condition and DD filtering ability. Finally, individual differences in suppression in ED and VWMC and distractor filtering ability were investigated. However, there was no significant correlation between suppression for ED and VWMC, or between suppression and ED or DD filtering ability (and there was no trend towards this). Individual differences in suppression in DD were not investigated as no suppression effect was observed in this condition.

The behavioural findings that accuracy in the remember scenes/ ignore faces task was lower than in the remember faces / ignore scenes task, and the finding that distraction effects for DD (lower performance in distraction conditions than no distraction condition) were only seen for the remember scenes / ignore faces task is in line with findings in chapter 3, which also finds this. As we did not find any distraction effects in the remember faces /ignore scenes task, it may be that this task was too easy, and the distractions were not distracting. This may be reflected in the non-significant findings for enhancement and suppression in neural activity in the active compared with passive conditions, seen in the remember faces/ignore scenes task. This may suggest that the task was too easy, as there was no evidence of significant enhancement and suppression effects. Due to this, the analysis and discussion of the neural activity focusses on activity associated with the remember scenes / ignore faces tasks, where we did see distraction effects, and significant enhancement and suppression effects, similar to previous studies (e.g. Gazzaley et al, 2005), as we were interested in modulations in activity associated with ignoring distraction. It should be noted that as we focussed on activity associated with the stimulus type remember scenes / ignore faces, this meant that we investigated activity in the PPA associated with enhancement, and activity the FFA associated with suppression, and so it is possible that using a different ROI could be a confound. However, previous studies investigating activity in task-specific sensory regions associated with WM and distraction, find similar findings in the FFA and PPA (Gazzaley et al, 2005a; Ranganath, DeGutis and D'esposito, 2004). For example, in Gazzaley et al. (2005a), in both the FFA and PPA, there was enhancement associated with remembering relevant stimuli compared with passive view, and when participants were asked to ignore stimuli there was a trend towards less activity in task-specific sensory regions, however this was only significant for the PPA. Similarly in Ranganath, DeGutis, and D'esposito (2004) activity in the FFA was significantly greater when faces were task-relevant (and participants had to ignore scenes) compared with when scenes were task relevant, and activity in the PPA was significantly greater when scenes were task relevant (and participants had to ignore faces) compared with when faces were task relevant. It does appear that effects might be stronger in the PPA than the FFA, for example, in Gazzaley et al (2005a), suppression compared with the passive view was only significant for the PPA, however there was still a trend towards suppression in the FFA. Additionally, they suggested that the lack of a significant suppression effect could be due to the FFA ROI being somewhat responsive to scene images, as well as faces. Based on these findings, in the current study we assume that modulations of attention in the FFA and PPA, are similar when remembering/ignoring faces and scenes, respectively.

Additionally, it should be noted that we averaged over left and right brain regions. in our data, we saw similar patterns of activity bilaterally, and a previous study using similar methodology also shows similar patterns of activity bilaterally (Gazzaley et al., 2005a). In Gazzaley et al., (2005a) they show a similar pattern of enhancement compared with the passive condition, and suppression compared with the passive condition for both the left and right PPA. In another similar study they only reported activity from the left PPA, but there is no explanation given for this (Gazzaley et al., 2005b). Therefore, as previous studies, where all of the data are reported show similar patterns of activity across left and right regions, and we saw similar patterns in our data, we decided to average over these regions.

PPA activity

Analysis of activity in the PPA when participants were asked to remember scenes, and in ED and DD conditions ignore faces, found that there was greater activity at the encoding period compared with the delay period, regardless of whether the participant is remembering or passively viewing the stimuli. This was expected as at the encoding period there were scenes on screen, whereas during the delay period there were not, and as the PPA is a scene-selective region, we would expect greater activity in this region when scenes are present. However, when participants were asked to remember scenes there was an increase in activity in the PPA compared with the passive view condition, at the encoding period. This increase in activity was observed for all three distraction conditions. Therefore, enhancement was observed when participants were asked to remember scenes, regardless of whether there was a distraction on screen, or whether they were expecting a distraction. This supports previous research (Gazzaley et al., 2005a and b) that also found enhancement, when trying to remember stimuli, compared with passively viewing stimuli. This enhancement of activity when participants were asked to remember stimuli, was only observed during the encoding period, when participants had to encode the scenes; it was not maintained during the delay period. Previous research by Ranganath, Degutis, and D'esposito (2004), suggests that activity in the PPA and FFA is sustained during the delay period in scene and face WM tasks, respectively. However, in this study they compared activity in the PPA and FFA at the delay period in the scenes WM task, with the faces WM task, rather than to a passive baseline, as in the current study. Therefore, it might be that there is some persistent activity in task-relevant visual regions during the delay in task-specific sensory regions, however the enhancement we see relative to the passive baseline, appears to be specific to the encoding period. Additionally, it may be that univariate analysis is not sensitive enough to identify sustained activity during the delay period, as previous studies such as Serences et al., (2009) observed sustained delay period activity in early visual regions using MVPA, which were not observed when they used univariate analysis.

By calculating an enhancement index (active – passive), we were able to look at individual differences in enhancement and WM performance. There was a trend towards a positive correlation between enhancement, in all three distraction conditions, and VWMC, however this was not significant. This is possibly due to low power as a post-hoc power analysis suggested we would need a sample of 64 participants to reach a power of 0.8, given an alpha level of .05. To the best of our knowledge previous studies have not reported correlations between enhancement and VWMC, however this was predicted as an association between enhancement and WM performance has been reported, for example by splitting the groups into low and high WM performance and comparing enhancement across groups (Padgaonkar, Zanto, Bollinger & Gazzaley, 2017). Similarly, there was a trend towards a positive correlation between enhancement in all three conditions, and ED filtering ability, and this was significant for enhancement in the DD condition (although after correcting for multiple comparisons was no longer significant). However, there were no correlations between enhancement in any of the conditions, and DD filtering ability. To the best of our knowledge, the association between individual differences in enhancement and filtering ability has not been investigated previously either. A positive correlation between enhancement and ED filtering ability would suggest that higher levels of enhancement at encoding is associated with more efficient filtering ability. This may be due to greater attention being paid to the relevant stimuli. This might be seen in ED but not DD, as in the ED condition, the distractions are presented at the same time and so the ability to attend more to the relevant stimuli, might result in less attention to the irrelevant stimuli, however as in the DD condition the distraction is presented at a different time the competition for attention is no longer there, and so is unlikely to affect distractor filtering ability.

FFA activity

Findings from the analysis of the activity in the FFA when participants were asked to remember scenes, and in the ED and DD condition ignore faces, show that there was greater activity in the distraction conditions, compared with the no distraction conditions, at the encoding period. This was expected as there were faces on screen in the distraction conditions, but not in the no distraction conditions, and the FFA is considered a face-selective region. Interestingly, there was also an increase in activity in the ND condition in the active compared with passive task, even though there were no faces on screen in either task. Previous research has found increases in task-relevant regions when participants were asked to remember stimuli compared with passive view (Gazzaley et al, 2005a and b), but have not reported findings of enhancement in task irrelevant regions. It is likely that this is due to the participants paying more attention in the active than the passive task, resulting in heightened activity generally across visual regions, regardless of the stimuli. Therefore, this effect is believed to be associated with attending to the task, rather than reflecting a WM specific process.

At the encoding period, in the passive task there was greater activity in the 'ED' condition than the 'ND' condition, as expected due to a face being on screen in the 'distraction' condition. However, in the active task when participants were asked to remember the scenes and ignore the faces, there was no significant increase in activity from the ND condition to the ED condition. This lack of enhancement in the FFA, when a face is on screen, could be considered a form of suppression, that has not been previously reported. In previous studies (Gazzaley et al 2005a and b) a suppression effect has been observed in the distraction condition, between the active and passive tasks. Given this, in the current study this suppression effect would correspond to a significant difference between the remember scenes / ignore faces and the passive task in the ED condition, however this was not significant (see figure 18). However, this study differs from previous, as previously targets and distractions have been presented sequentially, whereas in the current study they are presented simultaneously, and previous research finds that there are behavioural differences in presenting targets sequentially versus simultaneously (Ihssen, Linden, & Shapiro, 2010). In the current study, the timing of the distractions were also predictable, whereas in Gazzaley et al (2005a and b), targets and distractions were presented in a pseudo-random order, so the participants could not predict when a target or distraction would appear. Additionally, we do not see behavioural effects of ED (performance in ED was not significantly lower than ND), and so it may be that the task was not difficult enough to see these effects. However, it may be that the suppression effect observed in the current study provides a bigger picture of the suppression effects observed in previous studies, by showing that the comparison between activity in both the passive and ND conditions are important, as in Gazzaley et al. (2005a and b) there was not a matching ND condition.

However, this suppression effect was only observed when distraction was presented at the encoding period, not during the delay period, suggesting distinct neural mechanisms for ED and DD filtering. This could be due to a more task-selective mechanism required for ED filtering, as participants need to selectively attend to one stimulus and ignore another, whereas in DD filtering participants can ignore anything on screen regardless of stimulus type. Therefore, for ED filtering task-specific visual regions are recruited to selectively attend to the relevant and ignore the irrelevant. This might be related to activity in the basal ganglia, which is thought to be involved in selective gating of items into WM (Frank, Loughry and O'Reilly, 2001), and has been suggested to be involved in ED, but not DD filtering (McNab &

Dolan, 2014). It should be noted that behaviourally we find distraction effects for DD (significantly lower performance in DD than ND and ED), but we do not see any evidence of suppression in the fMRI analysis. However, it may be that suppression of task-specific regions is not necessary for DD filtering, regardless of difficulty, as it may not require task-selective filtering mechanisms. Instead DD suppression may be reflected in higher-level processing regions, such as the PFC, which were not analysed and have been previously associated with DD filtering tasks (Sakai, Rowe & Passingham 2002; Dolcos, Miller, Kragel, Jha, McCarthey, 2007; Minamoto et al., 2010; Feredoes, Heinen, Weiskopf, Ruff & Driver, 2011). Future research should investigate common and distinct activity in higher-level WM regions associated with ED and DD filtering.

Finally, by calculating a suppression index ((ED passive-ND passive) - (ED remember-ND remember)) we were able to look at individual differences in suppression of ED and WM performance. However, there was no correlation between suppression and VWMC or between suppression and ED or DD filtering ability. In particular, we would have expected ED suppression to correlate with VWMC and ED filtering, based on previous research that found a correlation between suppression and VWMC (Clapp & Gazzaley, 2012). There are a few explanations for these differences. Firstly, the suppression index used in this study was different to in previous, to account for activity in the ND condition as well as the passive. Previous studies have used the suppression index: active minus passive; however, we did not see a significant difference between the active and passive conditions. Secondly, behaviourally we did not see any distraction effects in ED, therefore it is possible that the scores did not vary enough to see effects of individual differences. Finally, this analysis might be underpowered as a post-hoc power analysis indicated that a sample size of 31 participants would be required for a power of a 0.8, with a similar effect size (0.5) to that seen in Clapp and Gazzaley (2012), whereas we only analysed data from 22 participants.

Conclusions

In conclusion, in this study we find evidence for common and unique mechanisms associated with ED and DD filtering. We find that enhancement in task-specific visual regions is common to both ED and DD filtering. However, there is a trend towards a correlation between enhancement and ED filtering, but not DD filtering, which might be related to perceptual or attentional competition between targets and distractions when targets and distractions are presented simultaneously in ED, which is not there when distractions are presented at a different time to the targets in DD. We find distinct neural mechanisms of suppression for ED and DD, as we see a suppression effect for ED, but not DD, in task-specific visual regions, possibly due to ED requiring a more task-selective filtering mechanism than DD. However, the suppression effect observed for ED, was relative to both a passive-baseline (as found previously in Gazzaley et al., 2005a and b), *and* a ND condition. This suppression mechanism has not been reported previously and might provide a bigger picture to the suppression effects previously observed using just the active and passive conditions.

Chapter 5: General Discussion

Overview of findings

The studies in this thesis aimed to understand the mechanisms underlying ED and DD filtering. In the first experiment, a smartphone game was used in order to collect data from a large number of participants, with the aim of understanding how ED and DD filtering mechanisms change over development and healthy ageing. The novel aspect of this study was to investigate ED and DD filtering during development, which has not previously been investigated. In the second study, we aimed to understand whether ED and DD filtering mechanisms generalise to visual-object WM tasks, as previous research has only investigated ED and DD filtering mechanisms in visuo-spatial WM tasks. In the final study, we used fMRI to investigate neural activity associated with ED and DD filtering, as this has not been directly compared in previous studies.

Firstly, using data from the smartphone game, we observed that ED filtering ability improves during development and deteriorates over healthy ageing, as expected. This fits in with previous research that finds children are more affected by distraction than adults (e.g. Olesen, Macoveanu, Tegner, & Klingberg, 2007) and older adults are also more affected by distraction than younger adults (e.g. Brown et al., 2015). There was a trend towards DD filtering ability also improving during development and deteriorating over healthy ageing, however this was not significant. A novel finding identified in this study is that ED and DD filtering each make a unique contribution to VWMC during development, and that DD becomes less predictive of VWMC over development. There was also a trend towards performance on ED becoming more predictive of WM over development, however this was not significant. These findings might be in line with the development of the basal ganglia, as

Ullman, Almeida and Klingberg (2014) found that activity in the basal ganglia predicted future VWMC during development and McNab and Dolan (2014) suggest that the basal ganglia might play an important role in ED filtering, but not DD filtering. We did not replicate previous findings that performance in DD declines more rapidly than performance in ED or that ED becomes more predictive of VWMC in older adults (McNab et al., 2015). However, this may be due to low numbers of older adults (as discussed in chapter 2).

Secondly, in the behavioural study comparing ED and DD filtering mechanisms across visual-spatial and visual-object WM, we found that VWMC significantly correlates across a visual-spatial and visual-object WM tasks. However, the correlation coefficients between the two visual-object tasks was numerically higher than the correlation coefficient between the visual-spatial and visual-objects tasks (although this was not statistically tested in this study). This is in line with previous research that finds lower correlations between visual object and visual spatial tasks, compared with between two visual-object tasks (Della Sala et al., 1999), however that visual-spatial and visual-object WM tasks are still moderately correlated (Gathercole, Pickering, Ambridge & Wearing, 2004), which suggests some general mechanism underlying performance on both types of WM task. We also found that DD filtering correlates across all three tasks (remember faces/ ignore scenes, remember scenes/ ignore faces, and remember the positions of red circles/ ignore yellow circles). This suggests similar mechanisms underlying DD filtering in both visual-spatial and visual-object WM tasks. Interestingly unlike with VWMC, correlations between two visual-object tasks were not numerically higher than the correlation between the visual-spatial and visual-object WM task (although again this was not statistically tested). This could indicate that a common DD filtering mechanism is having a strong influence on performance, regardless of WM task. However, we did not find that ED filtering significantly correlated across any of the WM tasks.

In this study we aimed to replicate previous findings that performance on ED and DD tasks uniquely predicted VWMC in a visual-spatial WM task, and extend this finding by showing that performance on ED and DD tasks uniquely predicted VWMC in visual-object WM tasks as well. However, we did not replicate previous findings that ED and DD performance uniquely predict VWMC in a visual-spatial task or find that ED and DD performance uniquely predict VWMC in the visual-object WM tasks. Previous findings that ED and DD performance uniquely predict VWMC in visual-spatial WM tasks have been replicated in the literature (McNab & Dolan, 2014, McNab et al., 2015), and in findings from the smartphone study in chapter 2. Therefore, it is likely that the findings in the current study are due to the design of the study, rather than ED and DD not predicting VWMC in visual-object WM tasks. In particular, in this study conditions were separated into blocks, rather than conditions being mixed, as in previous studies. This could result in less sensitivity to find ED and DD effects, as previous research suggests there are larger distraction effects for unpredictable distractions compared with predictable distraction (Carlson, Hasher, Zachs & Connelly, 1995; Sussman, Winkler & Schröger, 2003).

In the third study, using fMRI, we found an enhancement in activity in task-specific visual regions, relative to a passive-view baseline when participants were asked to remember stimuli. This was true for the ND, ED, and DD tasks. This is in line with findings from previous studies (Gazzaley et al., 2005a; Gazzaley et al., 2005b). There was a trend towards a positive correlation between enhancement in all three conditions (ND, ED, and DD) and VWMC, however this was not significant, possibly due to low power as a power analysis revealed that with a small effect size (r=.25) and an alpha of .05, a sample of 64 participants would be required to achieve a power of .80. As described previously an effect .25 was used, based on the results from this study, as previous research has not investigated this relationship between enhancement and VWMC. Previous research has found an association between VWMC and enhancement (Gazzaley et al, 2005a; Padgaonkar, Zanto, Bollinger & Gazzaley, 2017), however these studies did not directly investigate individual differences in enhancement and VWMC, for example Padgaonkar et al. (2017) split groups by low and high 'enhancement' and compared performance across groups. Next, we investigated suppression in task-specific visual regions. Previous research found that when participants are asked to ignore stimuli, there is a suppression of activity in task-specific visual regions relative to a passive view baseline (Gazzaley et al., 2005a; Gazzaley et al., 2005b, Clapp & Gazzeley, 2012). Whilst we found that activity in task-specific visual regions was lower when participants were asked to ignore stimuli, than in the passive-view baseline, this was not significant. However, we did find a significant suppression effect when comparing activity to both the passive view baseline *and* the ND condition. Although these differences in findings might be due to differences in the design of the tasks, as previously the targets and distractors were presented sequentially, and distractors were not predictable. However, the suppression effect observed in this study has not been reported previously and might provide a bigger picture of the suppression effect observed in previous studies, by showing that the comparison between activity in both the passive and ND conditions are important. Finally, we only observed this suppression effect for ED filtering and not DD filtering, which suggests that ED filtering requires selective suppression of task-specific visual regions, whilst DD filtering does not.

Findings from both chapter 3 and 4 support the theory that ED filtering requires a more task-selective mechanism than DD filtering. Firstly, as described in the previous paragraph, selective suppression in task-specific visual regions was only observed for ED and not DD filtering. A possible explanation for this is that in ED filtering, participants are required to selectively attend to the relevant information and selectively ignore the irrelevant information, and so selective mechanisms might be necessary to do this. However, in a DD task, when distractions are presented during the delay, participants can ignore any stimuli that is on screen at this point, regardless of what the stimuli is, so it might not be necessary to selectively filter certain stimuli. Instead, a more general suppression mechanism might be recruited. In the findings from chapter 3, we also found that DD filtering ability correlated across all three WM memory tasks (remember faces/ignore scenes, remember scenes/ ignore faces, and remember the positions of red circles/ ignore yellow circles), whereas ED filtering was not significantly correlated across any of these tasks. A possible explanation for this is that, if ED filtering requires task-selective mechanisms, ED performance might not correlate across tasks because it might require recruiting different brain regions for each task and so individuals might be better at selectively ignoring some distractions over other distractions. Whereas DD filtering might correlate across tasks because a more general suppression mechanism might be responsible for filtering distraction during the delay regardless of stimulus type. The theory that ED filtering requires a more task-selective filtering mechanism than DD, is also in line with the idea that the basal ganglia is involved in ED, but not DD filtering, which was suggested based on behavioural evidence in McNab and Dolan (2014). The basal ganglia is thought to underly the selective gating of items in WM (Frank, Loughry & O'Reilly, 2001; Gruber, Dayan, Gutkin, & Solla, 2006; McNab & Klingberg, 2008), and so if it is involved in ED, but not DD filtering, this is in line with our theory that ED filtering requires a more selective filtering mechanism than DD filtering.

In chapter 3 we also addressed a criticism of previous studies investigating ED and DD filtering, that participants could simply close their eyes when distractions are presented during the delay as a strategy to ignore distraction. If this is the case, then it could be that previous findings that ED and DD significantly and uniquely predict VWMC (McNab and Dolan, 2014; McNab et al., 2015) do not suggest dissociable internal mechanisms for ignoring ED and DD, instead it could be a result of this strategy by participants. In order to address this criticism, we used eye-tracking whilst participants were completing ND, ED, and DD conditions. Whilst we found that participants close their eyes significantly more often during the delay period compared with the encoding period, most likely due to focussed attention during the encoding period to remember stimuli, we found there was no significant difference between conditions. This suggests that participants were not closing their eyes more often during the delay period in the DD blocks, compared with the ND or ED blocks, which suggests that they were not using this strategy in order to ignore distractions presented during the delay. Whilst we only recorded eye-tracking during one study, we assume that this is similar across all of the studies.

Generally, across the studies we found that performance on DD was often significantly lower than performance on ED and ND tasks. This suggests that DD is more distracting than ED. This could be due to different factors. Firstly, it could be that when the distractors appear on screen after the encoding period, they might capture attention more than when distractors are presented at the same time as the relevant information, and so interfere more with items in WM. Secondly, when distractors are presented during the encoding period there are more stimuli on screen than when they are presented during the delay period, which means there is more competition for attention between stimuli. In Desimone and Duncan’s (1995) biased competition model they suggest that more stimuli increases competition, and decreases the attention allocated to each stimulus, however that attention can be biased towards goal-relevant stimuli. Therefore, in the ED condition, when there is more competition between stimuli we might encode more information about the target stimuli (as this is relevant to the task-goals), and less information about the distractor stimuli (as this is not relevant to task goals), whereas when distraction is presented during the delay period, when there are no relevant stimuli on screen and less competition between stimuli, we might attend more to the irrelevant stimuli on screen, which could interfere with items in WM. In particular in Oberauer's (2002; 2009; 2013) state-based model it is suggested that items that enter the focus of attention can interfere with other items in WM, and so it might be that in the DD condition distractors are more likely to enter the FOA, if we attend more to these stimuli, than in the ED condition, and so are more likely to interfere with items in WM.

The findings in these studies could have important real-world implications for WM training. Whilst findings from WM training are often inconsistent, and often show little transfer effects (Melby-Larvag & Hulme, 2013; De Simoni & Von Bastian, 2018), a study by Klingberg, Forssberg & Westerberg (2002) found that WM training improved performance on a non-trained WM task, and Raven's progressive matrices (a non-verbal reasoning task) in children with ADHD. Additionally, WM training tasks often include increasing WM load in line with performance (e.g. Klingberg, Fossberg & Westerberg, 2002; Morrison & Chein, 2011). However, as the ability to ignore task-irrelevant information is a crucial factor of WM (e.g. Vogel & Machizawa, 2004; McNab & Klingberg, 2008), it is possible that training that increases the difficulty of ignoring task-irrelevant information might result in greater improvements. In the findings from chapter 2, we show that different distraction mechanisms might contribute more to WMC across different individuals. In particular we found that DD performance was more predictive of WMC than ED performance in young children, and that this became less predictive over development, and previous research has found that ED performance became more predictive of WMC during healthy ageing (McNab et al., 2015). Therefore, it might be important to target WM training to the distraction mechanisms that contribute most to WMC in that individual.

Limitations

There are a couple of limitations of the studies that should be noted. Firstly, it is possible that the tasks were too easy as often we did not observe any distraction effects of adding distraction to the paradigm (i.e. performance was not lower in the distraction conditions than in the ND condition). This was the case in the findings from chapters 3 and 4. In chapter 3, we observed no distraction effects in the remember faces/ ignore scenes task, or when participants were asked to remember the positions of red circles/ ignore the yellow circles, and in the remember scenes/ ignore faces task we only saw distraction effects for DD not ED. Similar to the behavioural findings from chapter 3, in chapter 4, we again observed no distraction effects for the remember faces/ ignore scenes task, and for the remember scenes/ ignore faces task we only saw distraction effects for DD, not ED. If the tasks were too easy for the participants, this could have resulted in less modulation of activity in task-specific regions, as it was possibly not required to complete the task. This is one explanation for why we did not see significantly less activity in task-specific regions when participants were asked to ignore stimuli compared with a passive view baseline, as found in previous studies (Gazzaley et al., 2005a; Gazzaley et al., 2005b, Clapp & Gazzaley, 2012). Although there were also many differences in the task designs that could have resulted in the differences in findings (as discussed previously). In future work, pilot studies should be carried out to determine what target load, distraction load, timings etc. should be used in order to observe significant distraction effects.

One explanation for why the tasks might have been too easy compared with previous studies and another possible limitation of the studies, is that in the studies in chapters 3 and 4, each condition was presented in a separate block meaning that the timing of the distractions were predictable to participants and previous research has shown that predictable distraction is less 'distracting' than unpredictable distractions (Carlson, Hasher, Zachs & Connelly, 1995; Sussman, Winkler & Schröger, 2003). We also see that in the smartphone study where the conditions are mixed, distraction effects were observed, however there is also a higher load in the smartphone study, and it is possible that there were also some differences between the participants who came into the lab and those who took part in the smartphone game. Therefore, it is difficult to determine which differences in design are having an effect on performance. It is possible that this change in task design is why we did not replicate previous findings that ED and DD significantly predicted VWMC in chapter 3, as the previous study used the same task (with a lower load), but had blocks of mixed conditions. Future studies should directly compare the effects of mixing conditions versus blocking conditions on ED and DD performance.

Finally, a third limitation of the studies, is that there was no measure of whether participants encoded the distractions. Previous findings suggest that low VWMC individuals store irrelevant, as well as relevant information (Vogel & Machizawa, 2004; McNab & Klingberg, 2008). Therefore, it would have been useful to have considered a measure of how much of the irrelevant information participants encoded. With this analysis we could have investigated whether this correlated with their VWMC, which would support previous work. However, we could also have investigated how this relates to activity in task-specific sensory regions. In particular, whether participants who encode irrelevant material as well as relevant material show the same suppression effects as participants who more efficiently filter distraction.

Future direction

In addition to the future research that is suggested above to overcome limitations of the studies in this thesis, there are many other avenues for future research. With the fMRI data from chapter 4, we have investigated activity in sensory regions using ROI analysis. However, analysis should be carried out to understand the neural activity associated with ED and DD filtering in higher level processing regions. For example, many studies find areas in the prefrontal cortex to be involved in ED (McNab & Klingberg, 2008; Toepper et al., 2010) and DD filtering (Artchakov et al., 2009; Dolcos, Miller, Kragel, Jha, & McCarthey, 2007; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011). However, the activity in these regions should be directly compared, in order to disentangle the common and unique neural mechanisms associated with ED and DD filtering. Additionally, as discussed previously, another region associated with distractor filtering is the basal ganglia. In particular studies have found an association between the basal ganglia and ED filtering (McNab & Klingberg, 2008; Baier et al., 2010; Haeger, Lee, Fell, & Axmacher, 2015). However, there is some inconsistency with the role of the basal ganglia in DD filtering, as studies find that impairment of the basal ganglia is associated with improvements in distractor filtering (Cools, Miyakawa, Sheridan & D'esposito, 2010; Mehta et al., 2004), rather than with a decline in filtering ability, which would be expected if the basal ganglia plays an important role in DD filtering. McNab and Dolan (2014) suggest that this inconsistency might be due to the basal ganglia playing an important role in ED, but not DD filtering. However, this has not been directly compared and so using the data from Chapter 4 we could directly compare activity in the basal ganglia associated with ED and DD filtering. Additionally, as previous studies using MVPA, have found evidence of sustained activity across the delay period in sensory regions, that were not identified using univariate analysis (Serences, Ester, Vogel & Awh, 2009), MVPA analysis could be used to compare patterns of activity in sensory regions when presented with encoding distractions compared with delay distractions, using the data in Chapter 4. If delay distractions are more likely to enter the FOA than encoding distractions, as discussed above, it may be that distractions presented during the delay period are decodable from activity in sensory regions, however distractions presented during the encoding period are not. By identifying the neural mechanisms associated with ED and DD filtering, and getting a baseline understanding of what limits VWMC, we can investigate how this might differ in people with low VWMC. In particular, it could be useful in understanding developmental disorders in which WM is impaired, such as ADHD (Barkley, 1997; Martinussen, Hayden, Hogg-Johnson, & Tannock, 2005). This could lead to techniques to improve WM in these populations.

Another avenue for future research is to investigate how activity in task-specific visual regions changes over development and healthy ageing. In this thesis it was identified that during development DD filtering ability becomes less predictive of VWMC, and there was a trend towards ED filtering ability becoming more predictive of VWMC. This might be in line with increasing ability to ignore encoding distractions, and so the suppression effect observed during ED filtering might linearly increase during development. During healthy ageing, previous research has identified that DD filtering ability declines more rapidly than ED filtering, and that ED filtering ability becomes more predictive of VWMC (McNab et al., 2015). They speculate that the similarity between the ability to ignore encoding distraction and WM performance suggests more focused attention during encoding in older adults, making them better at the encoding distraction than the delay distraction task. It is suggested that this might be the case even when participants are not expecting distraction. Therefore, we might observe some suppression effects in task-specific visual regions at the encoding period for ND and DD tasks as well in the ED task, in older adults. This research would help us understand what is limiting VWMC in older adults, and could lead to techniques to improve WM.

Additionally, in the data presented in Chapter 3, eye-tracking data were collected for the purpose of investigating whether participants were closing their eyes during the delay period when distractions were on screen. However, with this data further analyses of gaze location and pupil diameter could be carried out in relation to performance. Analysing gaze location, would allow us to investigate length of time spent looking at/ looking away from distractions presented during encoding compared with the delay period, and how this relates to performance and VWMC. Analysis of pupil diameter could also provide further insights into the effects of distraction on WM, as a recent study found that pupil diameter provides a measure of what is in the 'focus of the mind' (Zokaei, Board, Manohar & Nobre, 2019). Therefore, changes in pupil diameter when presented with ED, compared with DD, and any relationship to performance could be investigated. In future studies, it would also be interesting to investigate the changes in pupil diameter in ED and DD over healthy ageing; in McNab et al. (2015), they found that over healthy ageing, DD performance declines at a faster rate than ED performance and propose that older adults might apply focussed attention during the encoding period to compensate for a decline in ability to hold items in WM over the delay, and so we might see changes in pupil diameter in line with these changes.

Conclusions

The studies in this thesis have investigated the mechanisms underlying ED and DD filtering. We have identified separable ED and DD filtering mechanisms during development. We also found that DD filtering ability becomes less predictive of VWMC over development and that there is a trend towards ED filtering becoming more predictive of VWMC over development. These findings might be important when designing techniques for improving WM during development. We observed evidence of similarities in performance on VWMC tasks between visuo-spatial and visual-object WM tasks, suggesting similar underlying mechanisms in the two types of WM tasks. We found that DD filtering, but not ED filtering correlated across visual-spatial and visual-object WM tasks, which might reflect that more task-specific filtering mechanisms underlie ED filtering, whilst more general filtering mechanisms underlie DD filtering. Finally, using fMRI we identified a novel suppression mechanism which relies on comparison between both a passive view baseline and a no distraction condition. As previous work has only identified a suppression mechanism relative to a passive view baseline, it is likely that the suppression mechanism identified in this thesis extends the suppression mechanisms identified and provides a bigger picture of the suppression occurring in task-specific stimulus regions when participants are asked to ignore stimuli. This suppression mechanism was only observed for ED filtering and not DD filtering, which further supports the theory that ED and DD filtering are separable mechanisms. It also supports the theory that ED filtering requires more task-selective suppression mechanisms, whilst DD filtering might require more general filtering mechanisms, perhaps in higher processing regions in the PFC. Further research is required to disentangle the neural mechanisms associated with ED and DD filtering, and how these change over development and healthy ageing. However, the studies in this thesis provide greater understanding of the mechanisms underlying ED and DD filtering, which can inform future research into conditions where VWMC is impaired, as well as during development and healthy ageing, and inform techniques for improving WM.

Appendices

Appendix 1; Mean accuracy and K-values for each condition in the out-of-scanner red circles task.

Measure	Working Memory Capacity	No Distraction	Encoding Distraction	Delay Distraction
Accuracy	89.77 (± 1.45)	97.73 (± 0.64)	96.67 (± 0.58)	94.09 (± 1.00)
K-value	3.65 (± 0.14)	2.82(±0.04)	2.79 (± 0.05)	2.68 (±0.05)

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