Examining the representation of spatial short-term memories through the lens of resource allocation theory

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Examining the representation of spatial short-term memories through the lens of resource allocation theory

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Abstract

This thesis aims to examine the nature of spatial representations in visuospatial working memory (VSWM) and the mechanism by which the oculomotor system supports VSWM maintenance. To examine these research questions, *Chapter Two* verifies the use of a continuous report task in measuring memory for spatial locations, showing that the representation of spatial locations is affected by the number of to-be-remembered items. In *Chapter Three*, a strong eccentricity effect in spatial, but not colour, working memory was observed. This result is argued to reflect that the resource involved in spatial working memory relies on topographic mapping. *Chapter Four* examined the distribution of resources across sequences of spatial locations. Results showed that the serial position effect, and therefore the distribution of resources, depends on whether the full sequence or a single probe is to be recalled. To examine the role of the oculomotor system, saccadic interference in spatial and colour working memory was examined in *Chapter Five*. Results showed that the oculomotor system is selectively involved in maintenance of spatial locations in VSWM. Performing multiple delay-period saccades resulted in an increase in guessing, but not imprecision, in spatial working memory. It is argued that spatial locations in VSWM are represented as activity peaks in a topographic cortical map. Within this map, the oculomotor system is involved in maintaining the signal to noise ratio of activity peaks for each of the to-be-remembered locations. This research makes an important and novel contribution to the literature by advancing understanding of the nature of representations within spatial working memory and interactions between VSWM and action systems.

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List of Figures

Declaration

I declare that no work in this thesis has been submitted elsewhere for qualification and is my own work unless referenced otherwise.

Published and Submitted Work

Part of Chapter One has been submitted as a chapter in an edited volume with authors Siobhan M. McAteer, Soazig Casteau, and Daniel T. Smith.

Chapter Two is under review in Vision Research with authors Siobhan M. McAteer, Anthony McGregor, and Daniel T. Smith.

Chapter Three is under review in Journal of Vision with authors Siobhan M. McAteer, Anthony McGregor, and Daniel T. Smith.

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Chapter Five has been published in Attention, Perception, & Psychophysics:
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Chapter 1

Literature Review

1.1 What is Visuospatial Working Memory?

Working memory is the ability to actively and temporarily maintain and manipulate information for use in broader cognitive tasks and behaviour (Baddeley, 2010, 2011; Baddeley & Hitch, 1974). Baddeley and Hitch (1974) proposed a multi-component model of working memory. This model conceptualises working memory as comprising two independent, domain-specific slave systems, each with their own characteristics and capacity limits, which are under the control of the central executive. This model of working memory has been influential across the field of psychology, and has provided a framework for much research examining the behavioural and neural underpinnings of memory and cognition (Baddeley et al., 2021; Nee & D'Esposito, 2018).

The retention and maintenance of visual and spatial information is proposed to take place in visuospatial working memory (VSWM). VSWM is a limited capacity store responsible for maintaining information about the appearance and spatial locations of objects in a visual array (Baddeley & Hitch, 1974). It has been shown that VSWM abilities are correlated with and predictive of general fluid intelligence (Colom et al., 2007; Colom et al., 2008; Unsworth et al., 2014), mathematical ability (Allen et al., 2019, 2020; Ashkenazi et al., 2013; Fanari et al., 2019; Swanson & Beebe-Frankenberger, 2004), and reading comprehension (Daucourt et al., 2018; Inhoff & Weger, 2005; Nouwens et al., 2017). Moreover, VSWM is affected by diseases such as Parkinson's Disease and Alzheimer's Disease (Grossi et al., 1993; Lee et al., 2010; Zokaei & Husain, 2019). The involvement of VSWM in such a broad range of behaviours highlights its role as a critical cognitive system in daily behaviour and higher-level cognition (Rösner et al., 2022). However, the representation of information within VSWM is still not fully understood in healthy populations.

1.2 Functional Organisation of VSWM

Baddeley and Hitch (1974) proposed separation between the maintenance of verbal information and visuospatial information in VSWM, with behavioural (Alloway et al., 2010; Berry et al., 2019; Cocchini et al., 2002; Logie et al., 1990; Pickering et al., 2001; Postma & De Haan, 1996; Shah & Miyake, 1996; Vandierendonck et al., 2004) and neurophysiological studies (Basso et al., 1982; Hanley et al., 1991; Rothmayr et al., 2007; Smith & Jonides, 1997, 1998; Vallar & Baddeley, 1984) supporting this view (but see Morey, 2018; Poirier et al., 2019). These studies have relied heavily on the dual-task paradigm, where the independence of two cognitive functions can be examined. In this paradigm, participants are asked to complete two tasks, a primary and secondary task, simultaneously. If performance on the primary task is disrupted by performing the secondary task, the two tasks are argued to rely on the same cognitive resources. Conversely, if performance of the primary task is not significantly disrupted by the secondary task, it can be argued that the two tasks are independent of each other. This method has also been used to support separation between memory for visual and spatial features within VSWM, which will be outlined in this section.

1.2.1 Behavioural Evidence

Using the dual-task paradigm, Tresch et al. (1993) reported a double dissociation between spatial and visual working memory. Participants were required to remember either the location of a dot or the form of an object, while concurrently performing movement or colour discrimination tasks. Memory for object form was selectively impaired by the colour discrimination task whereas memory for the dot location was selectively impaired by the movement discrimination task. However, the objects used were drawn from a small set of eight objects, which could be easily verbalised. Although a double dissociation was found, this potential verbalisation of the objects used calls into the question the validity of the task used to probe visual memory. Della Sala et al. (1999) developed the Pattern Span Task, where participants are asked to remember visual matrices of filled and unfilled squares. They compared pattern span performance to Corsi blocks performance while participants were presented with irrelevant visual input or were required to follow an arrangement of blocks with their hands (spatial tapping). Della Sala et al. (1999) observed a double dissociation: performance on the Visual Patterns task was selectively disrupted by irrelevant visual input whereas performance on Corsi blocks task was selectively disrupted by the spatial interference task. It was therefore concluded that there is behavioural dissociation in memory for spatial locations and memory for visual features.

The double dissociation reported in these examples (Della Sala et al., 1999; Tresch et al., 1993) has not been reliably replicated, with many studies reporting same-system interference only (e.g., Hecker & Mapperson, 1997), which suggests that this evidence is insufficient to conclude that there is separation within VSWM. Many of the studies investigating this issue have also used different interference tasks, for example passive visual input, such as presentation of abstract paintings, and active movements generated in space, such as spatial tapping (Della Sala et al., 1999). The differences in active and passive interference tasks might mean that they interfere with VSWM to different degrees, calling the validity of these tasks as pure VSWM interference tasks into question.

These issues prompted a more rigorous study of the independence of visual and spatial stores in VSWM to be carried out (Klauer & Zhao, 2004). Klauer and Zhao (2004) attempted to reproduce the double dissociation observed in previous studies (Della Sala et al., 1999; Tresch et al., 1993), while ruling out other potential explanations for the dissociation, such as similarity-based interference, short-term memory consolidation, and central executive involvement. Participants were required to remember the identities of Chinese ideographs and the location of dots. Interference tasks involved either detecting a stationary item within a moving array or to discriminate colours within a display. Across six experiments, memory performance in the visual task was significantly more disrupted by colour discrimination than by motion detection. Conversely, location memory was significantly more disrupted by motion detection than by colour discrimination. Klauer and Zhao (2004 argued) that these significant simple main effects provide strong evidence for a double dissociation between visual and spatial memory within VSWM. Additionally, these findings cannot be explained by other factors, such as central executive involvement, strengthening the argument for a functional dissociation between visual and spatial stores in VSWM. This dissociation has been confirmed by subsequent behavioural studies (Darling et al., 2009; Darling et al., 2007; Sanada et al., 2015; Smith, 2022; but see Vergauwe et al., 2009).

1.2.2 Neurophysiological Evidence

Extensive neurophysiological evidence bolsters the case for a dissociation between spatial and visual processing within VSWM. Using positron emission tomography (PET), Smith et al. (1995) found that spatial memory activated right hemisphere regions whereas object memory was associated with activity in the left hemisphere. They also reported a behavioural double dissociation, which implied that different working memory buffers are used for spatial and object information. Courtney et al. (1996) further showed that activity was significantly greater in fusiform, parahippocampal, inferior frontal, and anterior cingulate regions for visual working memory compared to location working memory. Likewise, activity was significantly greater in superior and inferior parietal cortex and the superior frontal sulcus in location working memory compared to visual working memory.

These findings have been supported by subsequent studies using functional magnetic resonance imaging (fMRI), providing greater spatial resolution and therefore greater support for a dissociation between spatial and object working memory at the neural level (Courtney et al., 1998; McCarthy et al., 1996; Ren et al., 2019). More recently, Konstantinou et al. (2017) carried out voxel-based morphometry to examine whether different structures might underlie capacity limitations in object and location working memory. They showed that object and location memory spans were not significantly correlated, providing behavioural evidence for a separation between visual and spatial working memory stores. Additionally, grey matter density and white matter volume of distinct cortical structures correlated with spatial and object spans. These distinct pathways shown by PET and fMRI are similar to the dorsal and ventral pathways that are involved in vision for action and vision for perception (Goodale & Milner, 1992), indicating that there is a functional significance of the separation of VSWM into visual and spatial stores.

However, this dissociation in neural pathways has not been widely accepted (McCants et al., 2019; Nee et al., 2013), and there is a growing consensus against using locations of neural activity to support domain-specificity within working memory (D'Esposito & Postle, 2015; Eriksson et al., 2015). fMRI studies by Nystrom et al. (2000) and D'Esposito et al. (1998) have suggested that the dorsal/ventral distinction between visual and spatial working memory is too simplistic, as it is not reliably found in when different VSWM paradigms are used. They argued that the areas proposed to be active during visual and spatial working memory are observed because they are also involved in non-memory processes, including attention and motor planning, which support memory processes. Sala et al. (2003) examined neural activity when houses, faces, and spatial locations are probed in VSWM tasks. They showed that activation was broadly consistent with the dorsal/ventral pathways, thereby supporting fractionation between visual and spatial VSWM at the neural level. As well as showing different patterns of neural activation, Sala et al. (2003) demonstrated a behavioural dissociation in performance, consistent with the claim that VSWM performance for faces is distinct, both behaviourally and neurally, from memory for houses and locations. Memory for houses was not distinct from memory for spatial locations. On first inspection, this pattern of data seems to suggest that there is no clear fractionation between visual and spatial working memory. However, studies employ different tasks and stimuli within these tasks, and these stimuli may comprise of multiple features, both visual and spatial. These differences in tasks and stimuli might underpin the conflicting results. For example, Nystrom et al. (2000) sequentially presented letters and shapes in distinct spatial locations, for both visual and spatial memory conditions (Experiments 2 and 3). It is likely that, despite being instructed to remember either the shape/letter or location, participants were encoding and retaining both spatial and visual features of the stimuli. This idea is supported by Foster et al. (2017), who showed that spatial locations are spontaneously represented in VSWM, even when irrelevant to task completion. This automatic encoding of spatial information during visual working memory tasks might be observed because spatial location aids in binding visual features together into coherent representations in VSWM (Pertzov & Husain, 2014; Wheeler & Treisman, 2002). Although there is a degree of separation between visual and spatial working memory (Courtney et al., 1996; Smith et al., 1995), this might be less pronounced than the separation between verbal working memory and VSWM because memory for spatial locations is typically required to support memory for visual features.

The failure to find consistent evidence supporting separate neural pathways underlying spatial and visual working memory processes is not too problematic for the modular view. The mapping within the cortex, especially within the prefrontal cortex, is many-to-many: many functionally distinct processes can activate the same regions within the brain. Furthermore, using cortical locations to support dissociation of functions, especially memory processes, is complex because it relies on accurately separating these cognitive processes. For example, memory must be separated from attention, and within memory, encoding, rehearsal, and retrieval processes must be separated. This separating of processes is complex, and there is still overlap at some levels, for example where location aids encoding into visual working memory, even when location is irrelevant to the primary memory task (Foster et al., 2017; Olson & Marshuetz, 2005). Nevertheless, the behavioural and neurophysiological evidence presented in this section broadly suggests that there is a degree of separability between visual and spatial working memory.

1.3 Measuring VSWM

As outlined, there are many important differences in the tasks being used to measure VSWM, which might result in different conclusions being drawn about the structure and function of VSWM. For example, Brooks matrix task (Brooks, 1967), in which participants are asked to remember a series of spatial locations or nonsense sentences, has been shown to employ the use of general-purpose executive functions (Salway & Logie, 1995), so is not specifically probing memory for spatial locations. A variety of tasks are used to measure spatial and visual working memory, including Corsi blocks task, change detection tasks, and continuous report tasks, which will be outlined in this section.

1.3.1 Typical Measures of VSWM

When measuring spatial working memory, studies typically use Corsi blocks task (Milner, 1971), where participants are required to recall a sequence of block tapping. This task was developed as a spatial alternative to digit span, which is used to assess verbal working memory (Corsi, 1972). Corsi blocks task is a powerful test that has been employed by psychologists both in clinical and in laboratory settings to examine a myriad of different research questions about VSWM, for example, examining VSWM deficits in different patient groups (Kessels et al., 2000). However, there is a lack of standardisation in terms of procedure, especially with respect to display characteristics, such as block placement and block numbering, scoring, and determination of span measurement. As well as this, replication has been difficult because procedural information is not always reported, such as block tapping rate and trials performed at each level (Berch et al., 1998). This lack of standardisation means that the reliability and validity of Corsi blocks task as a measure of spatial processing has been difficult to verify, and has resulted in differences in estimates of capacity, ranging from around four items to seven items (Monaco et al., 2013). Kessels et al. (2000) proposed a framework for standardising Corsi blocks task, detailing important procedural and scoring concerns that should be consistent across studies, including task parameters such as block layout and scoring method. While the Corsi blocks task is widely used in experimental psychology, these parameters, or deviations from these parameters, are not widely reported or justified in studies with healthy participants so the issue of standardisation and the reliability of normative data remains (Arce & McMullen, 2021).

The nature of cognitive processes involved in Corsi blocks task has also been debated. Some scholars have argued that Corsi blocks task is not a pure measure of spatial memory, as both spatial locations and temporal order must be retained (Della Sala et al., 1999) and differences in procedures and experimental set-ups may mean that participants engage in different encoding and maintenance strategies (Berch et al., 1998). Vandierendonck et al. (2004) attempted to examine the nature of cognitive processes underlying performance of Corsi blocks task by using the dual-task paradigm in a series of experiments. Participants were required to complete the Corsi blocks task while also completing random generation, spatial tapping, or articulatory suppression tasks to assess whether Corsi blocks task probes spatial memory or a more domain-general process. It was shown that performance on the Corsi blocks task was significantly impaired in the spatial tapping condition, with random generation affecting performance only at intermediate and long sequences, where the central executive is engaged to support maintenance (Vandierendonck et al., 2004). This suggests that Corsi blocks task is probing memory for spatial locations, but as the task becomes more difficult, domain-general executive function mechanisms are required to support performance.

Visual working memory is typically measured by participants recalling information about simultaneously presented arrays of objects, such as in the Visual Patterns task (Della Sala et al., 1999). The Visual Patterns task and Corsi blocks task are commonly used to measure and compare performance across visual and spatial working memory. However, there are a number of differences between the tasks, which might cause potential comparisons between the tasks to be considered problematic. One difference between the Visual Patterns task and Corsi blocks task is in the mode of presentation. In Corsi blocks task, the blocks are tapped one at a time, with the presentation array being present throughout the task. In contrast, the visual patterns in the Visual Patterns task are presented simultaneously as arrays on cards. Having the presentation array being present throughout the trials in Corsi blocks task means that there are different potential sources of interference within the presentation of sequences. For example, as a function of sequence length, the amount of relevant and irrelevant information changes. On low span conditions, this might impair performance, as the number of irrelevant stimuli outnumbers the relevant stimuli and filtering settings, i.e. ignoring irrelevant stimuli, changes on a trial-by-trial basis (Jost & Mayr, 2016). In contrast, in the Visual Patterns task, half of the array is always filled, regardless of how large the matrix is. Additionally, the presented patterns change on each trial, which might influence how participants encode information into VSWM (Rudkin et al., 2007).

It might also be that the sequential nature of presentation in Corsi blocks task is inherently more difficult due to the requirement to retain spatial-temporal associations as well as mentally building and retaining relational information (Avons & Trew, 2006; Jiang et al., 2000), whereas simultaneous presentation of stimuli in visual working memory tasks like the Visual Patterns task does not necessarily require participants to encode and maintain the relational information between stimuli. This simultaneous presentation may result in increased visual span capacity. Lecerf and de Ribaupierre (2005) showed that recognition performance in a matrix task was greater when stimuli were presented simultaneously compared to when stimuli were presented sequentially (Gorgoraptis et al., 2011; but see Ihssen et al., 2010). It may therefore be that the Corsi blocks and Visual Patterns tasks are not probing visual and spatial working memory, but are probing memory for temporal sequences and memory for patterns, respectively. Mammarella et al. (2008) investigated this hypothesis in children using a battery of 13 working memory tasks, including Corsi blocks task, backwards and forwards digit span, Visual Patterns task, house recognition task, and static and dynamic maze tasks (more detail in Mammarella et al., 2006). The best fitting model to this data included separate components for verbal working memory, visual working memory, spatial-sequential working memory, spatial-simultaneous working memory, and an “active” component, which is involved mentally manipulating information (Mammarella et al., 2008). This model was subsequently confirmed in adults (Mammarella et al., 2013) and suggests that, although Corsi blocks task does measure spatial working memory, it is likely that there are different subcomponents of spatial working memory such that Corsi blocks task is measuring only one part of spatial working memory ability (Mammarella et al., 2013; Mammarella et al., 2008; Vandierendonck et al., 2004).

There are also distinct differences in the responses required on each task probing spatial and visual working memory, which might affect the measurement of VSWM. In the Corsi blocks task, participants are required to make a motor response, reproducing the sequence presented at encoding. In typical visual working memory tasks such as the Visual Patterns Task, participants are asked to verbally respond regarding which squares within a matrix were filled. In some visual working memory tasks, a motor response is required, such as clicking or shading which squares in a matrix were filled at presentation. However, the extra demands that are present in prototypical spatial working memory tasks require that participants respond with the temporal order presented during encoding. This requirement to reproduce the correct temporal order means that participants transform the stimuli and their representations in VSWM from retinotopic to spatiotopic representations to enable motor responding. In contrast, visual working memory tasks typically rely on two dimensional arrays, and there is no transformation from retinotopic to spatiotopic representations required to enable verbal responding. This lack of transformation means that there are fewer sources of noise present in visual working memory tasks, as retinotopic representations are more accurate than spatiotopic representations, where error accumulates over transformations (Golomb & Kanwisher, 2012; Shafer-Skelton & Golomb, 2018). These differences in response demands, as well as differences in presentation, limit the degree to which performance on the Corsi blocks task and Visual Patterns task can be compared.

1.3.2 Change Detection Task

One potential task that is matched in terms of presentation and response demands is the change detection task. This task involves presenting an array of items, such as coloured shapes. After a short delay, a test array is presented, which might involve a change in an item's colour, orientation, shape, or location. Participants are required to determine whether a change occurred between the test array and first presentation of the array. By changing the appearance or the location of stimuli within the array but keeping all other factors such as response demands and presentation mode consistent, the characteristics of visual and spatial working memory can be probed and directly compared. VSWM capacity (k) is calculated by measuring the proportion of trials in which a change is correctly (hit rate; h) and incorrectly (false alarm rate; f) detected relative to the number of items (N) presented in the array (Equation (1.1), Pashler (1988); Equation (1.2), Cowan (2001)).

$$k_p = N * \frac{h - f}{1 - f} \tag{1.1}$$

$$k_c = N * (h - f) \tag{1.2}$$

Most work using the change detection task has probed visual working memory by examining performance with changes in colour or orientation (e.g., Machizawa & Driver, 2011). The change detection task offers a reliable and stable estimate of VSWM capacity (Balaban et al., 2019; Dai et al., 2019). In a large-scale examination of the change detection task, Balaban et al. (2019) found that estimates of capacity were stable across trials, as well as over time in 3,849 participants. This was found in a ten-minute version of the task, indicating that even with few trials, the change detection task provides a reliable estimate of VSWM capacity (Balaban et al., 2019).

However, this task is not without its limitations. There are several factors in the change detection task that have been shown to affect performance, including the magnitude of change to be detected. Keshvari et al. (2013) have shown that the probability of reporting a change in an orientation change detection task increases with magnitude of the change to be detected at every set size, up to eight items. This was demonstrated by calculating capacity estimates at set size six for different magnitudes of change. At magnitudes between 0° and 9°, k was estimated to be 0, indicating that no items were retained. Conversely, when changes were large at magnitudes between 81° and 90°, k was estimated to be 3.8 items. They argued that, since capacity depends on the magnitude of change to be detected, this is inconsistent with the basic idea of a fixed capacity in VSWM. If there is a fixed capacity limit in VSWM, around three to four items should have been retained regardless of the magnitude of change to be detected. This finding therefore demonstrates that the change detection task must be tightly controlled to enable a reliable estimate of VSWM capacity to be obtained.

A further consideration for the change detection task is the way in which capacity estimates are calculated. Different calculations have been proposed depending on whether the recognition task is whole-display (Equation (1.1)) or single-probe (Equation (1.2)). The validity of these measures has been questioned because the estimate of capacity is biased by both the equation and the set size used to calculate capacity (Rouder et al., 2011). The equations used are valid only if N is greater than or equal to true capacity, k. For example, if a set size of four items is used, participants with a true capacity of three to four items will have a valid estimate of capacity, but if a participant has a capacity of five items, their estimate cannot be larger than four. The implication of this is that their estimate will be biased too low. This bias can be controlled by using larger set sizes, but using a large range of set sizes is not always practical and the decision of which set size will be large enough is not a straightforward one. Additionally, Cowan (2001) proposed that VSWM capacity is a latent property that is unchanging across stimulus and task properties, which has received mixed support in tasks using this measure of VSWM (Balaban et al., 2019; Keshvari et al., 2013). However, use of the measure proposed by Pashler (1988) results in an increasing k with increases in N (Equation (1.1)), contrary to the idea of a stable VSWM capacity (Cowan, 2001). Examination of these capacity measures highlighted that they are not opposing measures, but are valid for different tasks: Equation (1.1) is valid for whole report tasks, whereas Equation (1.2) is valid for single probe tasks (Rouder et al., 2011). However, many studies misreport measures based on their methods, resulting in inconsistencies across the field with respect to the ways in which VSWM capacity are measured and interpreted when using the change detection task (Rouder et al., 2011).

The change detection task provides a method of measuring and comparing VSWM performance for both visual and spatial features of stimuli. It is a useful, relatively straightforward, and reliable task that allows for a calculation of capacity estimates of visual and spatial working memory (Dai et al., 2019; Xu et al., 2018). However, there are several factors that might affect this reliability, and the appropriateness of the change detection task depends on the research question being investigated.

1.3.3 Continuous Report Method

A key issue with the Corsi blocks and change detection tasks is that they rely on discrete response spaces, producing a measurement of span (as in Corsi blocks task), or hit and false alarm rates (as in change detection tasks). Relying on such responses limits the degree to which inferences about the precision of the underlying representation can be made. In particular, in the Corsi blocks task, the primary measure is a span measure. It might be that the information from the presented array was encoded noisily, with little impact on performance at low set sizes. However, with increasing set sizes, the noise in representations increases, which increases the difficulty in selecting the correct block in the correct temporal position or in detecting changes, therefore resulting in more incorrect responses. Such tasks do not allow for detailed examination of the degree of noise in representations. More sensitive tasks have since been developed that permit more detailed examination of the precision in representations to be undertaken. One way to examine the noise within VSWM representations is to use a continuous report task (Wilken & Ma, 2004). In this task, participants are asked to reproduce a feature of a target stimulus along a continuous scale; for example, reporting the colour of a stimulus on a colour wheel or reproducing the orientation of a target. Computational models can then be applied to the data to examine the error distribution and the sources of response error. This task has been used to examine memory for a range of visual features, including colour (Bays et al., 2009; Zhang & Luck, 2008), orientation (Bays, Gorgoraptis, et al., 2011; Gorgoraptis et al., 2011), and motion direction (Zokaei et al., 2011).

The continuous report task has been argued to provide a more sensitive measurement of VSWM than tasks that span measures. Zokaei et al. (2015) examined VSWM performance on an orientation continuous report task in healthy children, young adults, and elderly adults, as well as in patients with Parkinson's Disease (PD). Participants performed a four-item orientation working memory task (three-item for children), and a single-item orientation working memory task with varied delay periods to control for the effect of the delay period on VSWM. PD participants, children, and a subset of elderly participants also completed a sensorimotor task to control for sensorimotor coordination. As well as this, all participants completed forwards and backwards digit span, and PD and elderly participants completed forwards and backwards versions of the Corsi blocks task. Precision on the continuous report working memory task was positively correlated with backwards digit span for all participants, and positively correlated with backwards Corsi span for elderly participants. This correlation indicates that the continuous report task reflects the complex nature of VSWM because backwards span tasks emphasise both storage and processing of memoranda whereas forwards span tasks emphasise storage only (Groeger et al., 1999; but see Rosen & Engle, 1997). In the continuous report task, visual and spatial features must be stored correctly in VSWM, but at recall, one feature, such as colour, must be used to retrieve the correct probed feature, such as orientation. A correlation between backwards span and VSWM precision indicates that the continuous report task places additional demands on VSWM that are not always required in traditional measures of VSWM. This also supports the claim that the continuous report task provides a method for examining the quality of VSWM representations because participants are asked to reproduce a feature of a remembered item. This task provides greater insight into VSWM processes and representations, which is beyond the information obtained by using a binary response task, such as the change detection task (Zokaei et al., 2015).

The continuous report task may be considered a more difficult task than the change detection task because of the additional demand to reproduce a visuospatial feature. This increased task difficulty may lead to a reduced capacity estimate. The differences between change detection tasks and continuous report tasks can be considered similar to the differences in recognition and recall memory tasks, where recognition judgements may be based more on a decision regarding familiarity whereas recall is a more effortful retrieval process requiring both search and decision processes (Kintsch, 1970). However, such a distinction between recall and recognition tasks has received little support. A more parsimonious position argues that recall and recognition memory are related functions in memory (Haist et al., 1992), which may rely on similar retrieval mechanisms (Tulving & Watkins, 1973). In this view, the differences in recall processes between the change detection and continuous report tasks should not be considered problematic because they rely on similar underlying processes within VSWM.

There are a variety of methods used to measure VSWM capacity, each with their own strengths and limitations. Span measures and change detection tasks are useful for carrying out studies to gain an estimate of VSWM capacity relatively easily. However, these methods rely on binary responding, so these tasks are not appropriate in cases where a more sensitive measure of VSWM is required, for example, in investigating how well information is encoded and retained. In these cases, a continuous report task may be more appropriate, though this task might be more difficult to carry out and may place additional demands on VSWM processes. Both the change detection task and continuous report methods have been used to examine the nature of capacity limitations in VSWM across multiple visual and spatial features. In this thesis, the continuous report task is used to measure the precision with which spatial and colour information about coloured dots is maintained in VSWM. Using the continuous report task, as opposed to other measures of visual and spatial working memory allows for more detailed insight into how spatial locations are represented in VSWM because participants are asked to reproduce the spatial location exactly as they remember it. In addition, more meaningful comparisons between spatial and visual working memory can be made because the influence of potential confounding variables, that may be present when performance across Corsi blocks and Visual Patterns tasks is compared, for example, is minimised: the only difference between the colour and spatial continuous report tasks is the feature to be recalled.

1.4 Models of VSWM capacity

One of the key characteristics of VSWM is that it has a limited capacity (Baddeley & Hitch, 1974), with high inter-individual variability being observed in capacity estimates (Machizawa & Driver, 2011). However, there is debate surrounding the nature of this capacity limitation, with opposing views being put forward to explain it. Slot models argue that there is a limit on the *number* of items that can be retained in VSWM (Zhang & Luck, 2008). In contrast, the resource model argues that all task-relevant information can be retained, with limitations on the *fidelity* with which information can be encoded and maintained in VSWM (Bays et al., 2009). In this section, an overview of these models and their supporting evidence will be discussed.

1.4.1 Slot Model

The slot model proposes that there are a limited number of slots available to maintain information about objects at a fixed resolution. When all slots are filled, additional memory items are not encoded into VSWM. The slot model therefore proposes that VSWM is all-or-none: items are either encoded completely, as bound representations, or not at all. This model of VSWM has been widely accepted and supported, and the use of a single capacity estimate in the form of "how many slots are available" is useful for comparing across individuals, task conditions, and tasks, including across modalities.

Luck and Vogel (1997) argued that VSWM has an upper limit of approximately four objects. In their experiment, participants were asked to complete orientation and/or colour change detection tasks, with between one and twelve items. It was found that participants were almost 100% correct on trials in which up to four items were presented. As the number of presented items increased beyond this, performance steadily declined. This was found for colours, orientations, and conjunctions of colour and orientation (Luck & Vogel, 1997). It was therefore argued that VSWM capacity is around four objects, rather than four features: participants could recall information about eight features distributed across four objects (conjunctions of colour and orientation). As well as this, participants could recall information about four features (colour or orientation) in a single-feature change detection task. Despite there being a greater number of features to be recalled in the conjunction condition, performance was similar to that in the single-feature condition, suggesting that conjunctions of features are held as bound representations in VSWM (Luck & Vogel, 1997; Vogel et al., 2001). This limit of around four items has been widely replicated and accepted across the field (Fukuda et al., 2010; Luck & Vogel, 2013). A limit of around four objects is also consistent with limits found in visuospatial attention and in perception, making it a useful measure of VSWM for comparison with other cognitive processes (Cowan, 2001).

Neurophysiological studies using electroencephalography (EEG) and fMRI have offered additional support for an item limit in VSWM (Todd & Marois, 2004; Vogel & Machizawa, 2004; Xu & Chun, 2006). This item limit has been demonstrated by measuring contralateral delay activity (CDA), which is a sustained posterior ERP response in the hemisphere opposite to the location of to-be-remembered items (Feldmann-Wüstefeld et al., 2018; Luria et al., 2016). The amplitude of CDA has been shown to be sensitive to the number of objects that must be remembered, increasing as the number of items increases before plateauing when set size reaches and exceeds the individual's maximum capacity (Villena-González et al., 2020; Vogel & Machizawa, 2004). Similarly, activity in the posterior parietal cortex has been shown to increase with increases in set size before reaching an asymptote when set size reaches the individual's maximum capacity (Todd & Marois, 2004).

However, this strict form of the slot model fails to acknowledge that different characteristics of the stimuli, such as object complexity, affect whether and how information is retained in VSWM. Alvarez and Cavanagh (2004) showed that VSWM capacity was reduced when complex objects, such as shaded cubes, were to be remembered, compared to when simple objects, such as colours, were to be remembered (see also Eng et al., 2005; Taylor et al., 2017). It was therefore argued that VSWM is not fixed, but depends on the amount of information to be retained about each object. This proposal that VSWM capacity might not be fixed but that it depends on the amount of information to be remembered has been challenged. Awh et al. (2007) argue that the observed reduction in VSWM capacity with increased object complexity was due to increased similarity between sample and test items for more complex objects, which might interfere with comparing sample and test items at recall, rather than the information load of the to-be-remembered objects. Awh et al. (2007) therefore argue that object complexity is not a challenge for the slot model.

A particular challenge for the strict form of slot model comes from the use of predictive cues in VSWM. Studies show that recall is more precise at the cued location compared to uncued locations when the cue is presented during encoding (Botta et al., 2010; Griffin & Nobre, 2003; Palmer, 1990) or during maintenance when the array is no longer visible (Pertzov et al., 2013; Souza et al., 2016). This is a challenge to the assumption of all-or-none, fixed resolution encoding put forward by the slot model, where items should be encoded and maintained with relatively equal precision. This finding does not necessarily challenge the existence of a limited number of slots. Instead, these findings challenge how VSWM slots are utilised and how the to-be-remembered objects are distributed amongst the slots. This view is a challenge to the traditional, stricter slot model, which proposes that each object is represented only once in VSWM (Luck & Vogel, 1997). In response to this challenge, Zhang and Luck (2008) revised this model, called the slot+averaging model.

1.4.1.1 Slot+Averaging Model

In the slot+averaging model, there are a limited number of independent slots available to retain information in VSWM with a fixed precision. The critical difference from the traditional slot model is the way in which these slots are used. According to the slot+averaging model, multiple slots can be used to retain information about the same item before the representations are averaged together at recall.

Zhang and Luck (2008) used the continuous report task to probe memory for colour, and applied a mixture model to examine the sources of response error (Equation (1.3)). They found that response error, defined as the distance between the response colour value and the original colour value, followed a normal distribution centred on the original colour value ($\phi_\sigma(\hat{\theta})$). The standard deviation of this distribution (σ) represents the precision of memory representations. Although no significant effect of set size was observed for precision, Zhang and Luck (2008) found that precision decreased slightly between set sizes one and three, indicative that multiple slots were allocated to one item and averaged together at recall. A plateau in precision was observed between set sizes three and six. This was interpreted as evidence that maximum VSWM capacity is around three items: a plateau in precision indicates that each item is represented once, up to the maximum number of slots available. Consistent with the all-or-none assumption of the slot model, incorrect responses were proposed to be guesses, where participants responded at random. The probability of guessing was therefore proposed to come from a uniform distribution (γ), where all possible responses were equally likely. The probability that the target item was encoded into VSWM (P_m) was therefore modelled as $1 - \gamma$, where it was assumed that, if the participant was not responding at random, they were responding with the target value. P_m declined slowly between set sizes one and three, before rapidly decreasing between set sizes three and six. The results from this modelling, both in terms of precision and the probability of reporting the target, suggest that there is an item limit of around three items in VSWM, and this was highly correlated to the measure of capacity obtained using a change detection task (Zhang & Luck, 2008). The decrease in precision between set sizes one and three suggested that representations were averaged together at recall: when more than one slot is available to store a single representation, precision is highest, but as set size increases, and the number of representations of each item decreases, precision will decrease and the likelihood of guessing will increase as some items are not encoded into an available slot (Zhang & Luck, 2008).

$$p(\hat{\theta}) = (1 - \gamma)\phi_\sigma(\hat{\theta} - \theta) + \gamma\frac{1}{2\pi} \tag{1.3}$$

This revised model can explain why VSWM capacity is reduced for complex objects, where more than one slot may be required to store each representation in VSWM. Because more complex items require more than one slot, there are fewer slots available, resulting in fewer items being retained in VSWM, which would result in a decrease in capacity being observed. The results of studies using pre-cues can also be accounted for by the slot+averaging model, where the cued object is stored in multiple slots, therefore decreasing the likelihood that uncued items will be encoded (Zhang & Luck, 2008). Zhang and Luck (2008) examined the effects of cueing on VSWM and showed that P_m was significantly greater on valid trials but precision was only slightly, though significantly, increased on valid trials compared to invalid trials. There was no significant difference in precision between valid and neutral trials. This indicates that the cued location is stored in multiple slots and these slots are averaged together at recall. The magnitude of the difference between valid, neutral, and invalid trials was small, indicating that it is not possible to produce an imprecise representation if an item is encoded into VSWM. However, the facilitation of retro-cued items is less easily explained by the slot+averaging model, as this requires a degree of flexibility in the distribution of slots after encoding, which is not accounted for by the slot+averaging model.

Behavioural studies using both the continuous report task and the change detection task have offered supportfor this revised slot model (Adam et al., 2017; Barton et al., 2009; Donkin et al., 2013; Fukuda et al., 2010; Pratte et al., 2017). For example, Zhang and Luck (2011) used a colour continuous report task in which the number of distinct colours used was varied between 180 (high-precision) and 9 (low-precision) to examine whether there is a trade-off between the quantity and quality of representations in VSWM. In the high-precision condition, participants should prioritise encoding and maintaining high quality representations, so a decrease in VSWM capacity ($k = P_m * set\ size$) was hypothesised. In contrast, in the low-precision condition, a coarser representation can be used to complete the task, so if there is a trade-off between precision and capacity, an increase in k should be observed. Zhang and Luck (2011) showed that participants cannot retain more items than their VSWM capacity by decreasing the precision of these representations, as precision and VSWM capacity estimates were equal across both high- and low-precision conditions (see also Ramaty & Luria, 2018). The lack of a trade-off between precision and k is consistent with the idea that VSWM capacity is fixed, providing additional support for the slot+averaging model.

In their large-scale study, comprising data from 3,849 participants and over 500,000 trials in the change detection task, Balaban et al. (2019) showed that average VSWM capacity was around three items, consistent with previous reports of VSWM capacity (Fukuda et al., 2015). They further showed that participants have a bias towards reporting that a change occurs in the change detection task. The implication of this bias is that, when four items are presented, only around two to three of these items are represented in VSWM. At test, if the probed item is presented in its original colour but not represented in VSWM, the participant is more likely to respond with “different” because that item is not represented in VSWM. This bias increases as set size increases because the proportion of items that are not represented in VSWM increases. Balaban et al. (2019) argued that the change in memory strength (d'), which is a similar measure to precision, at set size eight correlated well with the change predicted from set size 4 ($r = 0.47$). The fact that this strength halves when set size doubles is consistent with the characterisation of VSWM as a flexible resource, which is distributed equally amongst all task-relevant memoranda (Bays et al., 2009). According to the slot model, memory strength is a mixture of two measures: one signalling the remembered items and one equal to 0 for the items that are not represented in memory (Zhang & Luck, 2008). Additionally, due to the all-or-none nature of encoding and storage, memory signal strength for individual items should be equivalent between set size four and set size eight. The memory signal strength for individual items at set size four (d'_{ss4}) can be calculated by $\frac{n * d'_{observed}}{k_n}$, where n is set size, $d'_{observed}$ is the observed memory signal strength at that set size, and k is calculated memory capacity at set size n. The observed d' at set size four was 2.48. Using this in the calculation of memory strength of individual items results in the finding that 2.79 items (k) were represented with d' of 3.56 (d'_{ss4}), while the remaining 1.21 items were represented with d' of 0 at set size four. Average d' at set size eight can be predicted using $\frac{d'_{ss4} * k_n}{n}$ to test the all-or-none nature of slots. This calculation resulted in the prediction that items are represented in VSWM with an average d' of 1.13 at set size eight, with k equal to 2.54, the observed k

at set size eight. That is, 2.54 items (k_{ss8}) are represented with d' equal to 1.13, while the remaining 6.46 items are represented with d' of 0 at set size eight. When memory strength was calculated in this way, the predicted memory strength values closely aligned with the observed data ($r = 0.83$). This suggests that memory strength, and thus precision, is equivalent across set sizes, supporting an item limit in VSWM and the assumption that a subset of items in supra-capacity arrays are represented in VSWM with a fixed resolution.

Using a whole-report task, Adam et al. (2017) offer additional support for the slot model of VSWM. They used the continuous report task to probe memory for colour and orientation. Participants were required to report all of the colours and orientations presented in a given trial. They showed that, as set size increased, variability in responses increased, similar to studies requiring a single response at test (Zhang & Luck, 2008). Notably, they showed when recall order was free, participants reported the most well remembered items first, with precision decreasing across the order of responding. Adam et al. (2017) also examined whether some responses were guesses and estimated individual VSWM capacity when six items were presented, using mixture modelling (Zhang & Luck, 2008). It was observed that the final responses in the set size six condition were guesses, with most participants showing a capacity limit between three and four items, consistent with previous work examining VSWM capacity limits (Robison et al., 2018; Todd & Marois, 2004). Adam et al. (2017) therefore provide evidence consistent with the slot+averaging model of VSWM, where responses become more variable as more items are to be remembered and where participants respond at random when the number of to-be-remembered items exceeds their VSWM capacity.

The slot+averaging model is not the only model that proposes an item-limit in VSWM, and a number of revisions to the slot model have been proposed. For example, the slot+resource model (Donkin et al., 2013; Standage & Paré, 2018; Zhang & Luck, 2008), is a similar model to the slot+averaging model with the exception that the precision within slots is dependent on a limited pool of resources, which are distributed in a continuous manner. However, the slot+averaging model is the most well-established revision to the slot model, and has received the most empirical support (Fukuda et al., 2010).

Overall, there is abundant behavioural and neural evidence to support an item limit in VSWM. Moreover, the slot(+averaging) model provides a relatively straightforward way to conceptualise limits in VSWM. The use of a single capacity estimate, the limit in the number of slots, is easy to interpret and permits comparison across individuals, tasks, conditions, and modalities. However, this model has been criticised as being overly simplistic as it ignores some of the complexities associated with the encoding, maintenance, and retrieval of information in VSWM. This issue is particularly important when multiple objects are to be remembered as the mixture model proposed by Zhang and Luck (2008) fails to accurately describe the pattern of responses observed at large set sizes (Bays et al., 2009). An alternative approach, which rejects the idea of an item limit in VSWM, is the resource model of VSWM (Bays et al., 2009).

1.4.2 Resource Model

Bays et al. (2009) argued that VSWM capacity is not limited by the number of items that can be retained, but is instead limited in terms of the quality of information that can be retained. They propose that the precision with which information is encoded and retained in VSWM is dependent on the fraction of memory resources allocated to each item. If a greater proportion of resources is directed towards an object, it will be remembered more precisely. They further argue that it is necessary to correctly bind object features together during maintenance and retrieval, enabling the information to be used in a meaningful way (Bays et al., 2009). For example, when participants were asked to recall the correct colour of an object, the target item was indicated by a location cue so both the correct location and correct colour must be recalled. Bays et al. (2009) thus proposed that there is no upper limit on the number of items that can be held in VSWM. Rather, representations within VSWM are noisy, with three main sources of recall error (Equation (1.4)): variability in the target representation (i.e., precision; σ), guessing (γ), and misbinding (β). Misbinding/swap errors occur when participants have encoded all the to-be-remembered features, but with incorrect identity-location binding information. These errors are modelled in a similar way to the target item: a Gaussian with precision σ

centred on the presented values ($\phi_\sigma(\hat{\theta} - \theta_i^*)$; Figure 1.1). These misbinding errors are not predicted by the slot models due to encoding and maintenance of information occurring in all-or-none independent slots.

$$p(\hat{\theta}) = (1 - \beta - \gamma)\phi_\sigma(\hat{\theta} - \theta) + \gamma\frac{1}{2\pi} + \beta\frac{1}{m}\sum_i^m \phi_\sigma(\hat{\theta} - \theta_i^*) \tag{1.4}$$

Bays et al. (2009) attempted to replicate Zhang and Luck (2008) while accounting for the occurrence of misbinding errors. They found that precision decreases gradually and continuously with set size, even beyond three to four items, consistent with a power law. Accompanying this decrease in precision was an increase in the probability of misbinding errors (β), even at set sizes of six items (see also Bays, 2016). When these misbinding errors are included in modelling of response error, the proportion of variability in the data accounted for by guessing responses is significantly decreased. Zhang and Luck (2008) found that guesses made up 62% of responses. However, when misbinding errors were included in the model, guesses made up only 14% of responses, indicating that a significant proportion of guessing responses observed by Zhang and Luck (2008) were not truly random (Bays et al., 2009). This result is inconsistent with the slot+averaging model: precision declines steadily with increasing number of items to be retained, and there is no rapid increase in the probability of guessing when set size exceeded VSWM capacity. Rather, the decrease in precision seems to be a result of incorrect item-location bindings at high set sizes. These findings are more consistent with the proposal that VSWM is a finite continuous resource that is distributed amongst all to-be-remembered items. Precision in VSWM therefore depends on the proportion of resource directed to each item: as the number of items to be remembered increases, there is less resource dedicated to processing each item, resulting in an increase in noise in the VSWM representation (Bays et al., 2009).

The resource model has been influential in VSWM research and there have been multiple proposals as to how the resource is allocated to items (Huynh Cong & Kerzel, 2021; Smith et al., 2018; van den Berg et al., 2012). For example, the variable precision model argues

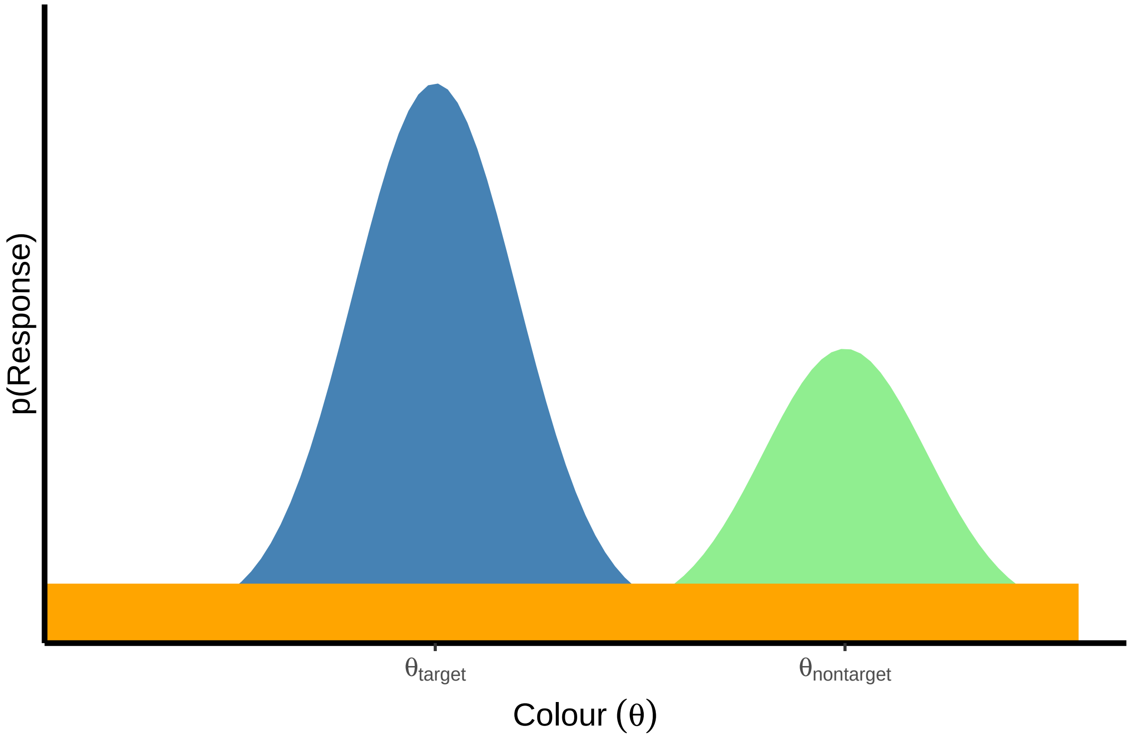

Figure 1.1: Graphical representation of Bays et al. (2009) mixture modelling. The blue curve represents the probability of responding with the target colour, while the green curve represents the probability of reporting the other presented colours (non-target). The standard deviation of these distributions represents the precision in responding. The orange uniform distribution represents the probability of guessing, where all responses are equally likely. Zhang and Luck (2008) included only the probability of responding with the target (blue curve) and the probability of guessing (orange uniform distribution) in their mixture model.

that the resource is not equally distributed across items and trials. That is, encoding quality is random, such that some items will be better remembered than others on a given trial, even if no cue is provided and items are equally salient (van den Berg et al., 2012). In the current thesis, the Bays et al. (2009) resource model, in which the resource is assumed to be equally distributed across all to-be-remembered items when no cue is available, will be discussed.

The finding of decreased precision with increased set size is reliably found across visual features, including colour (Bays, Wu, et al., 2011; Huang, 2010), orientation (Bays, Wu, et al., 2011; Bays, Gorgoraptis, et al., 2011; Gorgoraptis et al., 2011), and motion direction (Zokaei et al., 2011). Furthermore, studies where the relevance/saliency of an item is increased via cueing offer strong support in favour of the resource model over slot models (Bays, Gorgoraptis, et al., 2011). For example, Gorgoraptis et al. (2011) cued an item during encoding in an orientation continuous report task (Experiment Three). They showed that the cued item was recalled more precisely than non-cued items. This finding is consistent with an unequal distribution of resources, where VSWM resources are preferentially distributed to the cued item, with fewer resources directed to remembering the non-cued items. This finding of enhanced precision for cued items with a corresponding cost for non-cued items is reliably found (Bays, Gorgoraptis, et al., 2011; Bays & Husain, 2008). Retro-cuing has also been shown to increase precision of the cued item while decreasing the precision of the uncued item(s) (Kalogeropoulou et al., 2017; Pertzov et al., 2013; Schneider et al., 2018; Souza et al., 2016; Sprague et al., 2016; van Ede et al., 2019). This beneficial effect of retro-cues is a challenge for slot models, but can be easily explained by the resource model. VSWM resources are flexible and dynamic, so can be redistributed amongst memoranda even after encoding and during maintenance. Resources can therefore be redirected from uncued items towards the cued item even after encoding. This redistribution of resources results in a decrease in precision for uncued items as they receive a smaller proportion of resources compared to the cued item. In contrast, the cued item will be represented with greater precision due to receiving a greater share of VSWM resources.

To further strengthen the resource model position, Bays (2018) re-analysed data from eight studies that used the continuous report task, some of which offered support for an item limit in VSWM (Pratte et al., 2017; Zhang & Luck, 2008), while others supported a resource model of VSWM (Bays, 2014; Bays et al., 2009; Gorgoraptis et al., 2011; van den Berg et al., 2012; Wilken & Ma, 2004). According to the slot+averaging model of VSWM, capacity can be estimated from either frequency of guessing responses, or from the set size at which the standard deviation in response error (precision) begins to plateau. Critically, according to slot models, the two estimates should be equal (Zhang & Luck, 2008). Combining evidence across the studies revealed that there was weak evidence supporting a correlation between the capacity estimates (r = .25), even after standardisation (r = .21) and removal of participants who had capacity limits equal to the maximum set size used in the studies ($r = .09$). Examination of each experiment separately revealed that, in only one of the eight experiments, there was a significant correlation between the capacity estimates derived from frequency of guessing and precision. Bays (2018) also performed simulations to examine whether the correlation would be found when measurement error was corrected via bootstrapping ($r = .34$) and by fitting a Bayesian hierarchical model ($\textit{estimated mean posterior correlation} = .14$), observing no meaningful correlation under either simulation. This finding refutes the proposal that there is an item limit in VSWM, and suggests that such a model is not self-consistent. That is, the slot model proposes that capacity estimates derived from guessing and capacity estimates derived from precision should be equal, but this was not found. The weak correlations between capacity estimates, which explained less than 10% of the variance in the data, is strong evidence against the slot model assumption of discrete representations in VSWM. This finding does not fully discount the possibility of an upper limit on the number of items, which is independent of differences in precision, that can be retained in VSWM. However, models with a fixed capacity limit cannot adequately explain why precision decreases monotonically with increases in set size, unlike the resource model.

Neurophysiological evidence also supports the resource model. Previous evidence showed that there is an increase in neural activity before plateauing at individual VSWM capacity (Todd & Marois, 2004; Vogel & Machizawa, 2004). On first inspection, these findings are inconsistent with the predictions of the resource model, where delay period neural activity should be constant because the same resources are engaged regardless of set size. However, recent advances in analytical and modelling techniques have offered support for the resource model. Multivoxel pattern analysis (MVPA) is used with fMRI data to infer the functional role of networks within the brain by examining the relationship between patterns of activity and experimental conditions (Mahmoudi et al., 2012). Sprague et al. (2014) used MVPA to examine activity in the parietal, occipital, and frontal areas, and to construct the representations of items at remembered locations within these regions. They showed that, as set size increased from one to two locations, the activity in these regions became coarser, mirroring the decrease in precision in memory performance (see also Emrich et al., 2013). Electrophysiological work in monkeys offers additional support for a resource model of VSWM, suggesting that local field potentials during the delay period correlate with the precision of memory representations (Lara & Wallis, 2012, 2014). Electrophysiological correlates of both priority and precision have also been observed in humans, where delay period neural activity tracked the proportion of resources allocated to items, reflecting their precision within VSWM, providing additional neural evidence in favour of the resource model of VSWM (Salahub et al., 2019). Furthermore, the amplitude of CDA has been shown to correlate with the precision of recall, even at a set size of one item (Machizawa et al., 2012). These findings suggest that VSWM precision can be indexed by neural markers, and that a plateau in activity is not necessarily a marker of VSWM capacity. These findings therefore provide further evidence in favour of the view that VSWM is best characterised as a finite continuous resource rather than a store with an upper limit on the number of items that can be retained.

The characterisation of VSWM as a resource may be less easy to interpret compared to the single capacity limit proposed by the slot+averaging model (Rouder et al., 2011); it is difficult to quantify VSWM in terms of “how much” resource there is in VSWM. Additionally, the flexible and dynamic nature of a VSWM resource means that comparisons across tasks and domains are more complex compared to the single capacity measure provided by a slot model. However, the resource model is able to account for a wide range of behavioural findings, such as the benefit of retro-cues, that slot models cannot explain. Despite the nature of the resource being debated, this model has considerable explanatory power. Neural network models have provided a method for investigating the potential neural basis for VSWM resource by modelling neural spiking activity and relating patterns in this activity to VSWM precision. Neuronal activity is stochastic and spiking activity in neural models explain the presence of noise in VSWM representations (Bays, 2015; Schneegans et al., 2020). This assumption of stochastic variability in neuronal activity is incompatible with a slot model, where precision, and thus neural activity, should be relatively fixed for each item encoded into VSWM.

Bays (2014) investigated how noise in neural gain might relate to errors in an orientation continuous report task. He modelled memory for orientation through a population coding model. A decrease in neural gain with increases in set size was observed, and was similar to the decrease in precision with increases in set size observed in the behavioural task (Bays, 2014). This model provides a biologically plausible basis for a VSWM resource, and is consistent with single-cell and fMRI data, which showed a decrease in the amount of information about stimuli represented in neural activity as set size increases (Buschman et al., 2011; Emrich et al., 2013).

To model the probability of misbinding, the idea of specialised neurons for representing conjunctions of features can be included in the population coding model (Matthey et al., 2015), consistent with the proposal that, while features are maintained independently, information about the binding of features must also be maintained in VSWM (Bays, Wu, et al., 2011). A mixed population code includes a limited number of neurons, some of which are tuned to features and some of which are tuned to conjunctions of features independently of memory for the visual features, as observed in visual area V2 (Gegenfurtner et al., 1996). The proportion of units accounting for conjunctions of visual features has a strong effect on misbinding errors. The more conjunctive units there are within the population, the less likely misbinding errors are. In contrast, when only single features are coded (i.e., no conjunctive units), misbinding errors are overestimated when more than one item is to be retained. It is worth noting that the ratio between conjunctive units and feature units within the population depends on the number of items to be retained, reflecting the dynamic nature of the resource model. This mixed population coding model has been shown to fit behavioural data well, reproducing the decrease in precision and increase in misbinding errors that are observed with increases in set size (Matthey et al., 2015). This focus on population coding shows that the limit in the VSWM resource arises from the limited population of units that can be active, and their interactions with each other. Population coding models therefore argue that the notion of slots should be abandoned as there is little anatomical evidence to support their existence, whereas the resource model is a biologically plausible account of limits within VSWM.

There is growing behavioural and neurophysiological support for the idea that VSWM capacity can be characterised as a finite resource that is flexibly allocated across to-be-remembered items (Bays et al., 2009; Ma et al., 2014). The precise nature of this resource remains unclear, but the idea of population coding captures the different types of recall error observed in empirical studies (Matthey et al., 2015). One idea that has extended the proposal of population coding in VSWM is that resource allocation is constrained by the availability of neurons (Franconeri et al. (2013), refer to this is as cortical "real estate") to represent the memoranda in modality-specific, topographically organized cortical maps (Bays et al., 2009; Franconeri et al., 2013). The cortical maps hypothesis proposes that each position within the map represents a value in a specific information space (e.g. colour or spatial location). Items within an information space are represented as peaks of activity within the map that compete with each other for representation. Items from different spaces are represented in different maps and do not compete, reflecting the separability between spatial locations and visual features in VSWM outlined above (*Functional Organisation of VSWM*). In the case of spatial working memory, there is strong neurophysiological (Bisley & Mirpour, 2019; Lane et al., 2012), neuropsychological (Pisella et al., 2004; Smith & Archibald, 2020), and behavioural evidence (Ball et al., 2013; Pearson et al., 2014) that the cortical maps that represent spatial working memory are shared with maps used for the control of goal directed movements, such as saccades. This overlap indicates that the same cortical maps underlying motor control interact with the representation of spatial locations in VSWM. As a result, it is logical to propose that the resource responsible for maintenance of spatial locations in VSWM might be constrained by the availability of cortical space, and by the physiology of cortical regions involved in VSWM maintenance.

There is continued debate surrounding the nature of capacity limitations in VSWM. There is strong behavioural and neural evidence to suggest that VSWM is a continuous but finite resource (Bays et al., 2009; Fallon et al., 2016; Ma et al., 2014). That is, VSWM is limited by its ability to encode and retain accurate representations of all task-relevant or to-be-remembered items, rather than by a discrete upper limit. However, the strength of evidence in favour of a slot or resource model depends strongly on the methods used to measure VSWM as well as the assumptions made during modelling and analysis, such as the potential sources of error in responses. In addition, the precise nature of this resource allocation remains unclear.

1.5 The Role of the Oculomotor System in VSWM

Our ability to perceive and understand the world is dependent on our ability to construct and retain a stable internal representation of the world in VSWM via exploratory eye movements. The oculomotor system plays a critical role in visual perception (Land et al., 1999; Land & Hayhoe, 2001), but behavioural and neural overlap in the oculomotor system, visuospatial attention, and VSWM, especially in encoding and maintaining spatial locations in VSWM has also been observed (Pearson et al., 2014; Pearson & Sahraie, 2003). This section will outline research highlighting the selective involvement of the oculomotor system in spatial working memory, providing further evidence for fractionation between visual and spatial working memory, and discussing the involvement of the oculomotor system at all stages of VSWM processing.

As outlined in the previous section (*Resource Model*), the resource model of VSWM (Bays et al., 2009) provides a biologically plausible model of VSWM capacity. While this model does consider that shifting of resources is dependent on the oculomotor system (Bays & Husain, 2008; Ohl & Rolfs, 2017; Udale et al., 2022), it does not account for the overlap between the oculomotor system and VSWM in great detail. The extensive overlap between the cortical areas involved in VSWM and oculomotor control, chiefly posterior parietal cortex and prefrontal cortex (Ikkai & Curtis, 2011; Jonikaitis & Moore, 2019) suggests that any model of VSWM, regardless of whether they argue for a quantitative or qualitative capacity limit, should also consider the role of the oculomotor system in VSWM.

Early models that attempted to explain this overlap between VSWM and the oculomotor system argued that VSWM is “nothing more” than preparing a movement (Theeuwes et al., 2005), similar to the pre-motor theory of attention (Rizzolatti et al., 1987). However, studies have refuted this simplification of the role of the oculomotor system in VSWM, showing that saccadic interference impacts memory for location independently of memory for visual features (e.g., Postle et al., 2006), providing further support for their fractionation within working memory and giving an insight into the role of the oculomotor system in VSWM. In addition, studies using the eye-abduction paradigm have shown that performance on the Corsi blocks task was significantly disrupted by eye-abduction, where spatial span was reduced by approximately one item when stimuli were presented at locations that were outside of the oculomotor range (Ball et al., 2013; Pearson et al., 2014). Eye-abduction caused no disruption in visual or verbal working memory span as measured by the Visual Patterns, size estimation, and digit span tasks (Ball et al., 2013). Using the eye-abduction paradigm enables the effects of oculomotor control processes to be disentangled from attentional processes (Craighero et al., 2004), thereby ensuring that only saccadic programming is disrupted while covertly shifting endogenous attention is unaffected (Casteau & Smith, 2020; Smith et al., 2014, 2010). The findings reported by Ball et al. (2013) and Pearson et al. (2014) therefore indicate that the oculomotor system plays a functional role in memory for spatial locations, but is less involved in memory for visual features or verbal information.

The oculomotor system appears to play a critical role in VSWM, and studies using eye movements have played an important role in understanding the structure and mechanisms involved in VSWM. However, the precise functional role of eye movements in VSWM remains debated. There are several possibilities as to how the oculomotor system is involved at different stages of VSWM. It may be that the oculomotor system is primarily involved in encoding of spatial locations, perhaps via the pre-saccadic shift of attention ensuring that saccadic targets are attended and represented in VSWM. Saccadic eye movements during maintenance/rehearsal have also been shown to disrupt VSWM, indicating a role for the oculomotor system in maintenance, as well as encoding, of spatial locations. Finally, it remains possible that the oculomotor system is required for the retrieval of spatial information from VSWM, as outlined by scanpath theory (Noton & Stark, 1971) and the looking at nothing phenomenon (Ferreira et al., 2008). The following sections review the evidence for the different functional roles of the oculomotor system in VSWM.

1.5.1 Encoding

One possible role for the oculomotor system in VSWM is that eye movements facilitate encoding of information into VSWM. Consistent with this idea, saccades directed towards locations or items bias entry into VSWM, resulting in more precise representations of those objects and locations (Bays & Husain, 2008; Hanning et al., 2016; Shao et al., 2010; Udale et al., 2022). A notable example of this is described by Bays and Husain (2008). They asked participants to remember either the orientation or location of items in multi-item displays, and showed that the saccade target was remembered more precisely than the other items, even if the saccade item was extinguished before the saccade landed on the item. The mechanism by which encoding occurs might involve the pre-saccadic shift of attention, which is the mandatory shift of attention to the saccade target before the execution of a saccade. This pre-saccadic shift in attention increases sensitivity at the saccade location compared to other locations (Deubel, 1989; Zhao et al., 2012), which might result in that location having a more precise representation in VSWM.

This idea can be extended to explain variability in VSWM capacity, and it may be that saccades represent a way in which VSWM resources are preferentially shifted towards to-be-remembered locations, resulting in a more precise representation in VSWM (Ohl & Rolfs, 2017; Udale et al., 2022). Ohl and Rolfs (2017) demonstrated that saccades aid in consolidating information in VSWM. They showed that VSWM performance was improved for items at a saccade target, even if the saccade target was uninformative about the test location (Experiment One) or was unlikely to be the test location (Experiment Four). They argued that saccades aid in protecting and stabilising information in VSWM. They further proposed that individual differences in this saccadic behaviour might underpin individual differences in VSWM capacity limits, where the efficiency with which saccades are made might reflect the efficiency with which VSWM resources are shifted to ensure that items are encoded and maintained in VSWM with a high degree of precision (Ohl & Rolfs, 2017).

Other scholars have argued that if oculomotor activity has a specific role in encoding in VSWM, enforcing fixation (fixed viewing) during encoding should reduce memory performance relative to when eye movements are unconstrained (free viewing). Experiments comparing free and fixed viewing during encoding have produced mixed results. It has been shown that, in free viewing conditions, the number of fixations on task-relevant items and the duration of these fixations during encoding was positively related to recall performance (Saint-Aubin et al., 2007). However, increasing fixation duration on each item by slowing presentation rate did not improve recall performance for item order (Saint-Aubin et al., 2007). In addition, participants make few on-item fixations when encoding under free viewing conditions, and these on-item fixations are not strongly related to spatial memory performance (Lange & Engbert, 2013; Patt et al., 2014; Souza et al., 2020). These findings seem to suggest that oculomotor activity at the locations of memoranda is suppressed during encoding rather than being activated. Indeed, no difference in spatial span was observed when participants were asked to maintain central fixation compared to when they freely view memoranda during encoding in a Corsi blocks-style task (Czoschke et al., 2019). On first inspection, it seems difficult to explain how memory is enhanced at the saccade target (Bays & Husain, 2008) whereas others find no enhancement of items that have been fixated (Lange & Engbert, 2013; Patt et al., 2014; Souza et al., 2020). However, it is important to note that the pre-saccadic enhancement is only observed for the final item in a sequence (Bays & Husain, 2008; Udale et al., 2022), and not for all items within a sequence of saccades. Given that studies that correlate fixation with performance use many items, only one of which will benefit from fixation, it is easier to reconcile the two sets of data. The benefit of free viewing on memory span will be reduced when averaged across all items, thereby becoming almost undetectable.

An additional reason for studies comparing fixed and free viewing conditions reaching different conclusions is that they do not adequately disentangle the effects of oculomotor control processes from those of attentional control processes, which are known to be tightly coupled (Casteau & Smith, 2019; Smith & Schenk, 2012). It therefore remains possible that the oculomotor system plays a role in encoding because participants may engage in programming of saccades/covertly shifting attention while maintaining fixation, and this might underpin the relatively equal performance between free and fixed viewing observed in some studies (Czoschke et al., 2019). As discussed, the eye-abduction paradigm permits examination of the role of the oculomotor system independently of endogenous attentional processes in VSWM. Pearson et al. (2014) showed that, when eye-abduction was applied during encoding in the Corsi blocks task, there was a small but significant reduction in spatial span when items appeared at locations that could not become the goal of a saccadic eye movement. Notably, memory for visual features was not affected by the manipulation. Under normal viewing conditions, the visual transients associated with the appearance of memory items in Corsi blocks task activate saccade programs in the oculomotor system, and this activation supports the encoding of those spatial locations into VSWM. When eye abduction is applied, this activation in the oculomotor system is disrupted, which interferes with the encoding of information into VSWM. This explanation is consistent with evidence showing that eye abduction disrupts performance on Corsi blocks task, which uses sudden onsets, but not the arrow span task, which relies on symbolic cues to memorised locations (Ball et al., 2013). It is also worth noting that memory span was not abolished, but reduced, in the abducted condition. This finding emphasises that the oculomotor system plays a critical role in optimising encoding into VSWM (Ohl & Rolfs, 2017).

The data discussed in this section seem to suggest that the oculomotor system plays a functional role in encoding information into VSWM. Specifically, it appears that the oculomotor system has two partially dissociable functions. One role is to aid in the distribution of VSWM resources and to improve the precision of representations via the pre-saccadic shift of attention. The pre-saccadic shift of attention prioritises the encoding of information at the saccade goal with a high degree of precision, resulting in a precise representation of the saccade target in VSWM (Bays & Husain, 2008; Udale et al., 2022). The second role is that activation of oculomotor programmes supports the optimal encoding of spatial locations indicated by visual transients, supported by studies using the eye-abduction paradigm (Ball et al., 2013; Pearson et al., 2014).

1.5.2 Maintenance

The mechanism of rehearsal within VSWM was not specified in the original multi-component model of working memory (Baddeley & Hitch, 1974). The idea that motor traces act as associative links between visual snapshots acquired during encoding (Hebb, 1968) was extended to propose that rehearsal in VSWM may take place via an oculomotor loop (Baddeley, 1986). This idea argued that there is significant overlap in VSWM and the oculomotor system, and proposed that spatial locations are encoded as the goals of upcoming saccades, actively maintained via covertly planning saccades to remembered locations, and recalled through saccade plans, which guide selection of the remembered locations. This proposal has been supported by studies showing that irrelevant eye movements during the maintenance period significantly reduce VSWM span (Baddeley & Lieberman, 1980; Postle et al., 2006).

Considerable research has therefore been conducted to examine the role of the oculomotor system in maintaining and rehearsing information in VSWM. Two theoretical positions have largely dominated this debate. The attentional rehearsal view (Awh et al., 1998) proposes that maintenance and rehearsal in VSWM is achieved using attentional refreshing, during which covert attention is directed to different spatial locations in memory to maintain their representation. This view holds that oculomotor activity during rehearsal is an epiphenomenon of the close coupling between covert attention and oculomotor control. This attentional rehearsal hypothesis contrasts with the oculomotor loop hypothesis (Baddeley, 1986), which emphasises the functional role of the oculomotor system. It is difficult to differentiate these theoretical positions using neuroimaging approaches because of the large degree of overlap between regions involved in attention, VSWM, and oculomotor control (Awh & Jonides, 2001; Ikkai & Curtis, 2011; Zhou et al., 2022). Therefore, much of the focus has been on carefully designed behavioural experiments.

One approach has been to examine how holding something in VSWM affects orienting of attention. According to the attentional rehearsal hypothesis, covert attention should be directed to locations held in VSWM (Awh et al., 1998; Awh & Jonides, 2001). Consistent with this, Awh et al. (1998) showed that when a location is held in VSWM, perceptual processing is enhanced at that location. They further showed that spatial working memory performance was disrupted when attention was shifted away from memorised locations towards non-memorised locations during the delay period, suggesting that during the maintenance period attention is shifted towards memorised locations to retain their representation in VSWM. Further study has shown that, when participants are asked to perform limb movements during the maintenance of spatial sequences, spatial working memory performance is decreased (Lawrence et al., 2001). These findings provide additional evidence to support the attentional rehearsal hypothesis; shifts in attention precede both eye and limb movements (Shepherd et al., 1986), such that performance of limb or eye movements during the delay-period of a memory task disrupts the shifting of attention towards memorised locations, thereby reducing VSWM span.

In a similar vein, if the oculomotor system has a functional role in the maintenance of spatial information in VSWM, a correlation between delay-period fixations towards memorised locations and memory performance would be predicted. Consistent with this prediction, Tremblay, Saint-Aubin, et al. (2006) reported a positive correlation between the number of fixations towards a pair of serially presented locations and spatial memory. Similarly, Olsen et al. (2014) found that the degree of similarity between eye movements performed at encoding and eye movements during the retention interval predicts memory performance, but only when information about relative spatial locations was available during recall. This finding has been extended by Lilienthal et al. (2018), who showed that overt rehearsal leads to enhanced memory span, with delay-period fixations on memorised locations predicting memory performance when environmental support was available. However, these findings are not without their limitations. Specifically, in Tremblay, Saint-Aubin, et al. (2006), participants fixated at least one pair of locations on only around two thirds of trials. This indicates that eye movements might make a relatively minor contribution to rehearsal in VSWM. More problematically, in some studies the stimulus array remained on screen throughout the retention interval. This environmental support for rehearsal has been shown to influence both memory performance and delay-period oculomotor activity (Lilienthal et al., 2018; Souza et al., 2020). Indeed, Godijn and Theeuwes (2012) carried out a similar study to Tremblay, Saint-Aubin, et al. (2006) in which participants were asked to either freely view or maintain fixation on a single point during the delay-period of a spatial serial recall task. In this case, no difference in memory performance was found between free and fixed viewing conditions, indicating that in the absence of a stimulus array, delay-period eye movements are not functional, but are a reflection of covert attentional rehearsal processes in VSWM (see also Souza et al., 2020).

An alternative approach is to investigate the effects of holding a location in VSWM on the oculomotor system, specifically on the metrics of saccades. Theeuwes et al. (2005) showed that holding a location in VSWM causes saccade trajectories to deviate away from that location, similar to inhibition of return in attention (Taylor & Klein, 2000). Holding a location in VSWM has also been shown to increase latency of saccades directed to that location and this oculomotor inhibition is associated with decreased perceptual accuracy (Belopolsky & Theeuwes, 2009a, 2009b; Ostendorf et al., 2004). These studies appear to suggest that the oculomotor system plays a functional role in the maintenance of spatial information because deviations to saccade trajectories are driven by activation at the level of the superior colliculus (Godijn & Theeuwes, 2004).

Further support for the functional role of the oculomotor system in maintenance comes from saccadic interference studies, in which participants make eye movements to irrelevant locations during the maintenance period (Lawrence et al., 2004; Pearson & Sahraie, 2003; Postle et al., 2006). Using the selective interference paradigm, Pearson and Sahraie (2003) compared different types of interference performed during the retention interval of the Corsi blocks task, including saccadic interference, limb movement, and covert attentional interference. They showed that saccades performed during the retention interval disrupted spatial span significantly more than other interference conditions, a finding which has been supported in similar studies (Lawrence et al., 2004; Peterson et al., 2019). The finding that saccadic interference is significantly more disruptive than covert orienting is consistent with the claim that the oculomotor system and attentional systems make distinct and dissociable contributions to the maintenance of spatial information. However, making saccadic eye movements necessarily involves shifts of attention. To clarify the extent to which the oculomotor system contributes to maintenance independently of attentional control, Pearson et al. (2014) applied eye-abduction during the retention interval of the Corsi blocks task. They demonstrated that application of eye-abduction, and therefore the disruption of saccadic programming, during the retention interval significantly disrupted spatial span on Corsi blocks task but had no significant effect on performance on the Visual Patterns task. Because eye-abduction does not disrupt endogenous covert attention (Casteau & Smith, 2020; Smith et al., 2012), this study offers strong support for the idea that the oculomotor system has a functional role in maintenance of spatial information in VSWM that is independent of and in addition to the role of attention.

A final approach in examining the role of the oculomotor system in VSWM maintenance is to investigate how delay-period eye movements towards a location affect the representation of that location in VSWM. Ohl and Rolfs (2020) showed that memory for orientation was improved at a memorised location if a delay-period saccade was performed to that location, similar to Awh et al. (1998), who showed enhanced perceptual processing at memorised locations. Ohl and Rolfs (2020) further showed that this effect was spatially selective to the endpoint of the saccade, with very little enhancement for a stimulus at a location near to the saccade target. It should be noted that these studies were examining memory for non-spatial features such as colour and orientation or shape (Hanning et al., 2016; Ohl & Rolfs, 2017, 2018), whereas other studies have emphasised the functional role of the oculomotor system in memory for spatial locations (Ball et al., 2013). Nevertheless, they support the view that the oculomotor system plays a functional role in VSWM maintenance. This functional role in visual memory might occur via enhancement or protection of the representation at a specific location, which aids the representation of non-spatial features (Schneegans & Bays, 2019).

The behavioural experimental approaches discussed indicate that the oculomotor system plays a critical functional role in VSWM maintenance, above that of the role of covert shifts of attention. However, the specific mechanism by which the oculomotor system supports maintenance in VSWM is unclear. Saccadic interference studies may have found a disruptive effect of delay-period saccades because additional information was presented at saccade locations. This additional information might be encoded into VSWM, thereby interfering with or displacing information already in VSWM (Bays & Husain, 2008; Schut et al., 2017; Tas et al., 2016). Schut et al. (2017) showed that the decrease in precision following a delay-period saccade was equivalent to maintaining an additional item in VSWM. Tas et al. (2016) found that performance on a colour change detection task was significantly reduced when participants made a delay-period saccade towards a task-irrelevant object compared to when the task-irrelevant object was presented at fixation or when attention was covertly shifted towards the object. Additionally, delay-period saccades to empty space did not affect VSWM performance, suggesting that the saccade target is automatically encoded into VSWM and this is the mechanism by which delay-period saccades interfere with VSWM maintenance. This finding is consistent with the view that saccade targets are automatically encoded into VSWM (Ohl & Rolfs, 2017) to aid perceptual stability across saccades (Hollingworth et al., 2008). Peterson et al. (2019) provide additional support for this view, showing that guessing responses were increased in a spatial change detection task following the performance of a delay-period saccade compared to shifting covert attention. They further suggested that saccades "smear" working memory representations due to remapping of VSWM representations across saccades. They observed a directionally specific effect of saccades on precision in the change detection task: precision was significantly decreased when the change occurred along the axis of the saccade compared to when the change occurred along the orthogonal axis. This remapping proposal also suggests that VSWM representations and the oculomotor system share a common spatial representation, perhaps in a parietal priority map (Ikkai & Curtis, 2011), because areas that are active during both VSWM and oculomotor activity have a retinotopic organisation that undergoes updating (Golomb et al., 2008; Golomb & Kanwisher, 2012).

There is extensive evidence that both attentional and oculomotor processes are active during VSWM maintenance. Dual-task studies examining the effect of VSWM maintenance on saccade metrics, as well as the effect of delay-period saccade tasks on VSWM demonstrate that the oculomotor system makes a specific and functional contribution to the maintenance of spatial locations in VSWM that is independent of the role of attentional rehearsal. The mechanism of this contribution is not clear, but studies indicate that VSWM representations and saccade programs may be maintained within a common spatial map (Ikkai & Curtis, 2011; Jerde et al., 2012).

1.5.3 Retrieval

A final possibility is that the oculomotor system may be involved in aiding retrieval from VSWM. Early theories proposed that the degree of overlap between gaze patterns at encoding and retrieval is important for memory retrieval (scanpath theory; Noton & Stark (1971)). They proposed that, during encoding, visual features are linked with a motor component. At recall, the motor memory traces are reinstated and the presented visual features are compared to those stored in memory. Studies have shown a correlation between the similarity of oculomotor activity at encoding and retrieval and memory performance (Bochynska & Laeng, 2015; Laeng & Teodorescu, 2002). However, this finding has not been reliably replicated; eye movements made during retrieval are not necessarily a re-enactment of those made during encoding (Johansson et al., 2012). By experimentally manipulating the eye movements performed during recall, Foulsham and Kingstone (2013) showed that responses were more accurate if scanning behaviour during retrieval was constrained to the parts of the image presented during encoding compared to when random portions of the image were presented during retrieval. However, there was no significant recognition advantage for re-viewing the fixation sequence made by either self or another participant at encoding. Foulsham and Kingstone (2013) and Johansson et al. (2012) provide evidence against a strong interpretation of scanpath theory, because the fixation sequence in itself is not a predictor of memory performance.

A less strict interpretation of scanpath theory has been proposed in the looking at nothing phenomenon. According to this view, gaze is directed towards locations held in memory to facilitate the recall of information that was previously presented at that location.

Critically, this theory does not assume that the sequence of fixations is repeated between encoding and retrieval. This approach therefore has a greater degree of flexibility than scanpath theory, reflecting patterns of behaviour that have been observed in visual mental imagery tasks, visual long-term memory tasks, and verbal memory tasks (Brandt & Stark, 1997; Damiano & Walther, 2019; Ferreira et al., 2008; Spivey & Geng, 2001; Wynn et al., 2018). While receiving some empirical support, this theory, and therefore the role of the oculomotor system at retrieval, has been challenged. It has been proposed that oculomotor activity is epiphenomenal to covert shifts of attention towards memoranda at recall (Martarelli & Mast, 2013; Scholz et al., 2018). Scholz et al. (2018) asked participants to remember factual statements associated with locations on a screen. During retrieval, participants were asked to complete a tracking task, either covertly or overtly shifting attention to locations on screen, while judging whether the test statement was true. No difference between overt and covert disruption was found on memory accuracy, which was taken as evidence that looking at nothing is a reflection of covertly shifting attention to the associated location to aid retrieval. Similar results have been reported by Martarelli and Mast (2013), indicating that the oculomotor system has a limited functional role during recall.

The studies discussed with respect to the looking at nothing phenomenon and scanpath theory have mainly examined memory for verbal descriptions or memory for long-term visual memories, rather than VSWM. Early research suggested that the oculomotor system plays a limited role in retrieval during the Corsi blocks and Visual Patterns tasks (Pearson et al., 2014). Indeed, a patient with congenital horizontal gaze palsy has been shown to use a retrocue to guide retrieval in a delayed match-to-sample task, regardless of whether the cued stimuli appeared along the axis of paralysis (Masson et al., 2021). Other empirical research has challenged this conclusion, and shown that a saccade performed after masking of memoranda improved memory performance at that location (Ohl & Rolfs, 2020, 2018). In addition, microsaccades towards the position of the cued stimulus have been observed following presentation of a retro-cue in memory for colour and orientation. This gaze bias was predictive of memory performance (van Ede et al., 2019).

These findings suggest that the oculomotor system is involved in the selection of an item for recall in VSWM, similar to the looking at nothing phenomenon. More recently, Kinjo et al. (2020) examined the function and characteristics of eye movements in VSWM for visual images and locations by manipulating viewing conditions. The looking at nothing phenomenon was observed in free viewing conditions, but there was no difference in memory performance between free and fixed viewing conditions. These results appear to suggest that eye movements play a limited functional role in VSWM retrieval, and that individual differences and task requirements play a large role in the degree to which the oculomotor system is involved in VSWM retrieval. Kinjo et al. (2020) further proposed that there may be two modes for memory retrieval, a non-saccadic mode and a saccadic mode. The non-saccadic mode requires covert shifts of attention around a small internal representation to retrieve information. In contrast, the saccade mode is implemented when the internal representation is large, where covertly shifting attention is insufficient for retrieval from VSWM. This dual-mode approach can explain the seemingly conflicting results from previous studies: task demands may have meant that covertly shifting attention was sufficient for task performance.

The oculomotor system plays an important role in the encoding and maintenance of information, especially spatial locations, in VSWM. Behavioural evidence using a variety of methods provide support for this view, including demonstrating that the oculomotor system impacts what is maintained in VSWM, and the precision with which this information is maintained. The oculomotor system appears to play a critical role in encoding and maintenance, with a less important role in retrieval. However, the nature of the role of the oculomotor system during encoding and maintenance, and how this relates to VSWM capacity, remains unclear.

1.6 Chapter Summary

To briefly summarise this chapter, VSWM is involved in a variety of higher cognitive skills (Baddeley et al., 2021), and VSWM can be separated from verbal working memory both behaviourally and neurophysiologically (Baddeley & Hitch, 1974; but see Morey, 2018). VSWM also appears to be separated between memory for visual features and memory for spatial locations (e.g., Klauer & Zhao, 2004), though there is a degree of functional overlap in these stores (Nee et al., 2013; Schneegans & Bays, 2017). There is continued debate surrounding how the capacity limits in VSWM are characterised. One approach assumes that VSWM has a discrete item limit, where information about up to three to four items can be retained (Zhang & Luck, 2008). An opposing view is that VSWM is a finite but flexible resource, where VSWM precision is dependent on the proportion of resource dedicated to each item (Bays et al., 2009). Empirical studies have offered support for both views (see Fallon et al., 2016; Fukuda et al., 2010; Ma et al., 2014), but the resource model appears to have better explanatory power, and neural network models based on this model have offered biologically plausible mechanism by which noise in VSWM representations might arise (Bays, 2014, 2015).

The oculomotor system appears to play an important functional role in VSWM, especially in spatial working memory. The role of the oculomotor system is independent of and additional to the role of attention, especially during the encoding and maintenance stages in spatial working memory (e.g., Pearson et al., 2014). Because there is extensive neural overlap between the oculomotor system and VSWM, a range of behavioural studies have been carried out to examine the functional role of the oculomotor system. Studies have utilised a variety of methods including experimentally manipulating oculomotor behaviour, limiting the ability to execute saccades using the eye abduction paradigm, and examining the bidirectional links between VSWM and oculomotor activity by examining the effects of VSWM on saccade characteristics. A functional role of the oculomotor system in VSWM is consistent with the oculomotor loop hypothesis (Baddeley, 1986) in which spatial locations are encoded as the goals of upcoming saccades, potentially via the pre-saccadic shift in attention. These locations are actively maintained by the oculomotor system, potentially via covertly planning saccades towards the maintained locations. The role of the oculomotor system at retrieval is less clear, but recent evidence suggests that the degree of involvement depends on task demands, where saccade plans guide selection of memorised material.

1.6.1 Research Aims

There is little research examining the nature of spatial working memory and the specific role of the oculomotor system. The continuous report task has not been used to examine spatial working memory as often as visual working memory (Pertzov et al., 2012; Schneegans & Bays, 2016). As a consequence, the representation of spatial locations in VSWM and the distribution of resources within spatial working memory remains unclear. Additionally, studies examining the role of the oculomotor system in VSWM rely on binary response tasks such as the Corsi blocks (Pearson et al., 2014) and change detection tasks (Peterson et al., 2019), so the nature of saccadic interference effects and the specific role of the oculomotor system on spatial working memory remains unexamined. The implication of using these tasks is that there is limited scope to examine the potential sources of recall error, which would provide greater insight into the representation of information within VSWM and the role of the oculomotor system in VSWM.

The aims of this thesis are twofold:

1. to examine the representation of spatial locations, and distribution of resources, within VSWM; *and*
2. to examine the specific role of the oculomotor system in VSWM.

Across four studies, these two aims were investigated. *Chapter Two* examined the nature of spatial working memory capacity limitations and the distribution of VSWM resources in spatial working memory across set sizes using a spatial continuous report task. *Chapter Three* more directly tested the cortical maps hypothesis by examining whether and how eccentricity might constrain the distribution of VSWM resources and the representation of spatial locations in VSWM across the visual field. *Chapter Four* investigated the distribution of resources across serial positions in sequences of spatial locations in VSWM using whole- and partial-report continuous report tasks. Finally, *Chapter Five* directly compared the effect of saccadic interference in a visual and spatial continuous report task to examine the effects of delay-period activation of the oculomotor system on response errors in visual and spatial working memory.

Preface to Chapter Two

Memory for spatial locations is important for supporting many functions of cognition and behaviour, such as motor control (Van der Stigchel & Hollingworth, 2018). The continuous report task provides a sensitive measure of VSWM, giving an insight into how the sources of recall error in memory of visuospatial features might change in different task conditions (Zokaei et al., 2015). The primary focus of VSWM research has been on the nature of representations of visual features such as colour and orientation (Fallon et al., 2016). When compared to the study of visual features, the continuous report task has not been used as widely to examine the representation of spatial locations in VSWM. Because of the lack of evidence that the continuous report task can be reliably used to examine memory for spatial locations, my first study aimed to replicate and extend previous work using such a task (Schneegans & Bays, 2016). Schneegans and Bays (2016) is one of only two published studies that have used a spatial version of the continuous report task. I decided to firstly try to replicate the results reported by Schneegans and Bays (2016) to verify the use of a spatial continuous report task to measure spatial working memory.

This study attempted to retain the general methods reported by Schneegans and Bays (2016), such as the number of trials per condition, the stimulus timing, and the stimulus size. Using the parameters reported by previous work that has used such a similar task provided a useful starting point for experimental design throughout this thesis.

Chapter Two has been submitted for publication in Vision Research with authors Siobhan McAteer, Anthony McGregor, and Daniel T Smith.

Chapter 2

Saccadic Programming May Produce a Non-linear Distribution of Resources in Spatial Working Memory

The capacity of visuospatial working memory (VSWM) is limited. However, there is continued debate surrounding the nature of this capacity limitation. The resource model (Bays et al., 2009) proposes that VSWM capacity is limited by the precision with which visuospatial features can be retained. Many studies have shown a monotonic decrease in precision for visual features with increases in set size. However, few studies have examined this relationship within spatial working memory. The current study examined the changes in precision and the sources of recall error in memory for spatial locations across increases in set size. Consistent with the resource model there was an exponential increase in localisation error and monotonic increases in the probability of misbinding and guessing with increases in set size. These data indicate that items are encoded into VSWM with increasing noise as more items are to be remembered, providing additional support for a resource model of VSWM. However, an unexpected result was that imprecision did not increase between set sizes of two and eight. It was hypothesized that guiding the mouse pointer to the memorized location afforded a look-then-click strategy in which participants fixated the memorized location to accurately position the pointer which many have compensated for the increased imprecision of the underlying memory representations at set sizes of two or more. This result illustrates the flexibility of the action system in producing accurate, memory guided movements even under conditions where the underlying memory representation of the action goal is noisy.

2.1 Introduction

Although we can perceive a rich visual world, we cannot retain all the information presented to us at any given time (Adam et al., 2017; Luck & Vogel, 2013; Ma et al., 2014). Visuospatial working memory (VSWM) is the cognitive system that allows us to temporarily maintain and manipulate limited amounts of visual and spatial information about objects (Baddeley, 2000). There is continued debate surrounding the nature of the capacity limitation in VSWM. One influential proposal is that there is a flexible limit on VSWM capacity, where the limit is based on the fidelity with which items can be retained in VSWM (Bays et al., 2009; Zokaei et al., 2011). This resource model of VSWM draws primarily on studies that utilise the continuous report task (Wilken & Ma, 2004), which requires participants to reproduce a visual feature, such as colour or orientation of a probe after a short delay, along a continuous dimension. The distribution of recall error can therefore be examined to probe the sources of recall error and provide an insight into the precision with which representations are encoded and stored, providing a more sensitive measure of VSWM compared to span methods (Zokaei et al., 2015).

Using this approach, Bays et al. (2009) showed that precision significantly decreased when set size increased, even with an increase from one to two items. The decrease in precision was accompanied by increasing misbinding errors, where a feature of a non-probed item was reported, as set size increased, even up to six items. This finding indicates that all visual features in an array are encoded into VSWM, but with increasing noise as more features need to be retained. Bays et al. (2009) argued that when participants are retrieving items from VSWM, all visual and spatial features of each item must be correctly bound together. As a consequence, when participants incorrectly respond on a given trial, they may be responding with the feature of another presented item from the original array (misbinding), or they may be responding at random (guessing). Consistent with this view, when misbinding errors are accounted for, the proportion of variance in the data explained by guessing significantly decreases (Bays et al., 2009).

This finding has been replicated across a variety of non-spatial (visual) features, including colour, orientation, and motion direction (Gorgoraptis et al., 2011; Zokaei, Ning, et al., 2014; Zokaei et al., 2011). However, fewer studies have modelled the precision and error in spatial working memory. Given the well-established dissociations between memory for visual features and spatial locations in VSWM (Darling et al., 2006; Darling et al., 2009), it is likely that the pattern of response errors in memory for spatial locations might differ from those observed in memory for visual features.

Pertzov et al. (2012) modified the continuous report task to probe memory for locations, by asking participants to relocate objects to their original locations at test. They found that, as set size increased from one to five objects, localisation error increased. Moreover, the probability of committing misbinding errors increased with set size. This finding indicates that the representation of spatial locations within VSWM can be characterised by the resource model. However, the use of naturalistic objects in this study is problematic due to their complexity, which may have reduced precision overall (Chen et al., 2017).

Schneegans and Bays (2016) addressed these criticisms by presenting coloured dots to participants in a spatial continuous report task. As set size increased from one to eight items, they found a monotonic increase in localisation error with a corresponding increase in the prevalence of misbinding errors. This increase in misbinding errors indicates that all items had been encoded into VSWM. There was also a monotonic increase in the imprecision of memory representations as more items were to be retained, with a statistically significant increase between four and eight items. However, Schneegans and Bays (2016) had the fixation cross present throughout each trial, which may have allowed for the global configuration of the array to be encoded, without the absolute positions of each item being encoded and retained (Jiang et al., 2000). The use of a landmark would therefore reduce the cognitive load of the task, leading to an improvement in overall VSWM performance. Furthermore, only a limited number of set sizes were examined (1, 2, 4, and 8 items), so the claim of a linear increase in localisation error with increases in set size should be treated with caution.

The current experiment therefore sought to examine whether memory for spatial locations in the absence of a landmark is characterised by a monotonic increase in localisation error, imprecision, and misbinding with increasing set size.

2.2 Method

2.2.1 Participants

We carried out an *a priori* power analysis using G*Power v3.1.9.7 (Faul et al., 2009) to determine the required minimum sample size. Based on Schneegans and Bays (2016), we required a sample of at least two participants to detect a large effect of set size on response error ($\eta_p^2 = .83$) with 95% power and an alpha level of .05. We recruited 14 volunteers ($M_{age} = 20.43$ years, $SD_{age} = 1.34$, 9 females, 4 males, 1 non-binary, 13 right-handed) from the Department of Psychology participant pool. Undergraduate participants who were enrolled on the Psychology course at Durham University were credited with participant pool credit for their time. The study received ethical approval from Durham University Psychology Department Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

2.2.2 Design

We used a within-subjects design. The independent variable was set size, with eight levels (set sizes 1 to 8). The dependent variable was localisation error, measured by the Euclidean distance between the participant responses and the original location of the probe item. Imprecision, probability of reporting a target, probability of misbinding, and the probability of guessing, which were obtained from the best fitting mixture model (Bays et al., 2009), were additional dependent variables.

Participants completed one practice block comprising eight trials, one of each set size, to familiarise themselves with the task. The practice block was identical to the experimental blocks, with the exception that participants were shown their own response as well as the original location of the probe stimulus after submitting their response. They then completed 400 trials, randomised across 10 blocks, with each set size being tested 50 times.

2.2.3 Stimuli and apparatus

The task was programmed using Matlab R2019a, using the psychophysics toolbox (Kleiner et al., 2007), and was based on Schneegans and Bays (2016). The stimuli consisted of arrays comprising between one and eight coloured dots (diameter of each dot = 1° VA) and a fixation cross (0.76° VA x 0.76° VA) positioned at the centre of the screen. The fixation cross was present only at the beginning of each trial and was not present during encoding, maintenance, recall. The colours of each dot were chosen without repetition from a bank of eight discriminable colours: red, orange, yellow, green, cyan, blue, magenta, and purple. The visual mask comprised 800 coloured dots, like those presented at encoding, filling the annular space five to ten degrees of visual angle around central fixation. Participants' gaze was monitored using a tower-mounted EyeLink 1000 eye tracker (SR Research). Stimuli were presented on a 20-inch CRT screen with a refresh rate of 85Hz. Participants sat 60cm from the computer screen, with the centre of the screen at eye level.

2.2.4 Procedure

Participants were instructed to maintain fixation on the centre of the screen throughout each trial. Trials began with presentation of a fixation cross at the centre of the screen for one second followed by a blank screen for 0.5s. The stimulus array, comprising between one and eight coloured dots, was then presented for two seconds. The location of each dot was randomly chosen within the annular region between five and ten degrees of visual angle around central fixation. Each dot was positioned at least 1.5° of visual angle from other dots to ensure no overlap in their locations. After presentation of the array, the visual mask was presented for 0.1s. A blank screen was then shown for 0.9s. At test, one of the stimuli from the array was randomly chosen and presented in the centre of the screen. Participants were required to move the mouse to click the location on screen where it first appeared. Participants could respond with any location on screen as they were unaware that the stimulus presentation area was restricted. There was no time limit for responding. A one second blank screen followed the response period, before the beginning of the next trial. Participants were permitted to take a self-paced break between blocks. An example trial is shown in Figure 2.1.

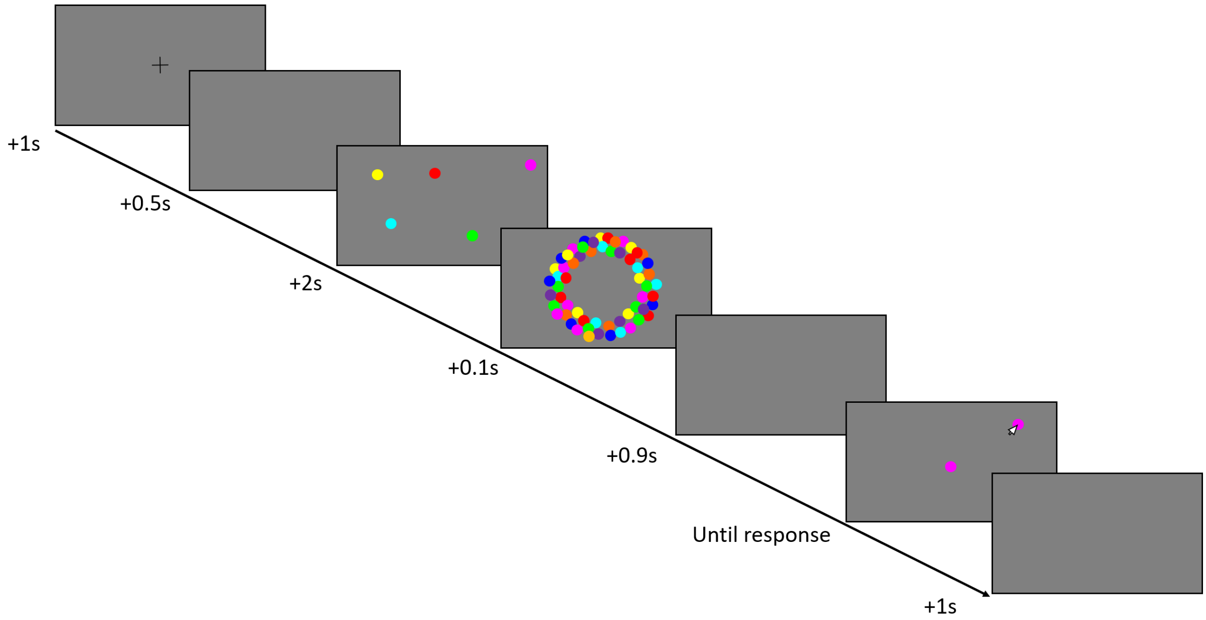

Figure 2.1: An example trial in Experiment One. Participants were shown an array of between one and eight dots. After a short delay, they were asked to click on screen where one of those dots first appeared.

2.3 Results

All inferential tests were carried out in R (R Core Team, 2019), using the `rstatix` package (Kassambara, 2019). Greenhouse-Geisser correction was applied if the assumption of sphericity was violated. Trials in which average saccade amplitude exceeded two degrees of visual angle during encoding and maintenance were removed from analysis to control for eye movements. This resulted in the full datasets of two participants being excluded due to missing data. Of the remaining 12 participants, 14.56% of trials were excluded due to eye movements.

Localisation error, measured by the Euclidean distance between the probed location and the participant's response on screen, was first examined to gain an overview of the pattern of response error. We then fit a series of mixture models to examine the sources of recall error and to gain a greater insight into the ways in which recall error varied with changes in set size. Localisation error can be considered a proxy for precision, but it does not assume the distribution from which the response is drawn.

2.3.1 Localisation Error

Mean localisation error is displayed in Figure 2.2. There is a clear increase in localisation error as set size increases, as confirmed with one-way repeated-measures ANOVA; $F(3.45, 37.97) = 24.18$, $p < .001$, $\eta_p^2 = 0.69$. Bonferroni-Holm corrected pairwise comparisons between adjacent set sizes revealed no significant differences; $p \geq 0.069$.

Simple linear regression was then carried out to examine whether set size predicts localisation error (Figure 2.2). Set size was a significant predictor of localisation error; $m = 21.7$, $SE = 2.09$, $p < .001$. However, the constant was not significant in this model; $c = 16.86$, $SE = 10.58$, $p = .114$. Additionally, this model accounted for only 53% of variance in the data; ${R^2}_{adjusted} = 0.53$, $F(1,\ 94) = 107.32$, $p < .001$. Examination of the data (Figure 2.2) suggested that an exponential model might provide a better fit to the data. An exponential model in the form $localisation\ error = a * exp(b * set\ size)$ was fit to the data. Both the constant [$a = 40.08$, $SE = 5.34$] and set size [$b = 0.21$, $SE = 0.02$] were significant; $p < .001$. Akaike Information Criterion values corrected for sample size (AICc) was calculated for both models to assess their relative fits to the data. Comparison of AICc values revealed that the exponential model provided a better fit to the data compared to the linear model; $\Delta AICc = 9.91$.

2.3.2 Mixture Modelling

2.3.2.1 Model comparison

Mixture modelling was then carried out using MemToolbox2D (Grogan et al., 2020; Suchow et al., 2013) to examine which model best fit the response data for each participant. We firstly compared the fit of the two-component mixture model (Zhang & Luck, 2008), which comprises a normal and uniform distribution to that of Bays et al. (2009), which

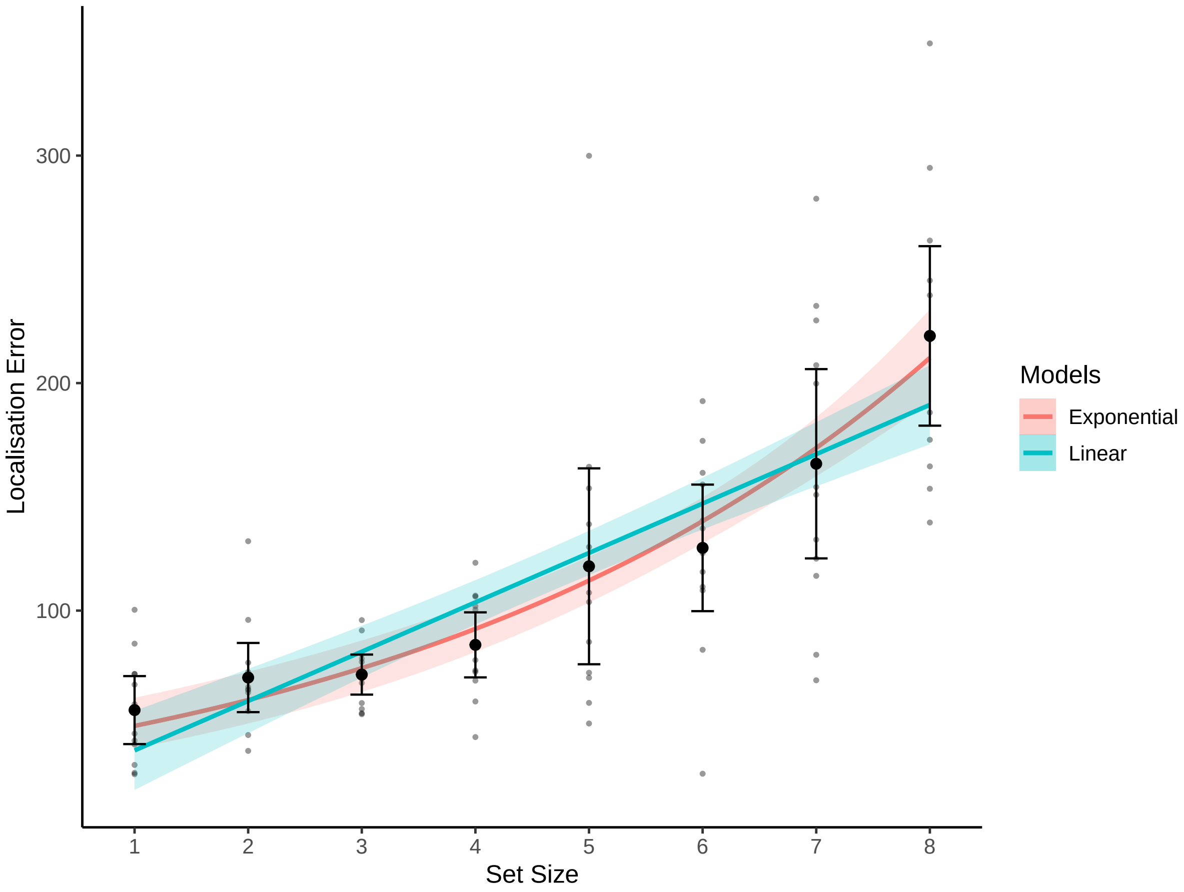

Figure 2.2: Localisation error as a function of set size for each participant, with the best-fitting linear and exponential models plotted. The shaded regions represent 95% confidence intervals. Mean values are shown in black, with the error bars representing 95% confidence intervals

comprises a normal distribution, misbinding errors and a uniform distribution. We also compared these models to a model that comprised only a normal distribution centred on the target location (Figure 2.3). The best fitting model across all participants, with the lowest AICc, was one that included a normal distribution centred on the target location, misbinding errors, and guesses corrected by assuming that responses were sampled from the annulus within which stimuli could appear, although this was only a marginally better fitting model compared to that which assumed no response sampling and was no different to the model without response sampling in some participants (Bays et al., 2009); *normal distribution only:* $M_{\Delta AICc} = 1053.57$; *normal distribution with guessing:* $M_{\Delta AICc} = 717.83$; *normal distribution with guessing, misbinding, and no response sampling:* $M_{\Delta AICc} = 6.04$.

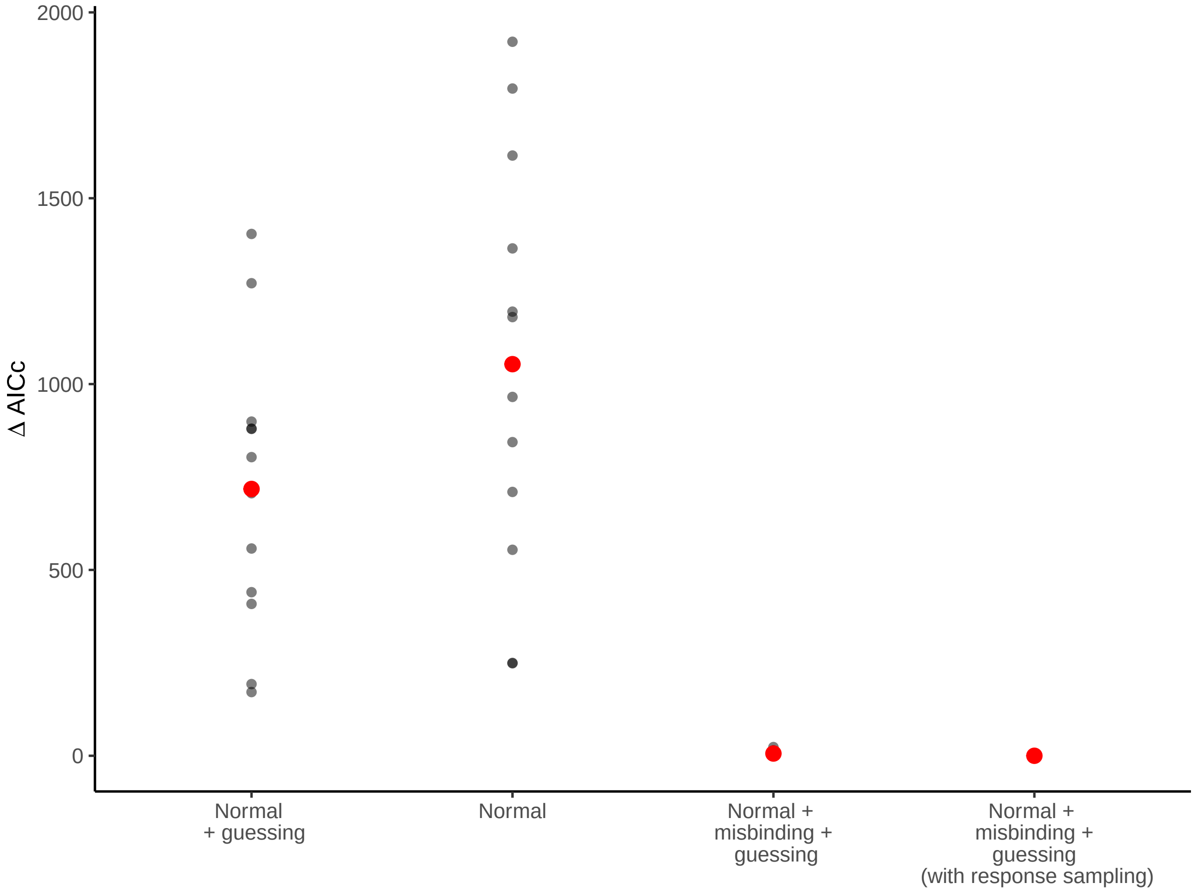

Figure 2.3: Difference in AICc scores of each mixture model for each participant compared to best fitting model. Mean difference is highlighted in red.

2.3.2.2 Sources of recall error

We fit the best fitting model, which included response sampling, to each set size condition and analysed how the sources of error changed across set sizes. Analysis of imprecision (Figure 2.4A) revealed a significant main effect of set size; $F(2.59,\ 28.48) = 3.58$, $p = .031$, $\eta_p^2 = 0.24$. Bonferroni-Holm corrected pairwise comparisons showed a significant increase in imprecision when set size increased from one item ($M = 41.32$, $SD = 13.68$) to two items ($M = 55.2$, $SD = 14.93$); $p = .016$. No other differences were significant; $p \geq 0.768$.

For the probability of reporting the target (Figure 2.4B), there was a main effect of set size; $F(2.45,\ 26.93) = 28.75$, $p < .001$, $\eta_p^2 = 0.72$. Bonferroni-Holm corrected pairwise comparisons indicated that participants were significantly more likely to report the target location at set size 3 ($M = 0.98$, $SD = 0.04$) than at set size 4 ($M = 0.92$, $SD = 0.08$).

The differences between set size 4 and set size 5 (M = 0.78, SD = 0.18), and set size 7 (M = 0.68, SD = 0.16) and set size 8 (M = 0.54, SD = 0.23) were also significant; $p \leq 0.045$. No other comparisons were significant; $p \geq 0.345$.

For the probability of misbinding (Figure 2.4C), a significant main effect of set size was observed; $F(3.04, 33.45) = 10.76$, $p < .001$, $\eta_p^2 = 0.5$. Bonferroni-Holm corrected pairwise comparisons showed that participants were significantly more likely to report a non-target at set size 4 (M = 0.09, SD = 0.08) compared to set size 3 (M = 0.02, SD = 0.04); $p = .031$. No other comparisons were significant; $p \geq 0.076$.

Finally, for the probability of guessing (Figure 2.4D), there was a significant main effect of set size; $F(7, 77) = 8.92$, $p < .001$, $\eta_p^2 = 0.45$. However, Bonferroni-Holm corrected pairwise comparisons revealed no significant differences between set sizes; $p \geq 0.061$.

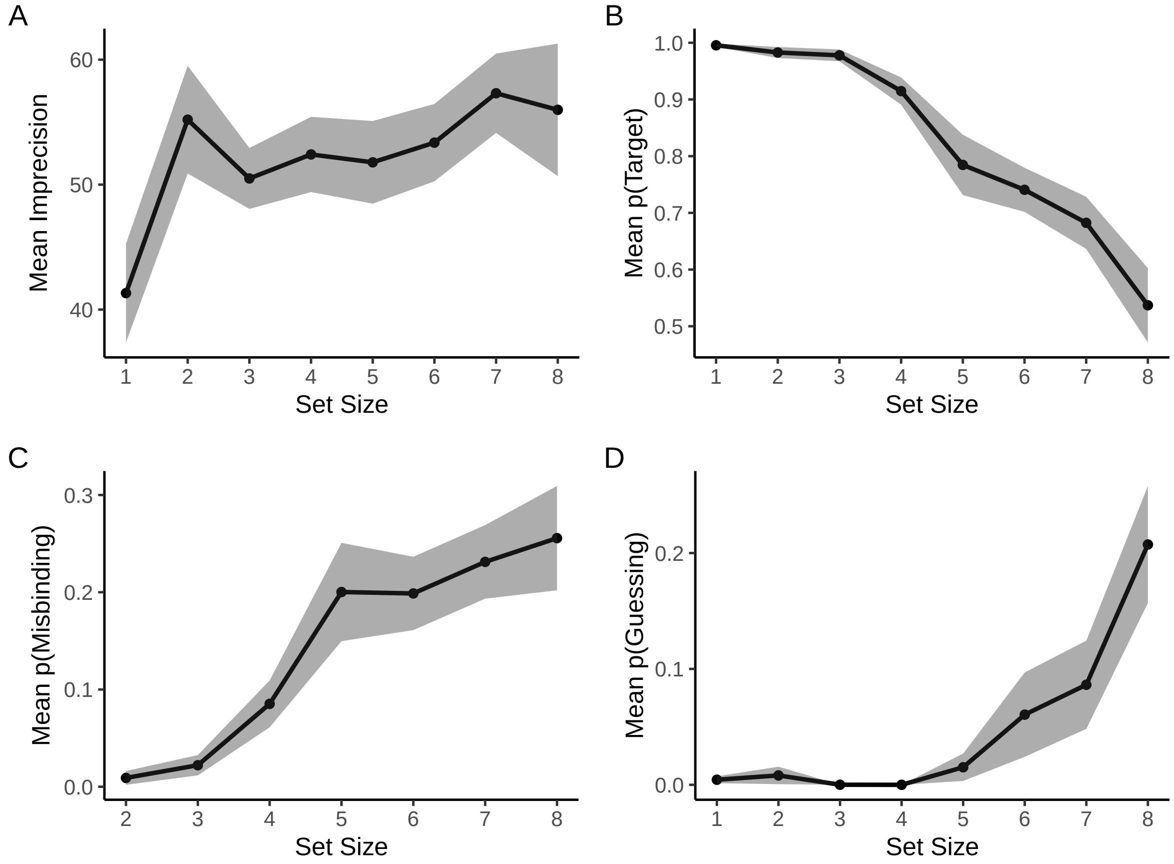

Figure 2.4: Mean imprecision (a) probability of reporting the target location (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) as a function of set size. Shaded regions represent SEM.

2.4 Discussion

This experiment showed that localisation error increased exponentially as set size increased from one to eight items. Mixture modelling (Bays et al., 2009; Grogan et al., 2020) showed that the best fitting model to our response data was one that includes misbinding errors (Bays et al., 2009) compared to a model that only includes a normal distribution and guessing (Zhang & Luck, 2008). When we examined the effects of set size on the parameters of this model, the probability of reporting the target location decreased with set size, accompanied by increases in misbinding and guessing, indicating that items were encoded into VSWM, but with increasing noise as set size increased. These findings are broadly consistent with previous work supporting the resource model of VSWM (Bays et al., 2009; Pertzov et al., 2012; Schneegans & Bays, 2016).

However, there are two ways in which our results differed from Schneegans and Bays (2016). Firstly, Schneegans and Bays (2016) reported that a linear model provided a good fit to their localisation error data. This linear effect was surprising, given the prior findings in non-spatial memory, where the relationship between recall error and set size follows a power law (Bays & Husain, 2008). In contrast, we found that localisation error changed rapidly at set sizes larger than four items, with the relationship between set size and localisation error being better characterised by an exponential model compared to a linear model [*linear model*: ${R^2}_{adjusted} = 0.53$, AICc = 1016; *exponential model*: AICc = 1006.09]. This observation suggests that when more items are to be remembered, less resource is directed to these items, resulting in greater noise in their representations. The most probable explanation for this apparent discrepancy is simply that by jumping from a set size of 4 to a set size of 8, Schneegans and Bays (2016) lacked the granularity to detect the exponential relationship.

Secondly, although we observed a monotonic increase in localisation error with set size, reflecting the fact that the absolute distance between the probed location and response location increased as set size increased, we observed no significant changes in imprecision after set size 2. In contrast, Schneegans and Bays (2016) reported a monotonic increase in both error and imprecision, which was largest between set size 4 and set size 8. When considering these data, it is important to recall that localisation error does not discriminate between correct responses that land near the veridical location, guesses, and misbinding errors, where the response is close to a non-probed location. In contrast, imprecision reflects the distribution of responses on correct trials only. The combination of a steep increase in localisation error and guessing errors, but flat curve for imprecision, suggests that when participants correctly recalled the probed location, they did so with a high degree of precision but were less likely to recall the correct location as set size increased. On first inspection, this pattern appears to indicate that imprecision in spatial working memory is unaffected by set size for set sizes more than two items, which is difficult to reconcile with Schneegans and Bays (2016) and previous studies in visual working memory, where a significant decrease in precision with each additional presented item is reliably reported (Ma et al., 2014).

There are two potentially important methodological differences between the current study and that of Schneegans and Bays (2016). Specifically, in the current study, fixation was enforced during encoding and maintenance but not during the response phase, and the hand was visible during probe localisation. In contrast, Schneegans and Bays (2016) occluded the hand during the experiment. They also recorded eye-movements, but did not report whether participants were instructed to maintain central fixation. Visually-guided localisation tasks, like the one used in the current study, afford a response strategy in which participants program and execute a combined eye-hand movement that initially fixates the memorised location, then move the pointer to that location (de Brouwer et al., 2021). Saccade programming is thought to be achieved via population coding, in which multiple units are activated for a specific location within a map and the saccade trajectory is determined by the weighted average of the activated population (Lee et al., 1988; Sparks et al., 1976). A consequence of this averaging is that small changes in the direction and amplitude of saccades are produced when multiple items are presented. Critically, Arai et al. (2004) found that increasing the number of distractors from none to one resulted in a decrease in initial dispersion and saccade latency, but increasing the number of distractors by more than one had minimal effects on the saccade metrics. This finding is consistent with the idea that the contributions of locations not intended to be the target of the upcoming saccade are relatively small, resulting in a small amount of noise in the response due to the averaging of activity.

It seems reasonable to suggest that when the hand is visible and the response is a visually-guided action, selection of the correct location in memory triggers a saccade averaging process to program the eye movements necessary to fixate the correct location and guide the mouse response. This process of saccade averaging will produce movements that are invariant with set sizes of two or more (Arai et al., 2004), therefore preserving the precision in the motor response despite an increase in noise in the underlying memory representation. The procedure used by Schneegans and Bays (2016) did not permit visually-guided responses because the hand was occluded, and this may have disrupted the compensatory effects produced by saccade averaging. This explanation may also account for our previous observation that saccadic interference increases guessing but not imprecision when a spatial localisation task is used (McAteer et al., 2023)[1]. The process of selecting a memorised item for a saccade target among distractors may also trigger the reallocation of resource from non-targets to the movement goal, thus maintaining precision (see Udale et al., 2022), even in the presence of many distractors.

There are two caveats to the current experiment which should be considered when interpreting these data. Firstly, there was some loss of data due to our exclusion criteria regarding eye movements. However, the medium and large effect sizes found for localisation error, imprecision, target responses, and misbinding are similar to previous findings (Pertzov et al., 2012; Schneegans & Bays, 2016) and the overall pattern of results did not change when data from all participants were analysed (see S1). Secondly, the distance of stimuli from fixation was not controlled in either the current experiment or Schneegans and Bays (2016), which may be important given there is evidence that attentional processing is less efficient with increasing set size and distance from fixation (Carrasco et al., 1995; Wolfe et al., 1998), and that changes in eccentricity influence VSWM encoding and

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[1] This refers to the data presented in Chapter Five.

maintenance (McAteer et al., 2021)[2].

In summary, our finding of a monotonic increase in error as set size increases is consistent with Schneegans and Bays (2016), demonstrating that memory for spatial locations becomes noisier as set size increases. Additionally, by using a larger range of set sizes, it was shown that localisation error increases exponentially with set size, rather than linearly, which supports that precision in VSWM is related to the proportion of resource directed to each item in VSWM. Imprecision in spatial working memory did not significantly increase when set sizes was larger than 2. It was hypothesized that the task afforded a visually-guided response and the saccade averaging processes associated with fixating the memorized location compensated for the increased imprecision of the underlying memory representations at set sizes of 3 or more. This result illustrates the flexibility of the action system in producing accurate, memory guided movements even under conditions where the underlying memory representation of the action goal is noisy. Comparison of models of VSWM and examination of the sources of recall error provide additional support for the resource model of VSWM.

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[2] This refers to the data presented in Chapter Three.

2.5 Supplementary Materials

2.5.1 S1: Experiment 1 analysis (no trials excluded)

2.5.1.1 Localisation Error

The results reported here include all data. Mean localisation error, measured by Euclidean distance between the probed location and the participant's response, is displayed in Figure 2.5. One-way repeated-measures ANOVA revealed a significant effect of set size; F(2.75, 35.81) = 73.95, $p < .001$, $\eta_p^2 = 0.85$. Bonferroni-Holm corrected pairwise comparisons between adjacent set sizes revealed significant differences between all adjacent set sizes ($p \leq 0.031$), except between set sizes 2 and 3; $p = .380$).

Simple linear regression was then carried out to examine whether set size predicts localisation error (Figure 2.5). Both set size [$m = 20.84$, $SE = 1.33$, $p < .001$] and the constant [$c = 17.88$, $SE = 6.71$, $p = .009$] were significant in this model. This model accounted for 69% of variance in the data; $R^2{}_{adjusted} = 0.69$, $F(1,\ 110) = 245.76$, $p < .001$. An exponential model in the form $localisation\ error = a * exp(b * set\ size)$ was also fit to the data. Both the constant [$a = 42.19$, $SE = 3.56$] and set size [$b = 0.19$, $SE = 0.01$] were significant; $p < .001$. Corrected Akaike Information Criterion (AICc) values revealed that the exponential model provided a better fit to the data compared to the linear model; $\Delta AIC = 10.58$.

2.5.1.2 Mixture modelling

2.5.1.2.1 Model comparison Mixture modelling was then carried out using MemToolbox2D (Grogan et al., 2020; Suchow et al., 2013) to examine which model best fit the response data for each participant. We firstly compared the fit of the two-component mixture model (Zhang & Luck, 2008), which comprises a normal and uniform distribution to that of Bays et al. (2009), which comprises a normal distribution, misbinding errors and a uniform distribution. We also compared these models to a model that comprised only a normal distribution centred on the target location. The best fitting model across all

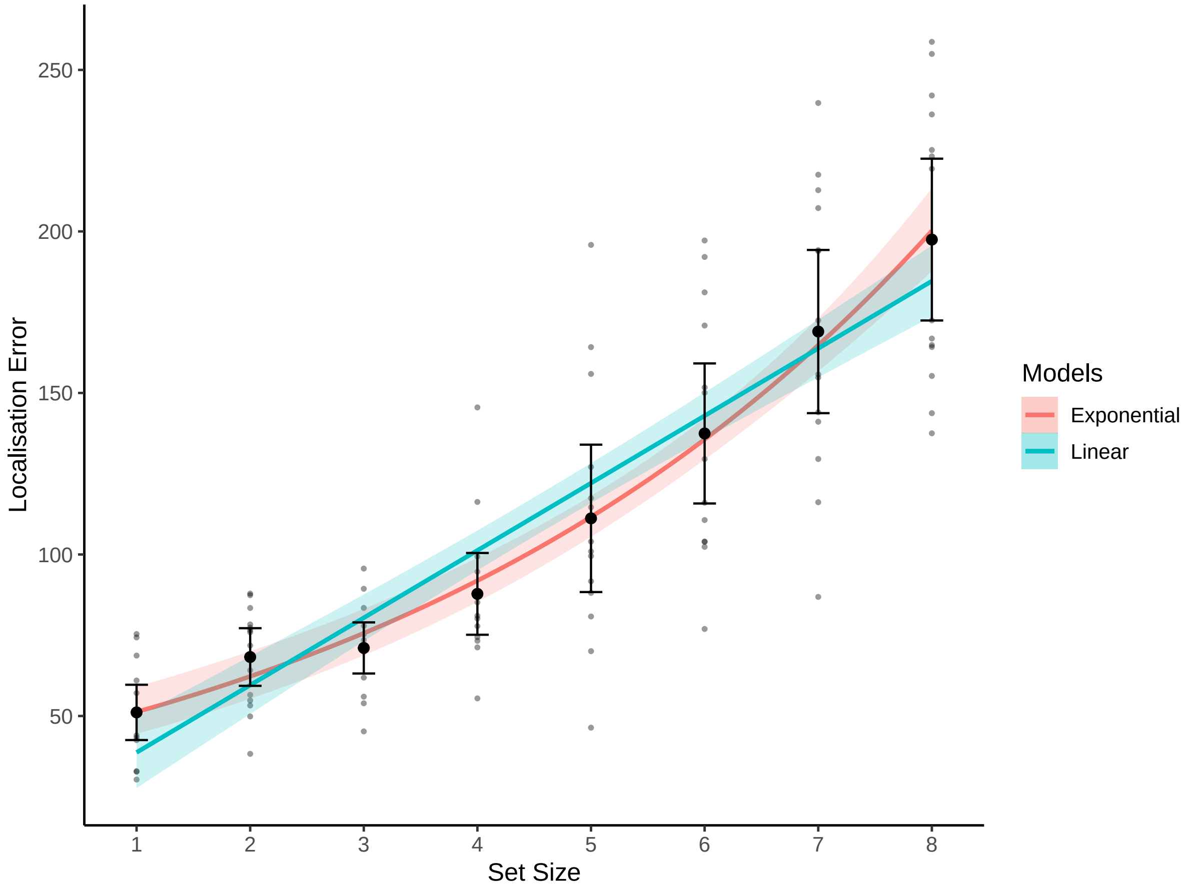

Figure 2.5: Localisation error as a function of set size for each participant, with the linear and exponential models plotted. The shaded regions represent 95% confidence intervals. Mean values are shown in black, with the error bars representing 95% confidence intervals.

participants, with the lowest AICc, was one that included a normal distribution centred on the target location, misbinding errors, and guesses (Bays et al., 2009); *normal distribution only:* $M_{\Delta AICc} = 1816.25$; *normal distribution with guessing:* $M_{\Delta AICc} = 1232.58$. This is displayed in Figure 2.6.

2.5.1.2.2 Sources of recall error A significant main effect of set size was found for imprecision (Figure 2.7A); $F(7,\ 91) = 11.13$, $p < .001$, $\eta_p^2 = 0.46$. Bonferroni-Holm corrected pairwise comparisons revealed a significant increase in imprecision between set size 1 ($M = 39.98$, $SD = 10.93$) and set size 2 ($M = 52.12$, $SD = 10.68$); $p = .003$. No other differences were significant; $p \geq 0.472$.

A significant main effect of set size was found for the probability of reporting the target location (Figure 2.7B); $F(2.14,\ 27.79) = 61.13$, $p < .001$, $\eta_p^2 = 0.82$. Bonferroni-Holm

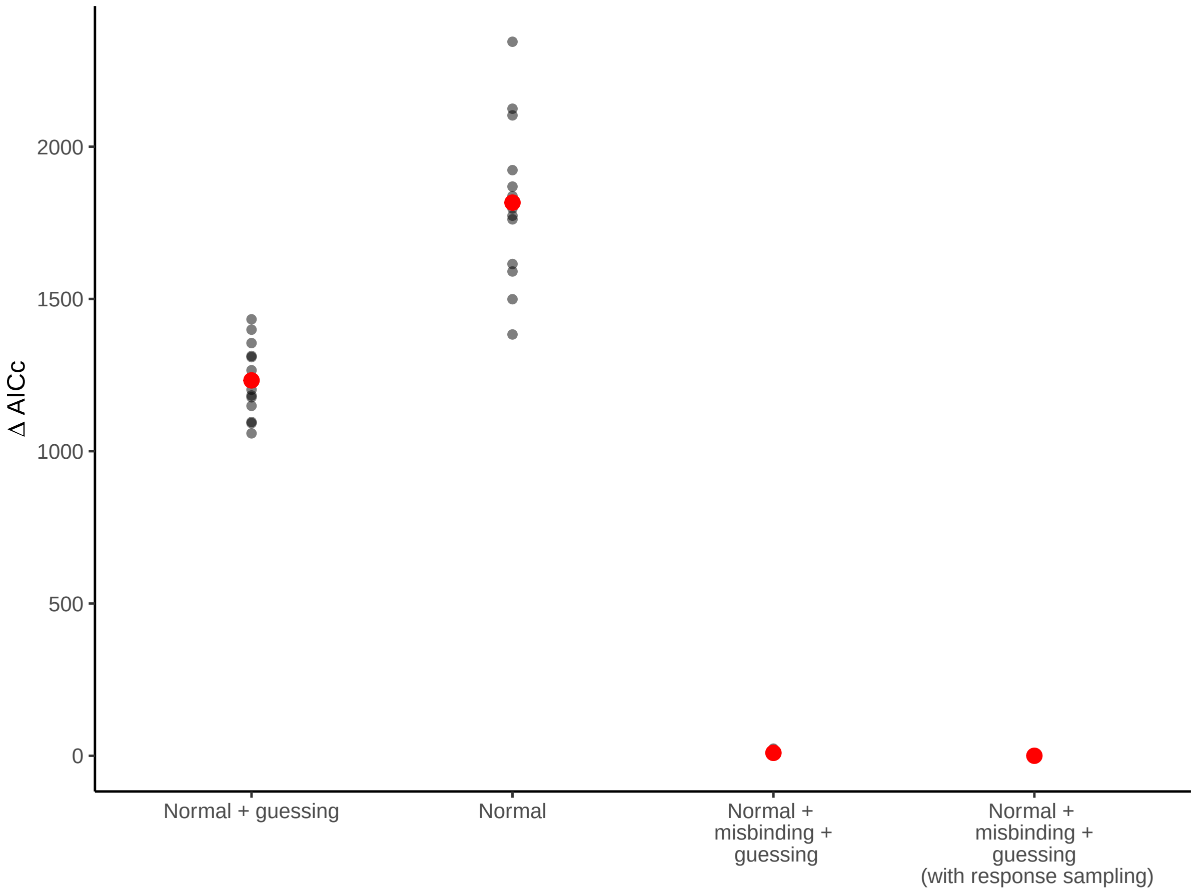

Figure 2.6: Difference in AICc scores of each mixture model compared to best fitting model for each participant. Mean difference is highlighted in red.

corrected pairwise comparisons revealed significant differences between all set sizes ($p \leq 0.044$) except between set size 1 and 2; $p = .240$.

A significant main effect of set size was observed for the probability of misbinding (Figure 2.7C); $F(2.43, 31.65) = 15.55$, $p < .001$, $\eta_p^2 = 0.54$). Bonferroni-Holm corrected pairwise comparisons showed that participants were significantly more likely to report a non-target at set size 4 ($M = 0.08$, $SD = 0.07$) than at set size 3 ($M = 0.02$, $SD = 0.03$), at set size 5 ($M = 0.15$, $SD = 0.12$) compared to set size 4, at set size 7 ($M = 0.21$, $SD = 0.13$) compared to set size 6 ($M = 0.19$, $SD = 0.14$), and at set size 8 ($M = 0.27$, $SD = 0.19$) compared to set size 7; $p \leq 0.006$.

A significant main effect of set size was found for the probability of guessing (Figure 2.7D); $F(1.84, 23.86) = 8.52$, $p = .002$, $\eta_p^2 = 0.4$. However, Bonferroni-Holm corrected pairwise comparisons revealed no significant differences between set sizes; $p \geq 0.680$.

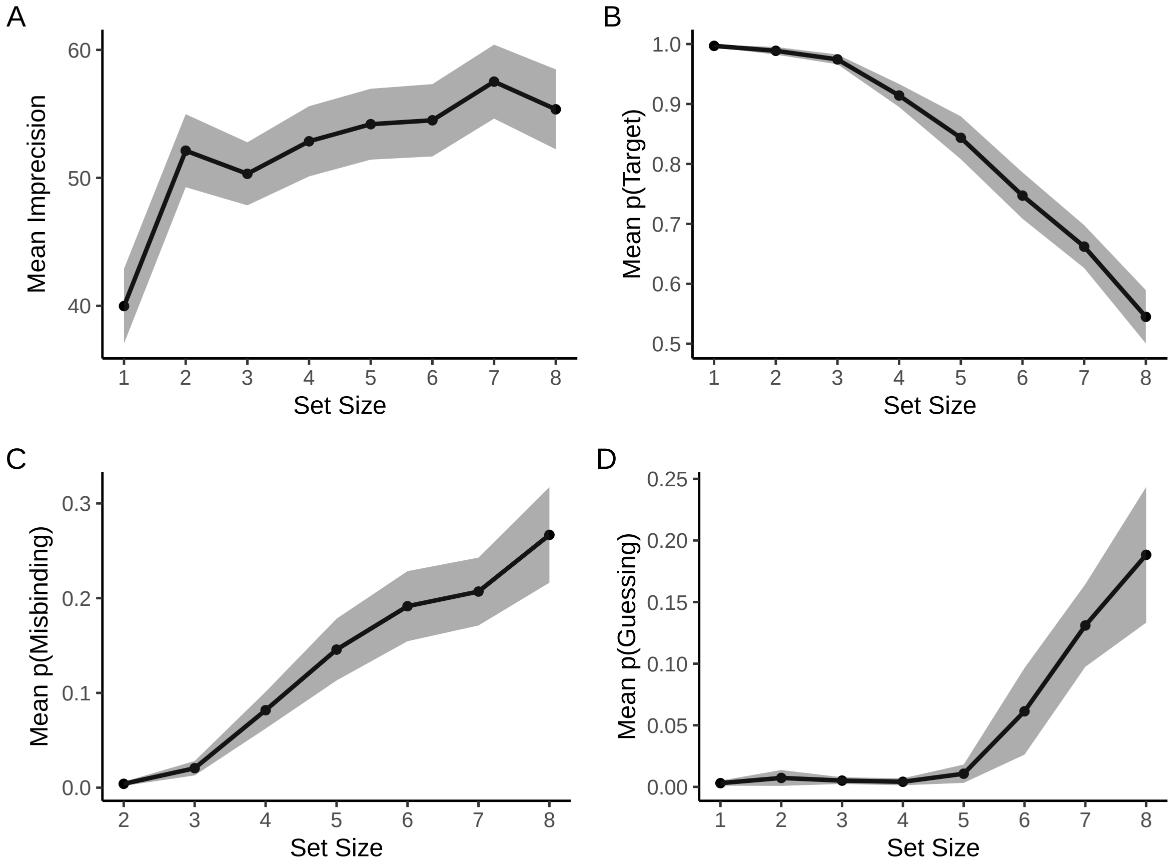

Figure 2.7: Mean imprecision (a), mean probability of reporting the target location (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) as a function of set size. The shaded region represents SEM.

Preface to Chapter Three

Chapter Two showed that the continuous report task and mixture modelling (Bays et al., 2009; Grogan et al., 2020) can be used to measure spatial working memory. However, the nature of the limitation in VSWM resources remains unclear. It has been proposed that spatial working memory relies on topographic maps in frontal and parietal regions, which integrate spatial information in VSWM and motor representations into a single coherent representation (Franconeri et al., 2013). A key prediction of this cortical maps hypothesis is that resource allocation is limited by the availability of cortical space to represent memoranda. Chapter Three attempted to investigate this hypothesis by examining whether the eccentricity effect, which is proposed to affect visual search performance due to cortical magnification (Carrasco et al., 1995), is observed in VSWM.

Chapter Two also highlighted that the requirement to maintain central fixation resulted in missing data, and therefore excluded datasets, as well as the exclusion of almost 15% of trials in the remaining datasets. As a result of this exclusion criteria, and the minimum number of trials being required for the mixture modelling (Bays et al., 2009) being 30 (Bays, n.d.), the number of trials per condition was increased to 60 in Chapter Three[3]. In addition to this increase, the total number of conditions was larger than Chapter Two (24 compared to 8). As a result, the decision was made to make this study a multi-session study. This decision was made in order to utilise a within-subjects design, while minimising the potential effects of fatigue on the task as participants would be completing four one-hour sessions in the multi-session study.

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[3] Although it is important to note that there was very little difference in the pattern of results when all data were included in Chapter Two (Supplementary Materials) compared to when trials in which saccades were made were excluded, indicating that the model parameters after data exclusion were reliable.

Note that this study was affected by COVID-19, where laboratory access was limited throughout data collection. A short-form version of the task, with only one session of 15 trials per condition, was conducted during this time. Results of this task are reported in the Supplementary Materials, and were used to inform the power analysis for the multi-session study, as an eccentricity effect was clearly observed. Although this effect was observed with such a small number of trials per condition, a larger number of trials per condition was used for the experiments reported in the main text to increase the reliability of the resulting model parameters.

Chapter Three has been submitted for publication in Journal of Vision with authors Siobhan McAteer, Anthony McGregor, and Daniel Smith.

Chapter 3

Precision in Spatial Working Memory Depends on an Item's Location Within the Visual Field: Evidence for an Eccentricity Effect in Spatial Working Memory

Visuospatial working memory (VSWM) has been characterized as a flexible resource that determines the precision with which memoranda are stored. The cortical map proposal conceptualizes resource allocation in terms of competitive interactions between representations in brain areas that code the mnemonic feature of interest. A key prediction is that resource allocation is limited by the availability of cortical space to represent memoranda. In the case of spatial working memory, locations are hypothesized to be encoded in retinotopic spatial maps used to control goal-directed action. These spatial maps are known to be inhomogeneous, such that regions representing the fovea have smaller and more densely packed receptive fields compared to regions representing more peripheral locations (Curcio et al., 1987; Rovamo & Virsu, 1979). If the cortical maps hypothesis is correct, this inhomogeneity should be reflected in differences in the amount of resource that can be allocated to increasingly eccentric locations, and therefore in the precision with which they can be represented. This prediction was tested in two experiments in which Bays et al.'s (2009) mixture model was used to examine how sources of recall error in spatial working memory changed across eccentricities. Consistent with the cortical map idea, precision monotonically decreased as eccentricity increased when central fixation was enforced (Experiment One) and in free viewing conditions (Experiment Two). No such effects were observed for colour memory (Experiment Three). These results demonstrate that resource allocation in VSWM is constrained by the availability of cortical resources as predicted by the cortical map theory of VSWM.

3.1 Introduction

Visuospatial working memory (VSWM) is a limited capacity system for the temporary maintenance of spatial and non-spatial (visual) information about items for upcoming task completion (Baddeley & Hitch, 1974). Although there is debate surrounding how this information might be represented within VSWM, there is growing behavioural and neurophysiological support for the idea that VSWM capacity can be characterised as a finite resource that can be flexibly allocated across to-be-remembered items (Bays et al., 2009; Ma et al., 2014). In this view, memory capacity is not constrained by a specific number of slots, but rather by the availability of memory resource to maintain representations at a functionally useful level of fidelity. The precise nature of this resource remains unclear, but one prominent idea is that resource allocation is constrained by the availability of neurons (Franconeri et al. (2013), refer to this is as cortical “real estate”) to represent the memoranda in modality-specific, topographically organized cortical maps (Bays et al., 2009; Franconeri et al., 2013).

The cortical maps hypothesis proposes that each position within the map represents a value in a specific information space (e.g. colour or spatial location). Items within an information space are represented as peaks of activity within the map that compete with each other for representation. Items from different spaces are represented in different maps and do not compete. Consistent with this idea, working memory for visual features and memory for spatial locations are dissociated within VSWM, both neurophysiologically (Courtney et al., 1996; Sala et al., 2003) and behaviourally (Darling et al., 2009; Darling et al., 2007; Klauer & Zhao, 2004). For example, it has been shown that cortical areas such as posterior parietal cortex and dorsolateral prefrontal cortex are selectively involved in the maintenance of spatial locations (Alekseichuk et al., 2017; Ren et al., 2019). These areas are similar to those areas involved in the vision-for-action pathway (Goodale & Milner, 1992), emphasising the role of spatial working memory in visually-guided behaviour (Manohar et al., 2017). In contrast, the cortical areas involved in memory for non-spatial features, such as shape and orientation, are more similar to the cortical areas involved in the vision-for-perception pathway (Ren et al., 2019).

In the case of spatial working memory, there is strong neurophysiological evidence that the cortical maps that represent spatial working memory are shared with maps used for the control of goal directed movements such as saccades. This argument stems from the observation of retinotopic maps within motor areas, especially in those areas involved in the programming of saccadic eye movements, such as superior colliculus, frontal eye fields (FEF) and lateral intraparietal cortex (Bisley & Mirpour, 2019). For example, microstimulation of FEF has been shown to trigger an eye movement towards the corresponding location in space, as well as enhancing responses at the corresponding locations in V4, highlighting the spatially-organised nature of cortical maps underlying motor control, and their coupling with perception (Moore et al., 2003). Critically, these cortical areas also maintain activation during delayed saccades (Curtis et al., 2004; Sommer & Wurtz, 2001), consistent with the idea that spatial working memories are maintained in cortical maps. In humans there is a body of neuroimaging evidence showing shared neural representations for action, attention, and working memory (Ikkai & Curtis, 2011) and the areas involved in the programming of eye movements such as the FEF have consistently been shown to be activated during VSWM tasks and attention (e.g. Campana et al., 2007; Lane et al., 2012; Smith et al., 2009, 2005).

Neuropsychological evidence also supports the idea of a common cortical map for action and spatial working memory. For example, patients with Progressive Supranuclear Palsy, a disease characterised by vertical paralysis of gaze, have significantly decreased spatial span along the axis of paralysis compared to the non-paretic axis (Smith & Archibald, 2020). Furthermore, patients with spatial neglect, characterised by an inability to orient and report sensory events in the contralesional side of space, show decreased performance in a spatial change detection task for locations presented in contralesional space (Pisella et al., 2004). Although this impairment was also shown in colour and shape memory, spatial memory was significantly decreased compared to memory for colour and shape in patients with parietal lesions (Pisella et al., 2004). It has been proposed that this deficit in spatial neglect is related to deficits in oculomotor search behaviour (Husain et al., 2001), highlighting the extensive overlap between spatial working memory and the oculomotor system. The implication of this overlap between the oculomotor system and VSWM is that they share a common representation, with motor maps for the generation of saccades being projected from superior colliculus to posterior parietal cortex for representation in a priority map that serves action, attention and VSWM (Christophel et al., 2012; Paré & Wurtz, 1997; Todd & Marois, 2005; Zelinsky & Bisley, 2015).

Behavioural studies lend further support to the proposition that action control and VSWM share a common spatial map. Studies using the dual-task paradigm with delay-period performance of saccades have shown that memory for spatial locations is disrupted (Lawrence et al., 2004; Pearson & Sahraie, 2003; Smyth & Scholey, 1994), and that this saccadic interference effect is specific to spatial memory (McAteer et al., 2023)[4]. The nature of this disruption in spatial memory has been argued to result from delay-period saccades reducing the signal-to-noise ratio of the activation peaks for the maintained spatial locations within the VSWM representation (McAteer et al., 2023)[5]. It has also been found that maintenance of a location in VSWM results in inhibition of saccades to that location (Belopolsky & Theeuwes, 2009a) and increased saccade curvature away from the remembered location (Theeuwes et al., 2005) and that experimentally constricting the ability to plan and execute saccades significantly reduces spatial memory span (Ball et al., 2013; Pearson et al., 2014). These findings illustrate how VSWM and saccade control draw on a shared cognitive process, consistent with the idea that performing saccades creates competition for resource between saccade targets and memory item, thus reducing the availability of resources for mnemonic representations in a shared cortical map of space.

The cortical maps hypothesis is also consistent with the evidence that physiological differences across the visual field are inherited by VSWM. For example, Carrasco et al. (2001) demonstrated that the horizontal-vertical anisotropy in perception (reduced perceptual performance for locations along the vertical meridian compared to iso-eccentric locations along the horizontal) is present in visual working memory (Carrasco et al., 2001). This

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[4] This refers to the data presented in Chapter Five.

[5] This refers to the data presented in Chapter Five.

anisotropy has been explained in terms of low-level physiological differences in the visual system, specifically with respect to the densities of retinal ganglion cells and cones, which is not radially symmetric across eccentricities in the visual field (Carrasco et al., 2001). Similar anisotropies can be seen in oculomotor behaviour, whereby large horizontal saccades have shorter latencies and higher accuracies compared to saccades along the vertical plane (Irving & Lillakas, 2019), and in spatial working memory, where spatial span and capacity is significantly reduced for locations presented along the vertical meridian compared to locations presented along the horizontal meridian (Smith, 2022).

Another prediction that derives from the cortical maps model is that the spatial locations of memoranda should affect the competitive interactions between them, such that closer items will compete more than items with greater spatial separation. The relative spatial positions of memoranda should therefore predict the precision with which items will be retained. One way in which these competitive interactions have been demonstrated within VSWM is by using a spatial crowding paradigm. Crowding effects have been demonstrated in both perception and VSWM, where precision is lower when a target is placed in close proximity to flankers compared to when the distance between flankers and targets is increased, which has been argued to reflect the decreased inter-item competition when inter-item distance is increased (Tamber-Rosenau et al., 2015; Yörük et al., 2020). This pattern of data supports the idea that perception and VSWM share a common representation, which might be restricted by neurophysiological limits, although it should be noted that Harrison & Bays (2018) have argued against crowding effects in VSWM when items are presented serially.

To summarize, the cortical maps hypothesis argues that spatial working memory relies on topographically organized cortical maps used to represent space. The considerable overlap between neural systems involved in oculomotor control and VSWM, combined with behavioural evidence of dual task interference between motor control and spatial working memory is strong evidence of the view spatial memory relies on cortical maps that integrate spatial information in VSWM and motor representations into a single coherent representation. The cortical maps hypothesis also holds that the fidelity of representations in VSWM is constrained by the physiology of the cortical regions maintaining the map. However, the evidence for this position is less direct, as it draws on studies examining how perceptual anisotropies affect memory span (as opposed to the precision of memory representations, Smith (2022)) and from related phenomena such as visual crowding (Yörük et al., 2020).

One way to address this issue is to make use of the eccentricity effect in vision. It is well-documented that both reaction time and accuracy decrease with increasing eccentricity and set size in visual search tasks (Carrasco et al., 1995; Wolfe et al., 1998) and object recognition (Jüttner & Rentschler, 2000). This eccentricity effect has been explained in terms of cortical magnification, whereby there are fewer cortical resources dedicated to processing each degree of visual angle as the visual field moves further into the periphery (Rovamo & Virsu, 1979; Virsu et al., 1987; Virsu & Rovamo, 1979). Indeed, increasing stimulus size as a function of cortical magnification was found to abolish the eccentricity effect (Carrasco et al., 1995), although it should be noted that this cortical magnification has not been reliably observed to neutralise eccentricity effects(e.g. Staugaard et al., 2016). The eccentricity effect therefore offers a more direct way to examine the cortical maps hypothesis in VSWM, in particular with respect to the key prediction that resource allocation is limited by the availability of cortical resource, which is retinotopically mapped across the visual field and declines with eccentricity.

The current study examined the eccentricity effect in visual and spatial working memory using a continuous report task to characterise the pattern of response errors in VSWM while systematically varying eccentricity and set size. If the cortical maps hypothesis is correct, precision in spatial working memory should decrease with increasing eccentricity. Analogous effects should not be observed in visual working memory because of the separability in memory for visual features and memory for spatial features, in which memory for spatial locations but not visual features is hypothesised to occur in spatially-organised maps.

3.2 Experiment One

3.2.1 Methods

3.2.1.1 Participants

An *a priori* power analysis based on the effect size for a significant main effect of eccentricity observed in a pilot experiment ($\eta_p^2 = .71$; see Supplementary Materials), indicated that we required a sample of at least three participants to observe a significant effect of eccentricity for imprecision ($\alpha = .05$, power = 95%). Six volunteers ($M_{\text{age}} = 28$ years, $SD_{\text{age}} = 4.24$, 5 females, 1 male, 5 right-handed) were recruited from Durham University. All participants reported having normal or corrected-to-normal vision. Participants received compensation at a rate of £12 per session for participation. This experiment received ethical approval from Durham University Psychology Department Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

3.2.1.2 Design

We used a within-subjects design. There were two independent variables: set size (eight levels: 1-8 items), and eccentricity, (three levels: 5°, 7.5°, and 10° of visual angle around central fixation). The dependent variables were localisation error, as well as imprecision, and the probabilities of misbinding and guessing. Participants completed a total of 1440 trials, across four one-hour sessions. Sessions were completed at approximately the same time on separate days. Each session comprised a practice block of 8 trials, where participants were shown the original location as well as their own response, and 360 experimental trials, with no feedback presented, randomised across 15 blocks.

3.2.1.3 Stimuli and apparatus

The task was programmed using Matlab R2019a, using the psychophysics toolbox (Kleiner et al., 2007). The stimuli consisted of arrays comprising between one and eight coloured dots (diameter of each dot = 1° VA) and a fixation cross (0.76° VA x 0.76° VA) positioned at the centre of the screen. The colours of each dot were chosen without repetition from a bank of eight discriminable colours: red, orange, yellow, green, cyan, blue, magenta, and purple. The visual mask comprised 800 coloured dots, like those presented at encoding, filling the annular space five to ten degrees of visual angle around central fixation. Participants' gaze was monitored using a tower-mounted EyeLink 1000 eye tracker (SR Research). Stimuli were presented on a 20-inch CRT screen with a refresh rate of 85Hz. Participants sat 60cm from the computer screen, with the centre of the screen at eye level.

3.2.1.4 Procedure

Participants were instructed to maintain fixation on the centre of the screen throughout each trial. Trials began with presentation of a fixation cross at the centre of the screen for one second followed by a blank screen for 0.5s. The stimulus array, comprising between one and eight coloured dots, was then presented for two seconds. The locations of each dot were randomly chosen from eight equally spaced locations on imaginary circles with radius of either 5°, 7.5°, or 10° of visual angle from central fixation. After presentation of the array, the visual mask was presented for 0.1s. A blank screen was then shown for 0.9s. At test, one of the stimuli from the array was randomly chosen and presented in the centre of the screen. Participants were required to move the mouse to click the location on screen where it first appeared. Participants could respond with any location on screen as they were not informed that the stimulus area was restricted. There was no time limit for responding. A 1.5s blank screen followed the response period, before the beginning of the next trial. Participants were permitted to take a self-paced break between blocks. An example trial is shown in Figure 3.1.

3.2.2 Results

Mixture modelling (Bays et al., 2009) was carried out using MemToolbox2D (Grogan et al., 2020). This mixture model (Bays et al., 2009) assumes that there are three sources of recall error: Gaussian variability in the response (imprecision), the height of which indicates the probability of reporting the target location; the probability of guessing,

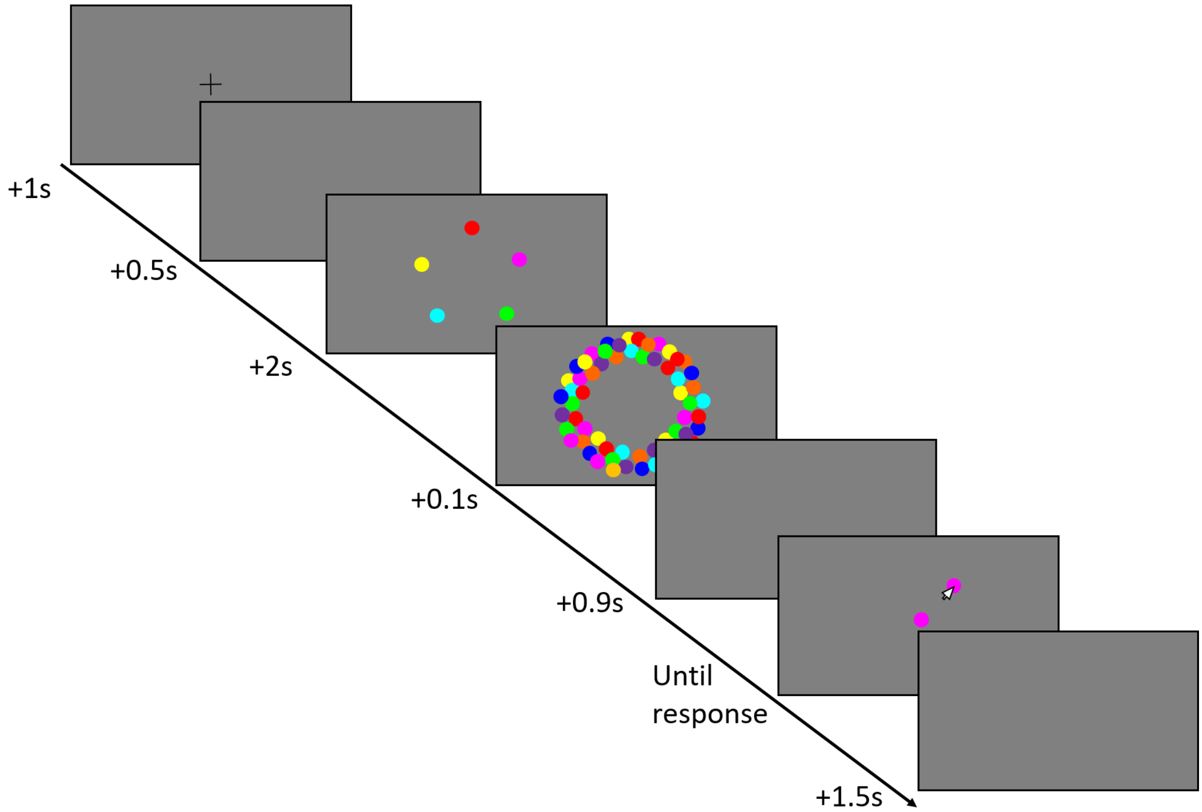

Figure 3.1: An example trial in Experiment One. Participants were shown an array of between one and eight dots. After a short delay, they were asked to click on screen where one of those dots first appeared.

which is drawn from a uniform distribution; and the probability of responding with a non-target (misbinding), which is drawn from a Gaussian centred on one of the non-probed items. Maximum likelihood estimates were obtained for these sources of recall error in each condition. The estimate of guessing was corrected by assuming that responses were sampled from the annulus within which items could appear.

Owing to the small sample size, we ran linear mixed effects model in R version 4.2.1 (R Core Team, 2019) using the `lmerTest` package (Kuznetsova et al., 2017), which applies Satterthwaite's method to estimate degrees of freedom and p values for the overall effects of set size and eccentricity. The model was run for each dependent variable to examine the effects of set size and eccentricity, which were included as fixed effects, after controlling for the random effect of participant[6]. Bonferroni-Holm corrected post-hoc contrasts of

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[6] The formula for the model was as follows for imprecision: imprecision ~ set size + eccentricity + set size:eccentricity + (1|ID)

the estimated marginal means were carried out to examine any significant effects using the `emmeans` package (Lenth, 2022).

Trials in which average saccade amplitude exceeded two degrees of visual angle were excluded from analysis. This resulted in the exclusion of 8.09% of trials.

For imprecision (Figure 3.2A), significant main effects of set size [$F(7, 115) = 11.79$, $p < .001$] and eccentricity [$F(2, 115) = 5.54$, $p = .005$] were observed. The interaction between set size and eccentricity was not significant; $F(14, 115) = 1.22$, $p = .271$. Bonferroni-Holm corrected pairwise comparisons between adjacent set sizes revealed that no differences between adjacent set sizes were significant; $p \geq .021$. Post-hoc comparisons between adjacent eccentricity conditions revealed that the differences between 5° VA ($M = 32.18$, $SD = 14.35$) and 7.5° VA ($M = 35.8$, $SD = 18.82$), and between 7.5° VA and 10° VA ($M = 43.51$, $SD = 29.81$) were significant; $p = .295$.

For the probability of misbinding (Figure 3.2B), a significant main effect of set size was observed; $F(6, 100) = 4.04$, $p = .001$. The main effect of eccentricity [$F(2, 100) = 9.34$, $p < .001$] and the interaction between set size and eccentricity [$F(12, 100) = 1.03$, $p = .428$] were not significant. Bonferroni-Holm corrected pairwise comparisons revealed a significant difference between set size 7 ($M = 0.09$, $SD = 0.1$) and set size 8 ($M = 0.09$, $SD = 0.15$); $p = 1.000$. No other differences were significant; $p \geq 1.000$.

For the probability of guessing (Figure 3.2C), significant main effects of set size [$F(7, 115) = 5.78$, $p < .001$] and eccentricity [$F(2, 115) = 5.53$, $p = .005$] were observed. The interaction between set size and eccentricity was not significant; $F(14, 115) = 0.93$, $p = .529$. Bonferroni-Holm corrected pairwise comparisons between adjacent set sizes revealed that no differences between adjacent set sizes were significant; $p \geq 1.000$. Post-hoc comparisons between adjacent eccentricity conditions also revealed that no differences between eccentricity conditions were significant after correction; $p \geq .184$.

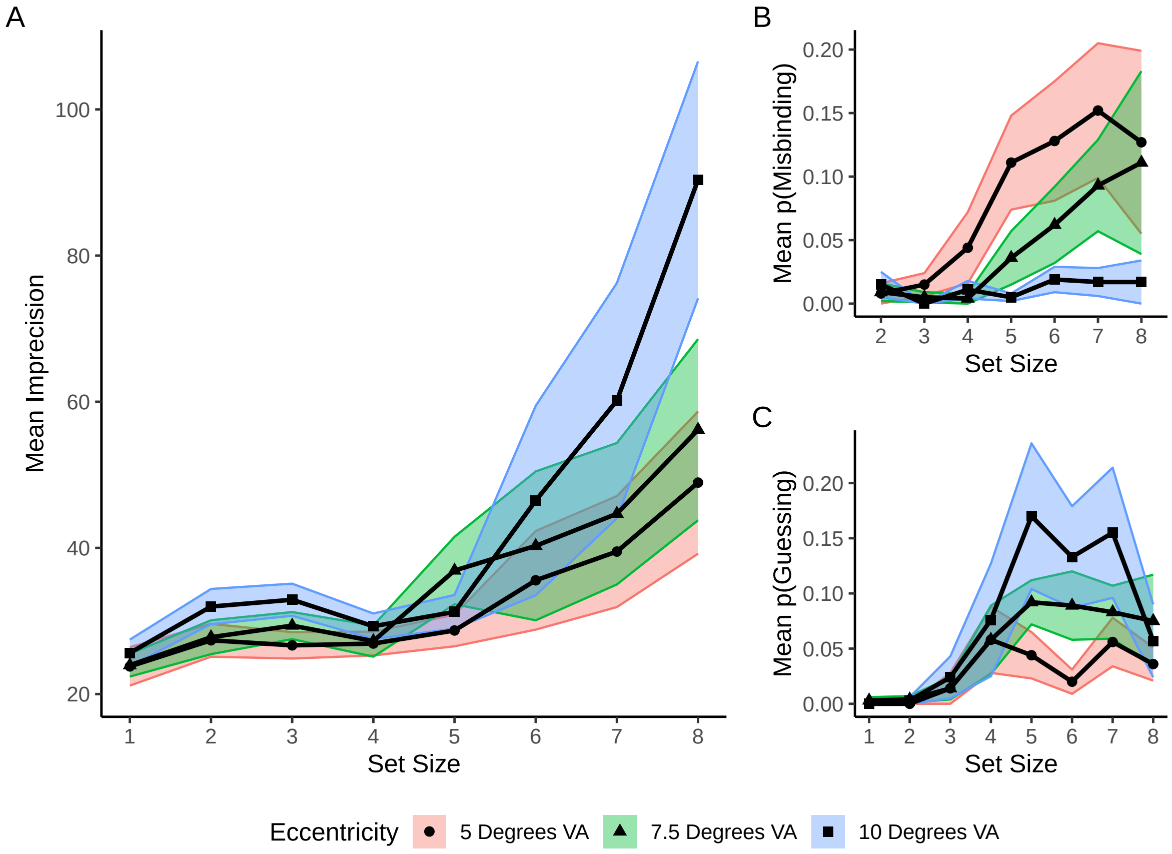

Figure 3.2: Mean imprecision (a), mean probability of reporting the target location (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) at each eccentricity and set size. The shaded regions represent SEM.

3.2.3 Discussion

This pattern of results indicates that there is an eccentricity effect in VSWM such that the noise in the representation, and therefore imprecision, increases as eccentricity increases. However, asking participants to maintain central fixation is not reflective of naturalistic viewing behaviour, and maintaining fixation during encoding and maintenance may result in decreased memory performance (Henderson et al., 2005). Therefore, we conducted a second experiment in which participants were free to move their eyes to examine whether the eccentricity effect is still present under naturalistic viewing behaviour.

3.3 Experiment Two

3.3.1 Methods

3.3.1.1 Participants

Six volunteers ($M_{\text{age}} = 26.67$ years, $SD_{\text{age}} = 2.42$, 2 females, 4 males, 4 right-handed) were recruited from Durham University. All participants reported having normal or corrected-to-normal vision. Participants received compensation at a rate of £12 per session for participation. This experiment received ethical approval from Durham University Psychology Department Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

3.3.1.2 Design

Design was as described in Experiment One.

3.3.1.3 Stimuli and apparatus

Stimuli and apparatus matched that of Experiment One.

3.3.1.4 Procedure

For each session, procedure followed that of Experiment One, with the exception that participants were instructed to view the screen in a natural manner and move their eyes freely.

3.3.2 Results

No trials were excluded from analysis. On average, approximately 17 saccades ($M = 17.23$, $SD = 4.25$, minimum = 1, maximum = 37) were made throughout encoding and maintenance on each trial. The same mixture model (Bays et al., 2009) and linear mixed effects models as used in Experiment One were used in Experiment Two, which included fixed effects of set size and eccentricity and participant ID as a random effect.

For imprecision (Figure 3.3A), significant main effects of set size [$F(7, 115) = 44.07$, $p < .001$] and eccentricity [$F(2, 115) = 59.98$, $p < .001$] were observed. The interaction between set size and eccentricity was not significant; $F(14, 115) = 1.37$, $p = .180$. Bonferroni-Holm corrected pairwise comparisons between adjacent set sizes revealed that the difference between set size 1 ($M = 17.37$, $SD = 3.86$) and set size 2 ($M = 37.77$, $SD = 9.79$) was significant; $p < .001$. No other differences between adjacent set sizes were significant; $p \geq .161$. Post-hoc comparisons between adjacent eccentricity conditions revealed that the differences between 5° VA ($M = 33.69$, $SD = 11.47$) and 7.5° VA ($M = 40.58$, $SD = 15.11$), and between 7.5° VA and 10° VA ($M = 48.69$, $SD = 16.27$) were significant; $p < .001$.

For the probability of misbinding (Figure 3.3B), a significant main effect of set size was observed; $F(6, 100) = 84.36$, $p < .001$. The main effect of eccentricity was also significant; $F(2, 100) = 13.89$, $p < .001$. The interaction between set size and eccentricity was not significant; $F(12, 100) = 1.55$, $p = .120$. For the main effect of set size, Bonferroni-Holm corrected pairwise comparisons revealed significant differences between set size 4 ($M = 0.07$, $SD = 0.06$) and set size 5 ($M = 0.14$, $SD = 0.09$), set size 5 and set size 6 ($M = 0.29$, $SD = 0.14$), and between set size 7 ($M = 0.31$, $SD = 0.14$) and set size 8 ($M = 0.39$, $SD = 0.14$); $p \leq .016$. No other differences were significant; $p \geq 0.089$. Bonferroni-Holm corrected pairwise comparisons between eccentricities showed that the difference between 5° VA ($M = 0.22$, $SD = 0.21$) and 7.5° ($M = 0.17$, $SD = 0.16$) was significant; $p = .010$. The difference between 7.5° VA and 10° VA ($M = 0.14$, $SD = 0.13$) was also significant; $p = .014$.

For the probability of guessing (Figure 3.3C), significant main effects of set size [$F(7, 115) = 21.12$, $p < .001$] and eccentricity [$F(2, 115) = 22.47$, $p < .001$] were observed. The interaction between set size and eccentricity was also significant; $F(14, 115) = 4.26$, $p < .001$. Bonferroni-Holm corrected comparisons between adjacent eccentricity conditions at each set size revealed that the difference between 5° VA and 7.5° VA was significant at set size 6 ($M_{\text{5DVA}} = 0.02$, $SD_{\text{5DVA}} = 0.03$; $M_{\text{7.5DVA}} = 0.09$, $SD_{\text{7.5DVA}} = 0.08$, $p = .002$) and at set size 8 ($M_{\text{5DVA}} = 0.04$, $SD_{\text{5DVA}} = 0.04$; $M_{\text{7.5DVA}} = 0.07$, $SD_{\text{7.5DVA}} = 0.1$, $p < .001$).

The difference between 7.5° VA and 10° VA was significant at set size 7 ($M_{7.5\text{DVA}} = 0.08$, $SD_{7.5\text{DVA}} = 0.06$; $M_{10\text{DVA}} = 0.16$, $SD_{10\text{DVA}} = 0.14$, $p < .001$) and set size 8 ($M_{10\text{DVA}} = 0.06$, $SD_{10\text{DVA}} = 0.08$, $p = .003$). No other differences were significant; $p \geq .064$.

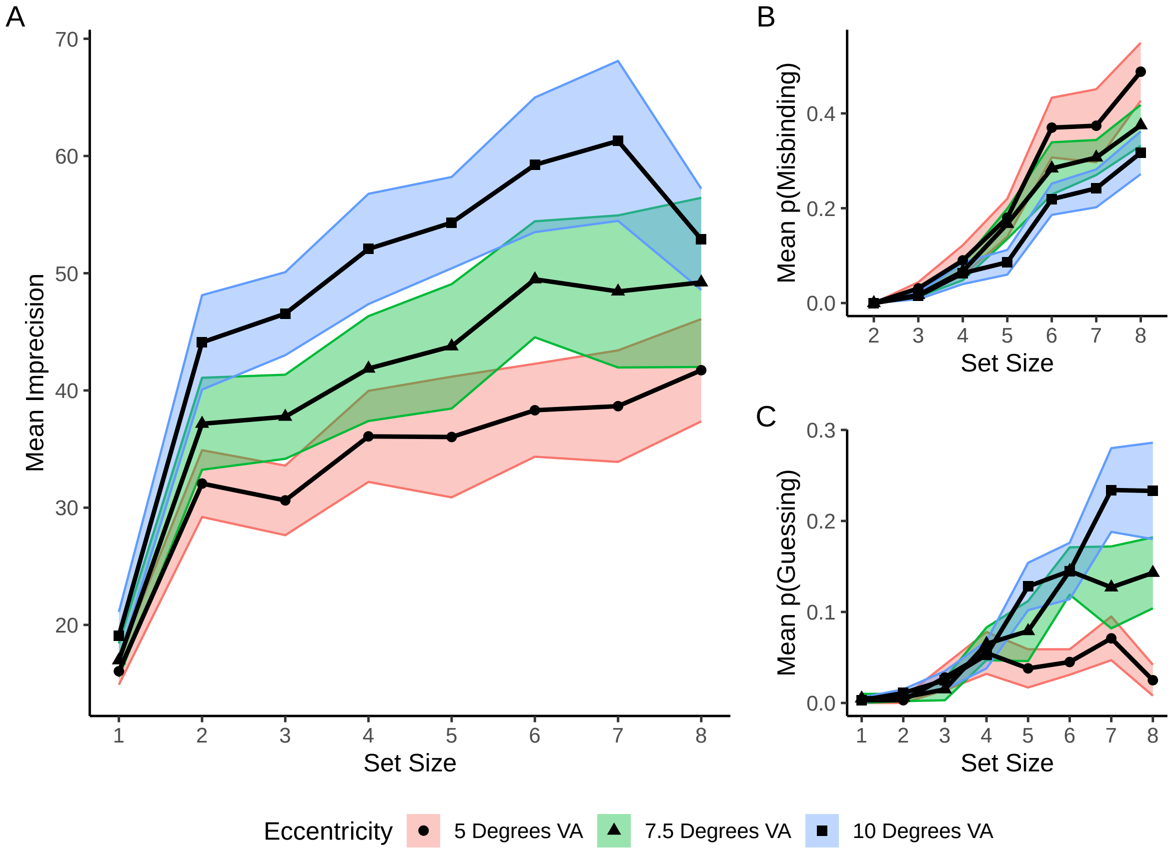

Figure 3.3: Mean imprecision (a), mean probability of reporting the target location (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) at each eccentricity and set size. The shaded regions represent SEM.

3.3.3 Discussion

Experiments One and Two demonstrated an eccentricity effect in the precision of spatial working memory that is consistent with the predictions of the cortical map hypothesis. Although Experiments One and Two showed broadly similar results, there were some interesting differences between fixed (Experiment One) and free viewing (Experiment Two). The eccentricity effect for single-item displays was abolished under free viewing. On first inspection, this result may seem hard to reconcile with the cortical maps hypothesis, which predicts that the availability of cortical resources depends on the position within the visual field. However, several studies have shown that fixating an item is associated with increased precision (Bays & Husain, 2008) and this facilitation of precision has been shown to be driven by a transient saccade-related boost to the resource available for encoding the saccade target (Udale et al., 2022). A pre-saccadic enhancement of precision may be sufficient to compensate for the lack of cortical real estate available for more eccentric items. Indeed, in visual search, it has been shown that the effect of eccentricity on accuracy was reduced for free viewing compared to fixed viewing (Carrasco et al., 1995). As set size increases larger than one item, participants tend to adopt the strategy to maintain fixation in the centre of the array (Fehd & Seiffert, 2008), which allows the eccentricity effect to emerge, even under free viewing. An alternative possibility is that, in single-item displays, participants simply fixated the item during the encoding phase, maintained fixation at that location throughout maintenance, and clicked where they were looking at recall.

The cortical maps hypothesis predicts that eccentricity effects should be specific to spatial working memory. Short term memory for features such as colour are hypothesised to be encoded in non-spatial maps, which do not exhibit a spatial inhomogeneity. To confirm that eccentricity effects are specific to spatial memory, a control experiment was conducted in which participants were presented with the same memory arrays as Experiments One and Two, but this time were shown the location of the target item and asked to recall its colour. It was predicted that imprecision, guessing and misbinding would increase with set size but be unaffected by eccentricity.

3.4 Experiment Three

3.4.1 Methods

3.4.1.1 Participants

Six volunteers ($M_{\text{age}} = 20$ years, $SD_{\text{age}} = 0.6235$, 3 females, 3 males, 5 right handed, 1 left handed, all confirmed normal or corrected-to-normal vision) were recruited from

Durham University. Participants enrolled on undergraduate courses in the Department of Psychology received credit for participation. This experiment received ethical approval from Durham University Psychology Department Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

3.4.1.2 Design

Design was as described in Experiment One.

3.4.1.3 Stimuli and apparatus

Stimuli and apparatus matched that of Experiment One with the exception that colours were randomly generated from a colour wheel with at least 30° angular separation between colours. At recall, participants were presented with a colour wheel 11° VA to 13° VA around central fixation.

3.4.1.4 Procedure

For each session, procedure followed that of Experiment One with the exception that participants were asked to recall the colour of each dot while maintaining central fixation throughout each trial. An example trial is shown in Figure 3.4.

3.4.2 Results

Trials in which average saccade amplitude exceeded two degrees of visual angle during encoding and maintenance were excluded from analysis. This resulted in the exclusion of one dataset from analysis. Of the remaining five datasets, 27.18% of trials were excluded from analysis. The same mixture model (Bays et al., 2009) and linear mixed effects models as used in Experiments One and Two were used in Experiment Three.

For imprecision (Figure 3.5A), a significant main effect of set size was observed; $F(7, 92) = 2.51$, $p = .021$. The main effect of eccentricity [$F(2, 92) = 1.19$, $p = .308$] and the interaction between set size and eccentricity [$F(14, 92) = 1.67$, $p = .075$] were not

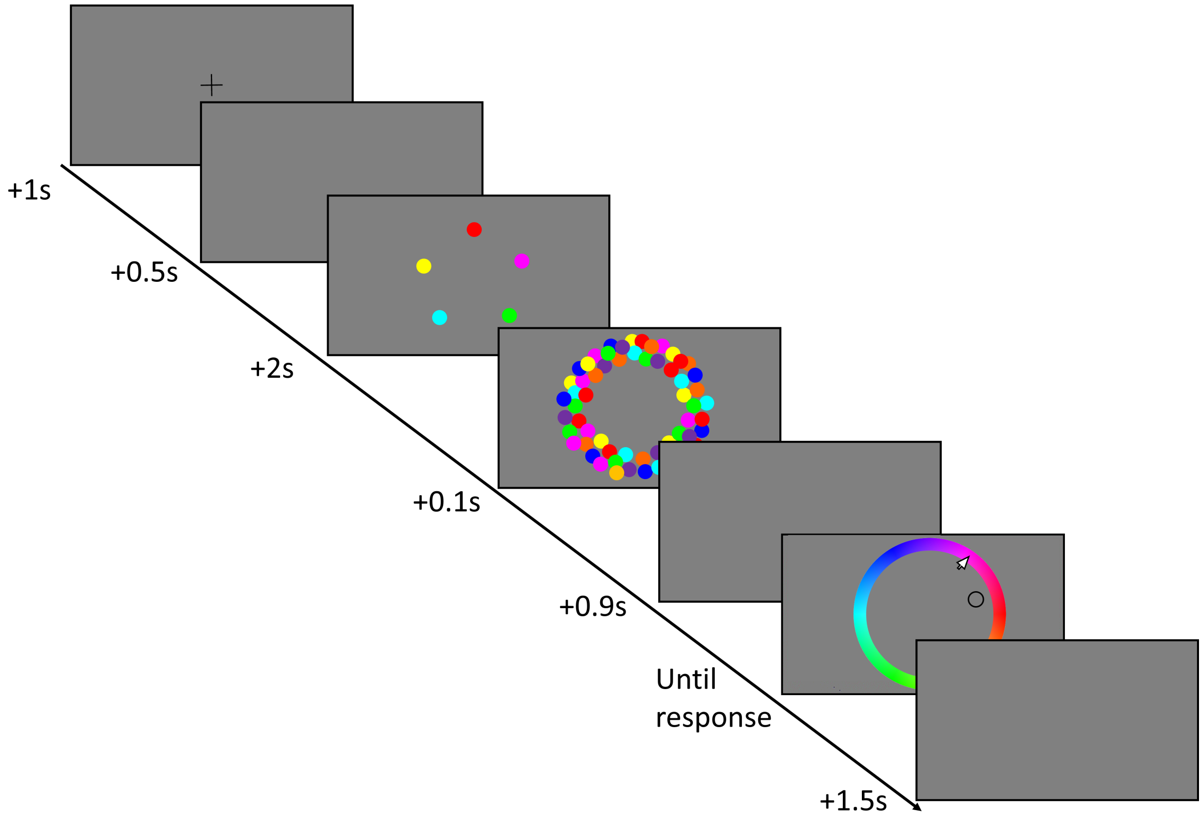

Figure 3.4: An example trial in Experiment Three. Participants were shown an array of between one and eight dots. After a short delay, they were asked to report the colour of one of those dots on a colour wheel.

significant. Bonferroni-Holm corrected pairwise between adjacent set sizes revealed no significant differences; $p \geq 1.000$.

For the probability of misbinding (Figure 3.5B), there was a significant main effect of set size; $F(6,\ 80) = 13.26$, $p < .001$. The effect of eccentricity [$F(2,\ 80) = 0.2$, $p = .817$] and the interaction between set size and eccentricity [$F(12,\ 80) = 0.85$, $p = .603$] were not significant. Bonferroni-Holm corrected pairwise between adjacent set sizes revealed no significant differences; $p \geq .125$.

For the probability of guessing (Figure 3.5C), there was a significant main effect of set size; $F(7,\ 92) = 2.93$, $p = .008$. The effect of eccentricity [$F(2,\ 92) = 0.78$, $p = .463$] and the interaction between set size and eccentricity [$F(14,\ 92) = 1.51$, $p = .123$] were not significant. Bonferroni-Holm corrected pairwise comparisons revealed no significant differences between adjacent set sizes; $p \geq 1.000$.

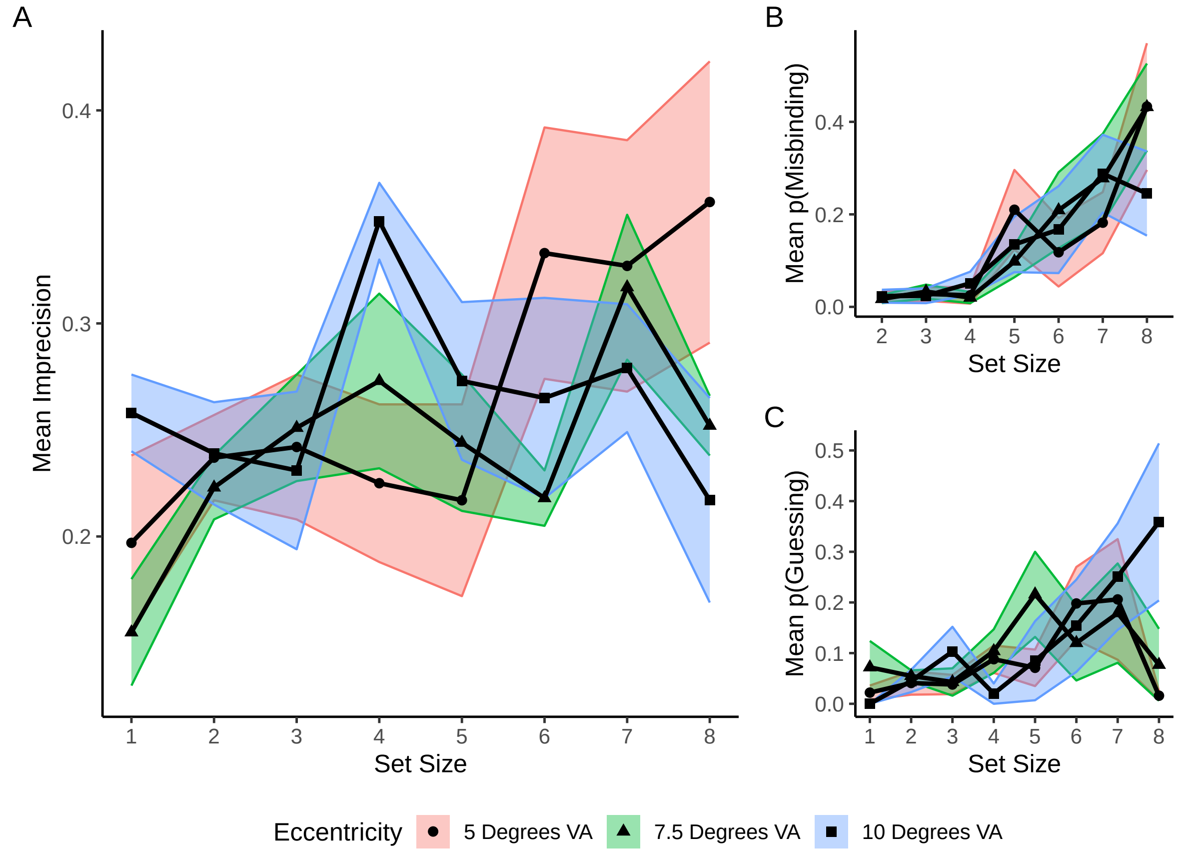

Figure 3.5: Mean imprecision (a), mean probability of reporting the target colour (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) at each eccentricity and set size. The shaded regions represent SEM.

3.4.3 Discussion

Experiment Three confirmed that imprecision, guessing, and misbinding in visual working memory increase with set size as resource is divided amongst a larger number of objects (Bays et al., 2009). Critically, these measures did not vary with eccentricity, confirming that the effects observed in Experiments One and Two are specific to spatial working memory, as predicted by the cortical maps hypothesis.

3.5 General Discussion

The current study investigated the cortical maps hypothesis by examining the eccentricity effect in visual and spatial working memory using a continuous report task. An eccentricity effect was found in spatial working memory (Experiments One and Two), which was characterised by increased imprecision with eccentricity. When memory for colour was examined (Experiment Three), no eccentricity effect was observed. These results are consistent with the cortical maps hypothesis in spatial working memory, which proposes that the distribution of VSWM resources is constrained by the availability of cortical space.

Imprecision within VSWM is hypothesised to be inversely related to the amount of cortical resource directed to each item in VSWM (Bays et al., 2009). The finding of increased imprecision with increasing eccentricity therefore reflects the fact that there was less resource available at the highest eccentricities to encode and maintain these locations in VSWM. This finding suggests the availability of VSWM resources is constrained by the availability of cortical space. However, this cortical space is unequally distributed across the visual field. The eccentricity effect for the probability of guessing provides additional support for the cortical maps hypothesis. As eccentricity increased and more items were to be retained, the probability of guessing in spatial working memory was increased, as evidenced by the significant interaction effect in Experiment Two. The probability of guessing indicates that some items were not represented in VSWM. Within the cortical maps hypothesis, this finding indicates that the availability of cortical space relates directly to the distribution of VSWM resources across the visual field. That is, VSWM resources are denser around central fixation, becoming scarcer as eccentricity increases. This explanation is comparable to the cortical magnification explanation of the eccentricity effect (Virsu et al., 1987). Consequently, when more items are presented at the highest eccentricity, not every item can be encoded as there is not enough resource present at these eccentricities to be distributed amongst all to-be-remembered items, causing some items not being encoded and resulting in an increase in guessing responses for these conditions. This observation therefore lends strong support to the idea that VSWM is a flexible but finite resource that depends on the availability of cortical space.

It was also found that misbinding was greatest for the stimuli closest to fixation. Although this was not statistically significant under fixed viewing (Experiment One), the same trend was observed for both viewing conditions. It seems plausible that this effect is an artefact of the decreasing spacing between stimuli at large set sizes. At small eccentricities the spacing may have been sufficiently low that some ‘guesses’ landed unintentionally close to the location of a non-target item, thus inflating misbinding. The stimuli were not scaled with eccentricity, so participants were unlikely to unintentionally place a guess on the position of a non-target item when arrays were presented at the more eccentric locations, even at larger set sizes.

Overall, these data are consistent with the cortical map hypothesis of VSWM (Franconeri et al., 2013) and the more specific claim that spatial working memory is represented in the same cortical maps used to guide actions such as eye movements (Ikkai & Curtis, 2011; Smith & Archibald, 2020; Zelinsky & Bisley, 2015). Indeed, the idea that visually-guided actions and spatial working memory share a representation is a computationally efficient way to temporarily maintain information for upcoming task completion. Networks already specialised for encoding detailed sensory information are recruited to aid maintenance of this information without requiring additional specialisation of cortical networks. This idea aligns with the broader theoretical position that the principle functional role of VSWM is the control of action (Heuer et al., 2020; Olivers & Roelfsema, 2020; Van der Stigchel & Hollingworth, 2018).

The finding that eccentricity affects spatial but not colour memory echoes a previous finding that oculomotor dual-task interference disrupts spatial but not colour memory (McAteer et al., 2023)[7]. This finding lends further support for the hypothesis that spatial locations and visual features are maintained in separate systems within VSWM and rely on separate neural mechanisms (Courtney et al., 1996; Konstantinou et al., 2017; Sala et al., 2003). In particular, memory for spatial locations relies on neural networks that are known to contain topographic maps, such as the frontoparietal network. In contrast, memory for visual features relies on right middle occipital gyrus and left superior temporal gyrus (Ren et al., 2019). These separate neural regions underlying VSWM sub-stores are similar to the two-streams hypothesis (Goodale & Milner, 1992) and emphasises the role

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[7] This refers to the data presented in Chapter Five.

of spatial working memory in visually-guided actions and behaving effectively within the environment (Manohar et al., 2017).

To summarise, we found an eccentricity effect in spatial working memory such that imprecision increased with increases in eccentricity. Given that the availability of cortical resources for encoding spatial locations declines with increasing eccentricity, these data suggest that the allocation of VSWM resources is constrained by the neural architecture of the visual system. These results converge with neurophysiological evidence for shared cortical representations for action goals and memorised spatial locations (Ikkai & Curtis, 2011), neuropsychological evidence that lesions to brain areas involved in visually-guided actions also disrupt spatial working memory (e.g. Smith & Archibald, 2020), and behavioural evidence that dual tasks that involve visually-guided actions disrupt spatial but not visual working memory (e.g. McAteer et al., 2023)[8]. Together, these findings support the idea that spatial working memory representations compete for representation within the spatial maps used to control action, as hypothesised by the cortical maps hypothesis.

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[8] This refers to the data presented in Chapter Five.

3.6 Supplementary Materials

3.6.1 Pilot Data

3.6.1.1 Methods

3.6.1.1.1 Participants Fifteen participants (*M* = 22.67 years, *SD* = 6.66, 12 females, 3 males, 15 right handed) volunteered. All participants reported having normal or corrected-to-normal vision. Participants received credit for taking part. This experiment received ethical approval from Durham University Psychology Department Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

3.6.1.1.2 Design We used a within-subjects design. There were two independent variables: set size (eight levels: 1-8 items), and eccentricity, (three levels: 5°, 7.5°, and 10° of visual angle around central fixation). The dependent variable was imprecision. Participants completed 8 practice trials before completing the experiment. There were 360 experimental trials, randomised across 15 blocks.

3.6.1.1.3 Stimuli and apparatus The task was programmed using Matlab R2019a, using the Psychophysics toolbox (Kleiner et al., 2007). The stimuli consisted of arrays comprising between one and eight coloured dots (diameter of each dot = 1° VA) and a fixation cross (0.76° VA x 0.76° VA) positioned at the centre of the screen. The colours of each dot were chosen without repetition from a bank of eight discriminable colours: red, orange, yellow, green, cyan, blue, magenta, and purple. The visual mask comprised 800 coloured dots, like those presented at encoding, filling the annular space five to ten degrees of visual angle around central fixation. Participants' gaze was monitored using a tower-mounted EyeLink 1000 eye tracker (SR Research). Stimuli were presented on a 20-inch CRT screen with a refresh rate of 85Hz. Participants sat 60cm from the computer screen, with the centre of the screen at eye level.

3.6.1.1.4 Procedure Participants were instructed to maintain fixation on the centre of the screen throughout each trial. Trials began with presentation of a fixation cross at the centre of the screen for one second followed by a blank screen for 0.5s. The stimulus array, comprising between one and eight coloured dots, was then presented for two seconds. The locations of each dot were randomly chosen from eight equally spaced locations on imaginary circles with radius of either 5°, 7.5°, or 10° of visual angle from central fixation. After presentation of the array, the visual mask was presented for 0.1s. A blank screen was then shown for 0.9s. At test, one of the stimuli from the array was randomly chosen and presented in the centre of the screen. Participants were required to move the mouse to click the location on screen where it first appeared. Participants could respond with any location on screen as they were not informed that the stimulus area was restricted. There was no time limit for responding. A 1s blank screen followed the response period, before the beginning of the next trial. Participants were permitted to take a self-paced break between blocks.

3.6.1.2 Results

Trials in which average saccade amplitude exceeded two degrees of visual angle were excluded from analysis. This resulted in three datasets being removed from the analysis. Of the remaining 12 datasets, 39.1% of trials being removed from the analysis. The mixture model (Bays et al., 2009; Grogan et al., 2020) was fit to the data to gain an estimate of effect size for the main effect of eccentricity on imprecision.

Eccentricity x set size repeated-measures ANOVA revealed significant main effects of set size [$F(3.04, 33.42) = 3.63$, $p = .022$, $\eta_p^2 = .248$] and eccentricity [$F(1.33, 14.67) = 26.45$, $p < .001$, $\eta_p^2 = .706$]. The interaction between set size and eccentricity was not significant; $F(14, 154) = 1.08$, $p = .375$, $\eta_p^2 = .090$.

Holm-Bonferroni corrected pairwise comparisons between eccentricity conditions revealed significant differences between 5° VA ($M = 34.56$, $SD = 15.73$) and 7.5° VA ($M = 47.38$, $SD = 19.53$; $p < .001$) and between 7.5° VA and 10° VA ($M = 60.96$, $SD = 24.96$; $p < .001$). The difference between 5° VA and 10° VA was also significant; $p < .001$.

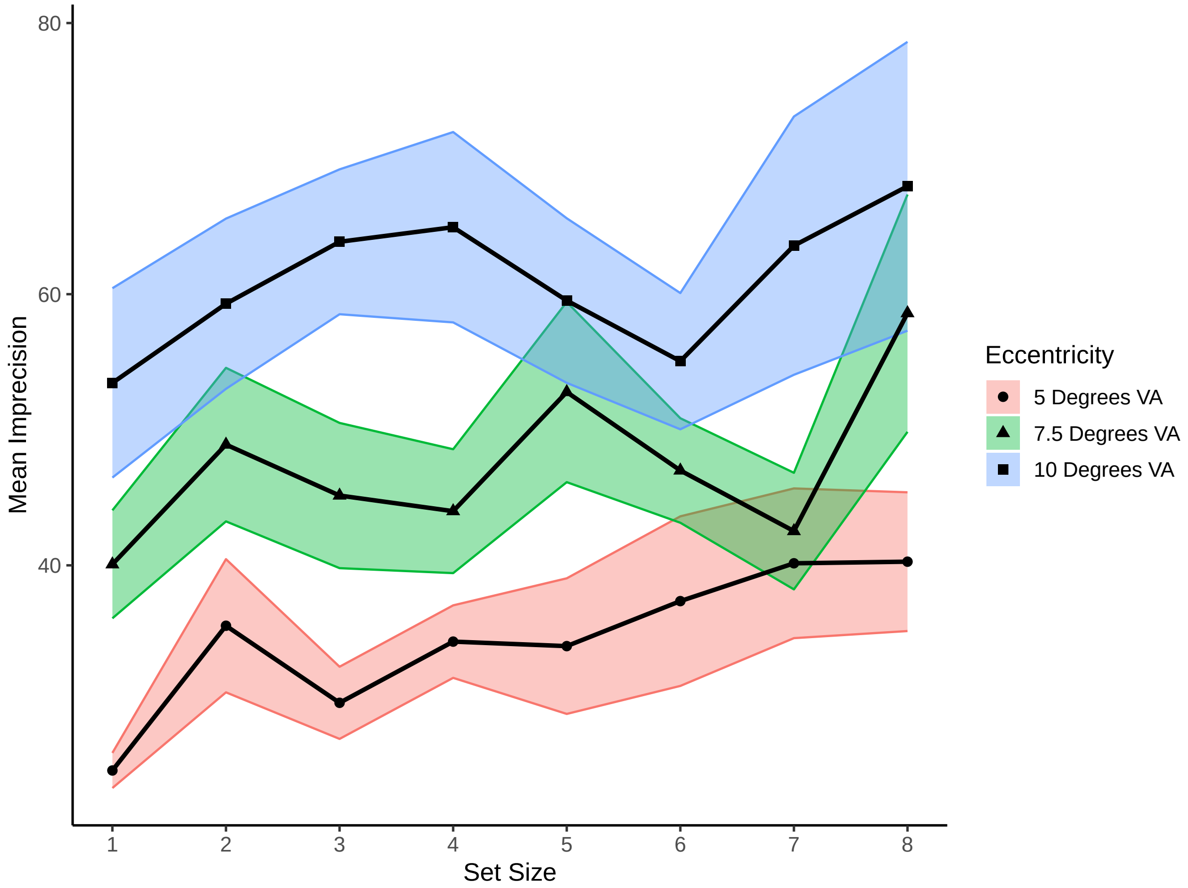

Figure 3.6: Mean imprecision as a function of set size for each eccentricity. The shaded regions represent SEM.

Holm-Bonferroni corrected pairwise comparisons between set size conditions revealed a significant difference between set size one (M = 39.47, SD = 19.76) and set size two (M = 47.92, SD = 21.4) only; p = .007. No other differences were significant; $p \geq =$ .906.

Preface to Chapter Four

The preceding experiments provided strong evidence for the resource model of VSWM, showing that the number and spatial location of memoranda can affect representation of spatial locations in VSWM. However, these experiments used simultaneously displayed arrays of memoranda. Previous tasks of spatial working memory have relied on participants remembering and recalling sequences of locations, such as in the Corsi Blocks task. There is little consensus on the distribution of resources across sequences of locations, with different serial position curves being observed during Corsi Blocks task (e.g. Guérard & Tremblay, 2008) and continuous report tasks (Gorgoraptis et al., 2011; Zokaei et al., 2011). Chapter Four aimed to examine whether these apparently conflicting serial position effects are due to differences in the nature of the recall task by directly comparing the serial position effects observed in whole and partial report continuous report tasks.

Note that the completion of this study was affected by restrictions imposed as a result of COVID-19. An online pilot study (n = 56) was carried out, which matched the procedural details reported in Experiment One, with the exception of the study being run on the participants' own devices. However, the results were unreliable due to the serial order curve in the sequential presentation condition being much weaker than reported in previously published studies. The power analysis for Experiment One was therefore based on Gorgoraptis et al. (2011). This study was chosen as the basis for the power analysis because it was deemed the most similar to the planned experiments, specifically with respect to the use of the continuous report task. However, it is important to note that the primary feature being recalled in Gorgoraptis et al. (2011) was orientation, whereas participants in Chapter Four were asked to recall spatial location. This difference in recalled features, and therefore the dissociation in the visual and spatial memory stores (Klauer & Zhao, 2004), meant that the power analysis was used as an indicative, rather than the definitive, minimum sample size.

In addition, the number of trials per condition was increased from 60 as in Chapter Two to 80. This decision was made to further increase the reliability of the model estimates after data were excluded due to eye movements. Because of the nature of the whole-report task, where one trial tested all serial positions, participants were able to complete the experiment in one session. However, in the single-report task, in which one trial was only testing one serial position, participants were tested across two sessions to minimise the effects of fatigue from the increased number of trials as participants were required to complete a total of 800 trials in Experiment Three compared to 320 trials in Experiments One and Two.

Chapter Four has been published in Journal of Vision: McAteer, S. M., Ablott, E., McGregor, A., & Smith, D. T. (2023). Dynamic resource allocation in spatial working memory during full and partial report tasks. *Journal of Vision, 23*(2), 10, 1-14, doi: 10.1167/jov.23.2.10.

Chapter 4

Dynamic Resource Allocation in Spatial Working Memory During Full- and Partial-Report Tasks

Serial position effects are well documented in working memory literature. Studies of spatial short-term memory that rely on binary response, whole-report tasks tend to report stronger primacy than recency effects. In contrast, studies that utilize a continuous response, partial-report task report stronger recency than primacy effects (Gorgoraptis et al., 2011; Zokaei et al., 2011). The current study explored the idea that probing spatial working memory using whole- and partial-report continuous response tasks would produce different distributions of visuospatial working memory resources across spatial sequences and, therefore, explain the conflicting results in the literature. Experiment One demonstrated that primacy effects were observed when memory was probed with a whole-report task. Experiment Two confirmed this finding while controlling eye movements. Critically, Experiment Three demonstrated that switching from a whole- to a partial-report task abolished the primacy effect and produced a recency effect, consistent with the idea that the distribution of resources in VSWM depends on the type of recall required. It is argued that the primacy effect in the whole-report task arose from the accumulation of noise caused by the execution of multiple spatially directed actions during recall, whereas the recency effect in the partial-report task reflects the redistribution of preallocated resources when an anticipated item is not presented. These data show that it is possible to reconcile apparently contradictory findings within the resource theory of spatial working memory and the importance of considering how memory is probed when interpreting behavioural data through the lens of resource theories of spatial working memory.

4.1 Introduction

Visuospatial working memory (VSWM) is the limited capacity store for the temporary maintenance and manipulation of spatial and non-spatial (visual) information (Baddeley, 2011; Baddeley & Hitch, 1974). There is continued debate surrounding the nature of capacity limitations in VSWM (Fallon et al., 2016; Luck & Vogel, 2013; Ma et al., 2014). One influential idea is that VSWM is a flexible and dynamic resource, which is distributed across all task-relevant items (Bays et al., 2009). The precision with which information is retained is dependent on the proportion of resource directed to each item. The resource model of VSWM has received considerable behavioural and neuroscientific support (for reviews, Fallon et al., 2016; Ma et al., 2014). However, the ways in which resources are distributed across visuospatial sequences are not well-understood. To examine the redistribution of resources across a sequence in VSWM, we investigated how memory for spatial locations and the corresponding response errors differ depending on set size and serial position.

Serial position effects have typically been examined in verbal memory tasks, where participants are asked to recall sequences of words. Studies have shown a primacy effect, where there is a sharp monotonic decrease in recall accuracy from the first serial position. There is also a small recency effect, where performance improves for the final item in the sequence (Murdock, 1968; Saint-Aubin & Poirier, 2000). These effects in verbal memory have been replicated in visuospatial memory (Guérard & Tremblay, 2008; Jones et al., 1995; Martín et al., 2017; Smyth & Scholey, 1996). Specifically, in spatial memory, Guérard & Tremblay (2008) asked participants to reconstruct a sequence of spatial locations after presentation of seven black dots. Performance was compared with a verbal memory task. The serial position curves observed in both spatial and verbal tasks were similar, exhibiting primacy and small recency effects. Transposition errors were more likely than omission errors, where no item is recalled, and this was found to increase across serial positions in both verbal and spatial tasks (Guérard & Tremblay, 2008). These effects have also been observed when visual-spatial movements (Agam et al., 2007, 2010,

2005) and auditory-spatial locations (Parmentier & Jones, 2000; Tremblay, Parmentier, et al., 2006) were examined, suggesting a reliable serial position effect across domains.

Studies examining serial position effects in VSWM have typically relied on binary response tasks, especially Corsi blocks task (Milner, 1971). While this task provides a reliable measurement of spatial working memory (Vandierendonck et al., 2004), the use of a binary response permits limited examination of the representations maintained in VSWM. The pattern of response errors across serial positions and how this might relate to the distribution of VSWM resources therefore remains unclear. The continuous report task (Wilken & Ma, 2004), which requires participants to reproduce a feature along a continuous dimension, permits a more detailed examination of VSWM representations and the sources of recall error (Bays et al., 2009; Zokaei et al., 2015). The continuous report task has been used extensively to investigate the representations of visual (Bays et al., 2009; Zhang & Luck, 2008) and spatial (Pertzov et al., 2012; Schneegans & Bays, 2016) features in VSWM. Behavioural studies using this approach to examine serial position effects indicate that the redistribution of VSWM resources across a sequence may not follow the serial position curve observed for quantized response tasks, in contrast to most models of serial order effects (Gorgoraptis et al., 2011; Zokaei et al., 2011). Specifically, Gorgoraptis et al. (2011) showed that, as the number of to-be-remembered items increased, precision in memory for orientation decreased monotonically. Across a sequence of to-be-remembered items, a strong recency effect was observed: precision was highest, with the lowest probability of misbinding, for the final presented item.

Such a strong recency effect was proposed to reflect dynamic redistribution of VSWM resources toward the most recently presented item. However, it is at odds with previous empirical work examining verbal and spatial working memory (Guérard & Tremblay, 2008) and is inconsistent with the predictions of computational models of serial position effects, which predict small recency effects (Hurlstone et al., 2014). One potential reason for this difference is that participants exposed to the continuous report paradigms did not necessarily have to rely on spatial representations to solve the task. The task used by Gorgoraptis et al. (2011) could be carried out without relying on spatial locations because the test orientation was probed by colour, even when spatial location was randomised in their Experiment 3. Their task relied only on memory for visual features rather than memory for visual-spatial conjunctions, which might explain why the serial position curve differed from previous findings in VSWM. The current study aimed to investigate the distribution of VSWM resources across sequences of spatial locations by examining the pattern of response errors across serial positions in a spatial continuous report task. This strategy permits the examination of whether performance in a spatial continuous report task, where visual and spatial features must be remembered, mirrors that of verbal tasks (Guérard & Tremblay, 2008), spatial tasks (Martín et al., 2017), or visual tasks (Gorgoraptis et al., 2011).

4.2 Experiment One

4.2.1 Methods

4.2.1.1 Participants

An *a priori* power analysis was carried out in G*Power v3.1 (Faul et al., 2007). We based this on Gorgoraptis et al. (2011), who reported a large effect of serial order on precision ($\eta_p^2 = .27$). We carried out a power analysis to detect a main effect of serial position using within-subjects analysis of variance with a factor of serial position with up to four levels, 90% power, and an alpha value of 0.05. The analysis indicated at least ten participants would be required for a set size of two, eight participants at set size three, and seven participants at set size four. We recruited eight students from Durham University ($M_{\text{age}} = 23.75$ years, $SD_{\text{age}} = 4.13$, 5 females, 3 males, 7 right handed, 1 left handed). Participants were compensated at a rate of £8/h for their time. This study received ethical approval from the Department of Psychology Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

4.2.1.2 Design

We used a mixed design with two independent variables. Our between-subjects independent variable was presentation mode (2 levels: sequential and simultaneous), and our within-subjects independent variable was set size (4 levels: 1, 2, 3, and 4 items). Serial position (up to 4 levels) was an additional within-subjects independent variable for the sequential presentation condition. The dependent variables were imprecision, and the probabilities of reporting the target location(s), non-target location(s), and guessing.

Participants were randomly assigned to one of the two presentation conditions. They first completed a block of eight practice trials, two of each set size. Practice trials were the same as the experimental trials, with the exception that participants were shown the correct locations as well as their own responses on screen. Once the practice trials were completed, participants completed 320 experimental trials, 80 of each set size, randomised across 16 blocks. Participants were free to take a self-paced break between blocks.

4.2.1.3 Stimuli and apparatus

The task was programmed using Matlab R2019a, using the psychophysics toolbox (Kleiner et al., 2007). The stimuli consisted of arrays comprising one, two, three, or four coloured dots (radius = 0.5° VA) and a fixation cross positioned at the centre of the screen (1° VA x 1° VA). The colours of each dot were chosen without repetition from a bank of seven distinct colours: red, orange, green, cyan, blue, magenta, and purple. The locations of the dots were chosen randomly within the annular region five to ten degrees of visual angle around central fixation, with at least 1.5° visual angle separating each dot. The visual mask comprised 800 coloured dots, like those presented at encoding, filling the annular space 5° to 10° of visual angle around central fixation. Participants were asked to respond as accurately and as quickly as possible. Participants were unaware that the area of stimulus presentation was constrained and were free to respond with any location on screen. Participants' gaze was monitored using a tower-mounted EyeLink 1000 eye tracker (SR Research). Stimuli were presented on a 20-inch CRT screen with a refresh rate of 85Hz. Participants sat 60cm from the computer screen, with the centre of the screen at eye level.

4.2.1.4 Procedure

Trials began with presentation of a fixation cross at the centre of the screen for 500 ms, followed by a blank screen for 500 ms. The stimulus array, comprising one, two, three, or four coloured dots, was then presented. In the simultaneous presentation condition, the array was shown for 2,000 ms. In the sequential presentation condition, each dot was shown for 500 ms, with a 500ms inter-stimulus delay. After presentation of the array, the visual mask was presented for 100 ms, followed by a 900 ms blank screen. Participants were then asked to respond with the locations of each dot presented on that trial, indexed by the coloured dot being shown at the centre of the screen and changing colour when the mouse was clicked. In sequential conditions, the order of responding was the same as the order of presentation. There was no time limit for responding. Responses were shown as an array on screen for 1000ms, after which a 1000-ms blank screen was shown, before the beginning of the next trial. An example trial for each condition is shown in Figure 4.1.

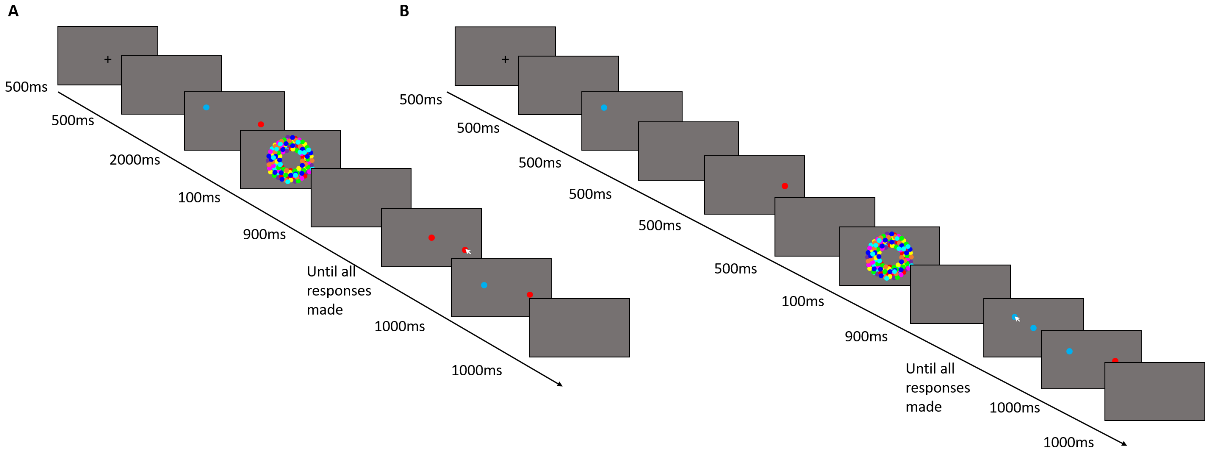

Figure 4.1: An example trial for simultaneous (A) and sequential (B) conditions.

4.2.1.5 Statistical analyses

Mixture modelling (Bays et al., 2009) was carried out using MemToolbox2D (Grogan et al., 2020). This mixture model (Bays et al., 2009) assumes that there are three sources of recall error: Gaussian variability in the response (imprecision), the height of which indicates the probability of reporting the target location; the probability of guessing, which is drawn from a uniform distribution; and the probability of responding with a non-target (misbinding), which is drawn from a Gaussian centred on one of the non-probed items. Maximum likelihood estimates were obtained for these sources of recall error in each condition. The estimate of guessing was corrected by assuming that responses were sampled from the annulus within which items could appear. Comparison of the corrected Akaike Information Criterion values for the model with and without this response sampling showed that the model that assumes response sampling provided a better fit in all experiments for all participants (*Experiment One:* ΔAICc = 20.19; *Experiment Two:* ΔAICc = 38.95; *Experiment Three:* ΔAICc = 30.69).

4.2.2 Results

An analysis of the effect of presentation mode is presented in Supplementary Materials S1. Briefly, there were no significant effects of presentation mode or interactions between presentation mode and set size. For the current analysis, we report only the data from the sequential presentation mode. We included all datasets in this condition. Examination of the eye tracking data revealed that, on average, approximately 20 saccades were made on each trial (M = 19.87, SD = 8.33, minimum = 1, maximum = 51).

Owing to the small sample size, we ran linear mixed effects model in R version 4.2.1 (R Core Team, 2019) using the `lmerTest` package (Kuznetsova et al., 2017), which applies Satterthwaite's method to estimate degrees of freedom and p values for the overall effect of serial position. The model was run on each set size to examine the effect of serial position after controlling for the random effect of participant. Serial position was included as a fixed effect and we included participant ID as a random effect.[9] Bonferroni-Holm corrected post hoc contrasts of the estimated marginal means were carried out to examine any significant effects, using the `emmeans` package (Lenth, 2022).

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[9] For all set sizes, the formula for the model was as follows for imprecision: imprecision ~ serial position + (1|ID)

For imprecision (Figure 4.2A), a significant effect of serial position was observed at set size four, $F(3,\, 9) = 4.96$, $p = .027$. The effect of serial position was not significant at set size two, $F(1,\, 3) = 0.37$, $p = .587$, or set size three, $F(2,\, 6) = 4.33$, $p = .069$. Post hoc pairwise comparisons between serial positions revealed a significant difference between the first and second item at set size four ($p = .037$). No other comparisons were significant ($p \geq 1.000$).

For the probability of reporting the target (Figure 4.2B), no significant effects of serial position were observed at set sizes two, $F(1,\, 3) = 0.55$, $p = .513$, three, $F(2,\, 6) = 1.12$, $p = .387$, and four, $F(3,\, 9) = 1.22$, $p = .357$.

For the probability of misbinding (Figure 4.2C), a significant effect of serial position was observed at set size four, $F(3,\, 9) = 4.67$, $p = .031$. The effect of serial position was not significant at set sizes two, $F(1,\, 3) = 2.73$, $p = .197$, and three, $F(2,\, 9) = 0.06$, $p = .946$. Post hoc pairwise comparisons between serial positions revealed no significant differences between items at set size four ($p \geq 0.145$).

For the probability of guessing (Figure 4.2D), the effect of serial position was not significant at any set size, *set size two,* $F(1,\, 3) = 0.96$, $p = .400$; *set size three,* $F(2,\, 9) = 0.35$, $p = .715$; *set size four,* $F(3,\, 12) = 0.62$, $p = .617$.

4.2.3 Discussion

This experiment aimed to examine the distribution of VSWM resources across sequences of spatial locations. We observed a weak primacy effect; the first presented item was remembered more precisely than items presented later in the sequence, although these effects did not reach significance. There were no effects of serial position or set size on the probability of guessing, indicating that all items were encoded into memory but with increasing noise as the sequence length increased. This pattern of results is broadly consistent with prior work that reports primacy effects in tasks that measure spatial working memory (Martín et al., 2017). However, these results are inconsistent with previous work using visual continuous report tasks (Gorgoraptis et al., 2011; Zokaei et al., 2011).

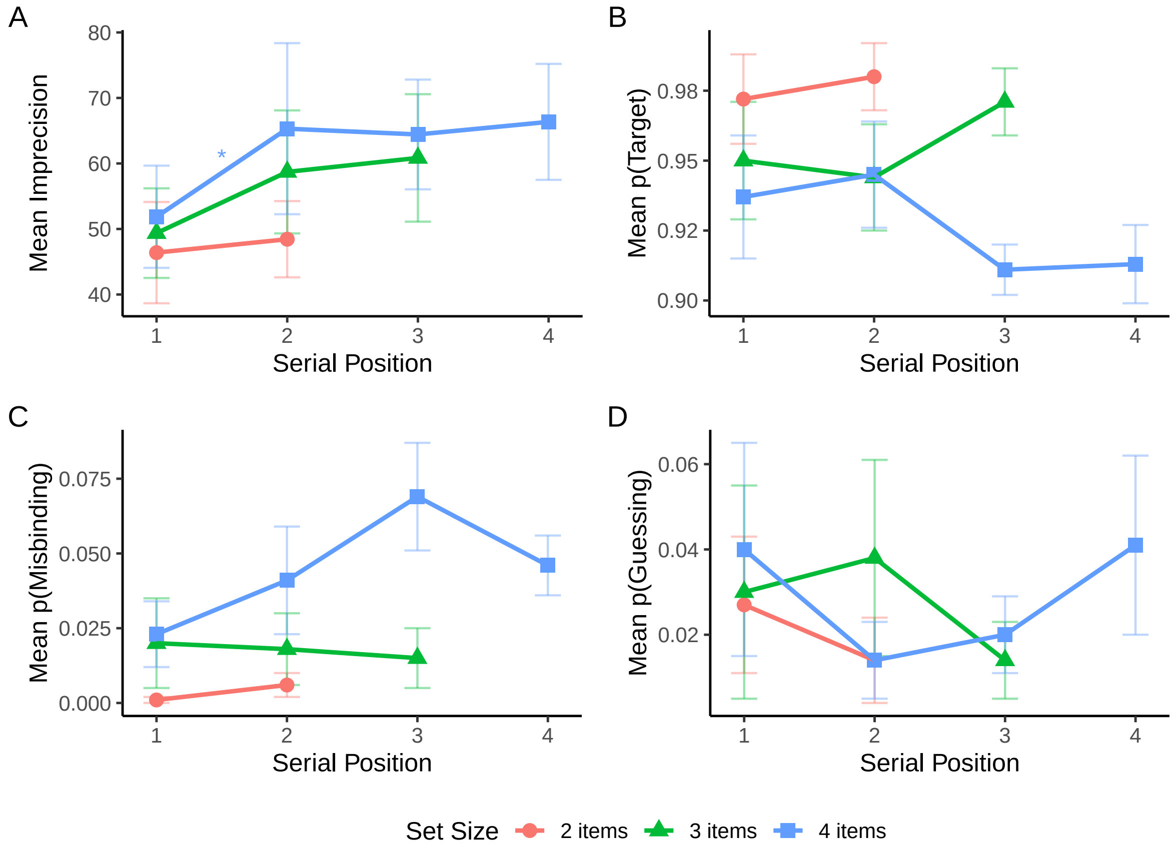

Figure 4.2: Mean imprecision (A), probability of reporting the target location (B), probability of misbinding (C), and probability of guessing (D) for each set size in the sequential presentation condition as a function of serial position. Error bars represent the standard error of the mean.

There are key differences in our task and previous work (Gorgoraptis et al., 2011; Zokaei et al., 2011), which might account for the differences in the serial position effects observed. First, central fixation was not enforced in our experiment but was enforced in Gorgoraptis et al. (2011). Although participants tend to make few on-item fixations when encoding under free viewing conditions (Lange & Engbert, 2013; Patt et al., 2014; Souza et al., 2020), Saint-Aubin et al. (2007) have shown that the number and duration of fixations on task-relevant items is positively correlated with recall performance. Similarly, Martín et al. (2017) observed that target-directed saccades improved recall accuracy for small set sizes. It may be that allowing participants to move their eyes freely throughout encoding and maintenance improved recall for the first item, but noise accumulated in the sequence of eye movements throughout encoding and maintenance, resulting in increased imprecision for these items.

The second key difference is that we used a whole report task, whereas Gorgoraptis et al. (2011) and Zokaei et al. (2011) used a single probe task. It is well-documented that the nature of the recall task affects recall performance (Sperling, 1960). Asking participants to recall one item from a sequence may result in VSWM resources being distributed across a sequence differently from when the whole sequence must be reported.

We carried out two further experiments to examine whether these differences underlie the primacy effect observed in the current experiment.

4.3 Experiment Two

We carried out a second experiment to examine whether the difference in viewing conditions between previous work (Gorgoraptis et al., 2011; Zokaei et al., 2011) and Experiment One might underlie the differences in the serial order curves observed.

4.3.1 Methods

4.3.1.1 Participants

We recruited 14 students from Durham University ($M_{\text{age}} = 29.43$ years, $SD_{\text{age}} = 9.18$, 9 females, 4 males, 1 nonbinary, 12 right handed). Undergraduate students enrolled on Psychology courses at Durham University ($n = 3$) were credited with participant pool time in exchange for their participation. Other participants ($n = 11$) were compensated at a rate of £8/h for their time. This study received ethical approval from the Department of Psychology Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

4.3.1.2 Design

The design was the same as Experiment One.

4.3.1.3 Stimuli and apparatus

The stimuli and apparatus matched those of Experiment One.

4.3.1.4 Procedure

The procedure followed Experiment One, with the exception that participants were asked to maintain central fixation throughout each trial.

4.3.2 Results

Trials in which average saccade amplitude exceeded 2° VA during encoding and maintenance were excluded from analysis. This process led to the exclusion of four datasets and the exclusion of 16.62% of trials from the remaining 10 datasets. An analysis of the effect of presentation mode is presented in Supplementary Materials S2 and S3. Briefly, there were no significant effects of presentation mode or interactions between presentation mode and set size, and free viewing improved recall precision of single-item displays. The linear mixed effects model matched the serial position analysis in Experiment One, which included serial position as a fixed effect and participant ID as a random effect.

For imprecision (Figure 4.3A), a significant effect of serial position was found at set size two, $F(1,\ 4) = 9.01$, $p = .040$, and set size four, $F(3,\ 12) = 4.32$, $p = .028$. The effect of serial position was not significant at set size three, $F(2,\ 8) = 3.41$, $p = .085$. Post hoc pairwise comparisons using Bonferroni-Holm correction between serial positions revealed no significant differences between items at set size four ($p \geq 0.084$).

For the probability of reporting the target location (Figure 4.3B), a significant effect of serial position was observed at set sizes three, $F(2,\ 8) = 7.9$, $p = .013$, and four, $F(3,\ 12) = 5.89$, $p = .010$. The effect of serial position was not significant at set size two, $F(1,\ 4) = 0.02$, $p = .884$. Post hoc pairwise comparisons using Bonferroni-Holm correction between serial positions revealed a significant difference between the first and second presented item at set size three ($p = .036$). No other differences were significant at set size three ($p \geq 0.435$) or set size four ($p \geq 0.095$).

For the probability of misbinding (Figure 4.3C), a significant main effect of serial position was found at set size four, $F(3,\ 12) = 4.84$, $p = .020$. There was no significant effect of serial position at set size two, $F(1,\ 4) = 2.58$, $p = .184$, or set size three, $F(2,\ 8) = 1.27$, $p = .331$. Post hoc pairwise comparisons using Bonferroni-Holm correction between serial positions revealed no significant differences at set size four ($p \geq 0.075$).

For the probability of guessing (Figure 4.3D), the main effect of serial position was significant at set size three, $F(2,\ 8) = 6.85$, $p = .018$. The effect of serial position was not significant at set sizes two, $F(1,\ 4) = 0.33$, $p = .599$, or four, $F(3,\ 12) = 2.3$, $p = .129$. Post hoc pairwise comparisons using Bonferroni-Holm correction between serial positions revealed no significant differences between items at set size three ($p \geq 0.053$).

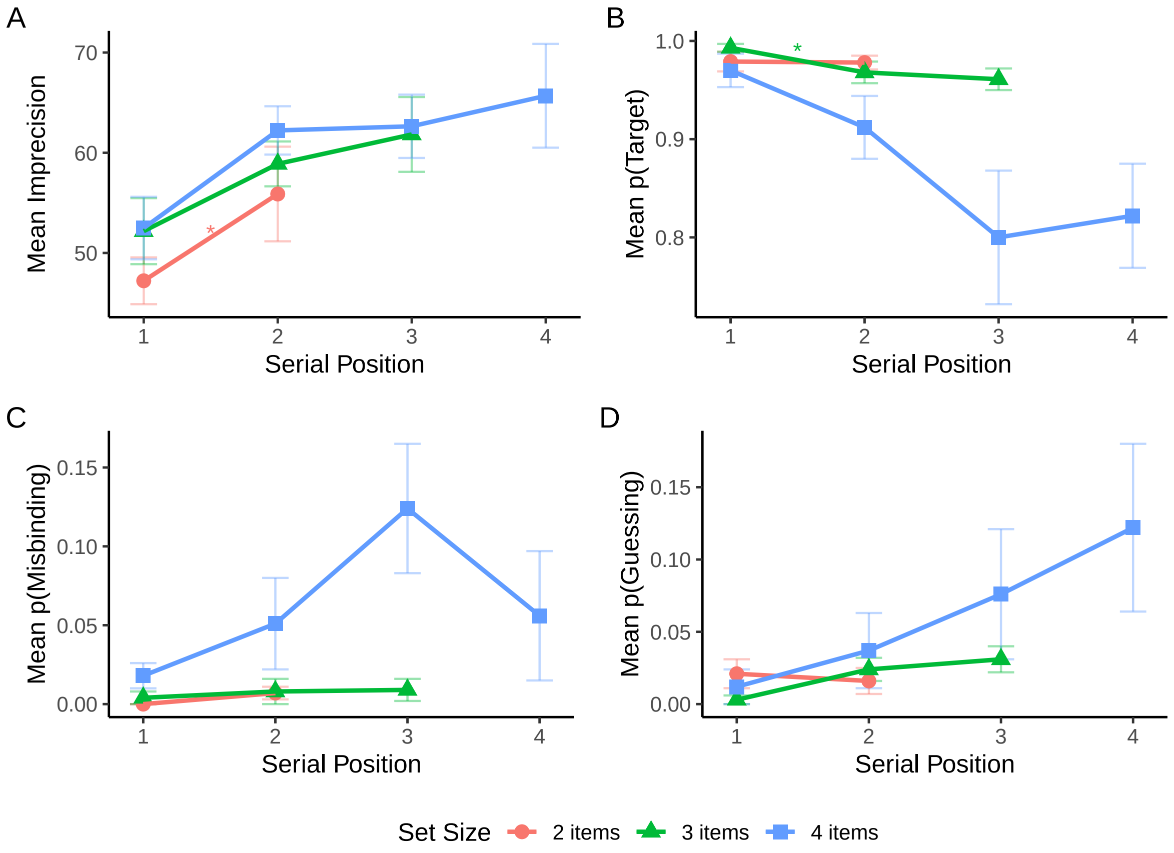

Figure 4.3: Mean imprecision (A), probability of reporting the target location (B), probability of misbinding (C), and probability of guessing (D) for each set size in the sequential presentation condition as a function of serial position. Error bars represent the standard error of the mean.

4.3.2.1 Comparison between free (Experiment One) and fixed (Experiment Two) viewing

We examined whether the instruction to maintain central fixation affected imprecision in VSWM using linear mixed effects model (Figure 4.4). Presentation mode and viewing condition were included as fixed effects, and participant ID was included as a random effect.[10]

There was no main effect of viewing condition on imprecision at any set size ($p \geq 0.573$). Serial position and viewing condition did not interact at any set size ($p \geq 0.178$). The effect of serial position was significant at set size two, $F(1, 7) = 5.88$, $p = .046$, set size three, $F(2, 14) = 7.67$, $p = .006$, and set size four, $F(3, 21) = 9.17$, $p < .001$. The difference between the first and second item was significant at set size three ($p = .026$) and set size four ($p = .002$). No other differences were significant ($p_{\text{ss3}} \geq 0.383$, $p_{\text{ss4}} \geq 0.806$).

4.3.3 Discussion

This experiment examined whether the requirement to maintain central fixation would reverse the primacy effect in spatial working memory observed in Experiment One to the recency effect observed in previous studies (Gorgoraptis et al., 2011; Zokaei et al., 2011). Contrary to this idea, we observed a primacy effect in Experiment Two. Indeed, when we compared imprecision across Experiments One and Two, the primacy effect was stronger in Experiment Two, with the first item of the list being represented more precisely in VSWM than subsequent items. This result appears to rule out the possibility that the discrepancy between our findings and those of Gorgoraptis et al. (2011) and Zokaei et al. (2011) can be explained by participants using different oculomotor strategies. An alternative explanation for the discrepant findings relates to the nature of the task. More specifically, we used a whole-report task, whereas previous work (Gorgoraptis et al., 2011; Zokaei et al., 2011) used a partial-report task that required participants to

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[10] The formula for the model was as follows: imprecision ~ serial position + viewing condition + serial position*viewing condition + (1|ID)

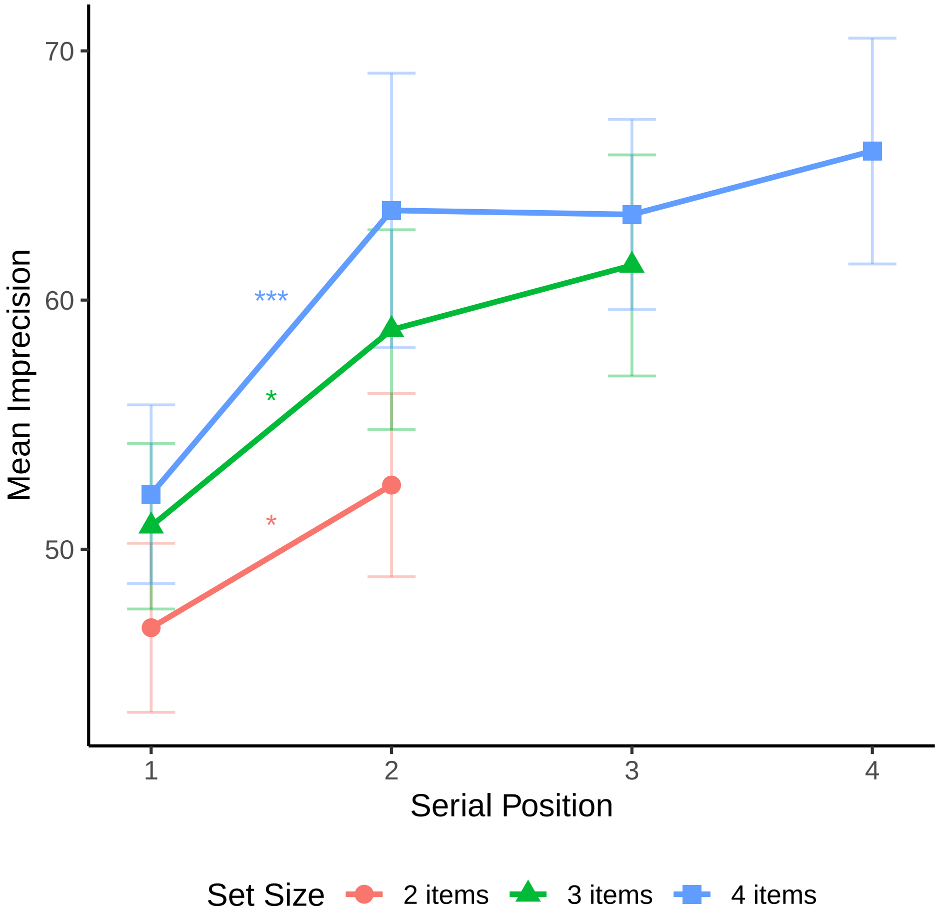

Figure 4.4: Mean imprecision for each serial position as a function of set size in the sequential presentation conditions collapsed across Experiments One and Two. Error bars represent SEM.

recall information about one of the presented items. This difference might have affected how resources were distributed throughout both tasks. In Gorgoraptis et al. (2011) and Zokaei et al. (2011), participants were unaware which item was task relevant. It was argued that resources were distributed towards the most task-relevant item, which was presumed to be the most recent item. Gorgoraptis et al. (2011) subsequently used a cue to explicitly indicate a task-relevant item. Precision was found to increase for the most task-relevant item regardless of serial position. In contrast, in our task, all items were equally relevant for successful task competition, which is likely to have resulted in resources being distributed differently compared with when only a single probe is used at recall. The possibility was examined in Experiment Three.

It is worth noting that imprecision was lower at set size one in free viewing compared with fixed viewing (see S3). This may be due to the fact that that item was fixated, resulting in a boost in its representation from an additional resource, as outlined in the model proposed by Udale et al. (2022).

4.4 Experiment Three

We carried out a third experiment to investigate the possibility that the contrasting effects observed in Experiments One and Two and previous work (Gorgoraptis et al., 2011; Zokaei et al., 2011) are due to differences in the nature of the task.

4.4.1 Methods

4.4.1.1 Participants

We based the minimum sample size on an *a priori* power analysis was carried out in G*Power v3.1 (Faul et al., 2007) based on Gorgoraptis et al. (2011), who reported a large effect of serial order for precision ($\eta_p^2 = .27$). We carried out a power analysis for within-subjects analysis of variance with factor of serial position, with up to four levels, with 90% power and an alpha of 0.05. To detect this main effect at set size three, we required a sample size of at least eight participants, and at least seven were required to detect the same effect at set size four. We recruited 10 students from Durham University ($M_{\text{age}} = 19.4$ years, $SD_{\text{age}} = 0.97$ years, 8 females, 1 male, 1 other/prefer not to say, 10 right handed). All participants reported having normal or corrected-to-normal vision. Participants were compensated £10 for their time. This study received ethical approval from the Department of Psychology Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

4.4.1.2 Design

Design was the same as Experiment Two with the exception that only sequential presentation mode was examined. Participants were asked to recall the location of one item from the display at test. Each set size and serial position was tested 80 times over 2 sessions.

Each session comprised 20 blocks of 20 trials, resulting in each participant completing a total of 800 trials.

4.4.1.3 Stimuli and apparatus

The stimuli and apparatus matched those of Experiments One and Two.

4.4.1.4 Procedure

The procedure followed Experiment Two.

4.4.2 Results

One participant was excluded from analysis as they did not complete the full experiment. No other data was excluded. The linear mixed effects models matched the serial position analysis in Experiments One and Two, which included serial position as a fixed effect and participant ID as a random effect for each set size.

For imprecision (Figure 4.5A), a significant effect of serial position was found for set size two, such that imprecision was higher for the first item than the second item in the sequence, $F(1, 8) = 34.46$, $p < .001$. The effect of serial position was also significant at set size three, $F(2, 16) = 5.97$, $p = .012$, but no pairwise comparisons were significant ($p \geq 0.455$). The effect of serial position was not significant at set size four, $F(3, 24) = 0.54$, $p = .661$.

For the probability of reporting the target location (Figure 4.5B), the effect of serial position was not significant at set size two, $F(1, 8) = 0.34$, $p = .575$, three, $F(2, 16) = 0.74$, $p = .492$, or four, $F(3, 24) = 1.21$, $p = .328$.

Similarly, for the probability of misbinding (Figure 4.5C), the effect of serial position was not significant at set size two, $F(1, 8) = 2.27$, $p = .170$, three, $F(2, 16) = 0.13$, $p = .876$, or four, $F(3, 24) = 0.9$, $p = .453$.

Finally, for the probability of guessing (Figure 4.5D), the effect of serial position was not significant at set size two, $F(1, 8) = 0.01$, $p = .917$, three, $F(2, 16) = 3.38$, $p = .060$, or four, $F(3, 24) = 1.41$, $p = .264$.

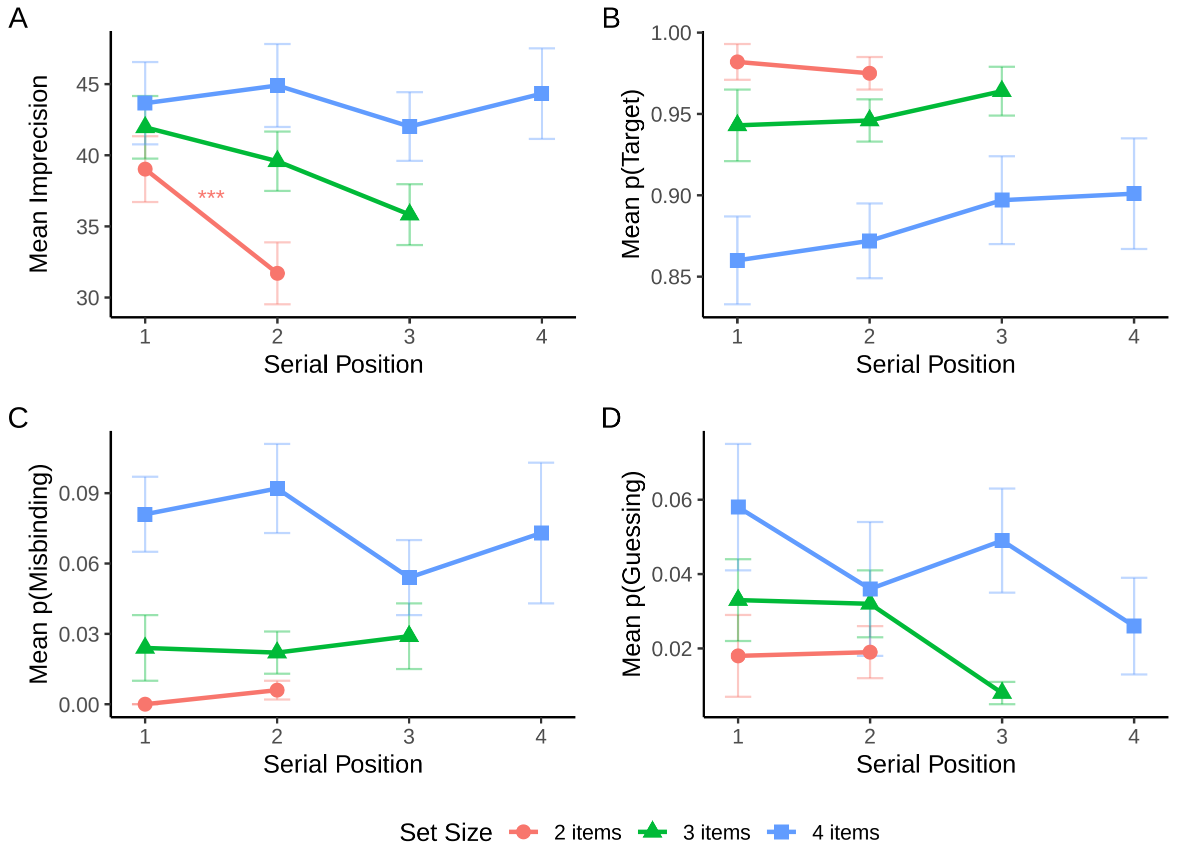

Figure 4.5: Mean imprecision (A), probability of reporting the target location (B), probability of misbinding (C), and probability of guessing (D) for each set size as a function of serial position. Error bars represent the standard error of the mean.

4.4.2.1 Comparison between whole-report (Experiments One and Two) and single-probe (Experiment Three)

We also compared imprecision between our whole-report tasks (Experiments One and Two) and our single-probe task (Experiment Three) to examine whether and how the serial position effect was affected by changing the nature of the recall task. The linear mixed effects model was carried out at each set size and included fixed effects of serial position, and recall task, as well as the interactions between recall task and serial position. We included participant ID as a random effect.[11]

We found a significant main effect of recall task at all set sizes, where imprecision in the

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[11] The formula for the model was as follows: imprecision ~ serial position + recall task + serial position*recall task + (1|ID)

whole-report task was significantly greater than in the single-probe task at each set size; *set size two,* $F(1,\ 16) = 13.05$, $p = .002$; *set size three,* $F(1,\ 16) = 18.92$, $p < .001$; and *set size four,* $F(1,\ 16) = 13.55$, $p = .002$.

A significant interaction between recall task and serial position was also observed at every set size; *set size two,* $F(1,\ 16) = 23.91$, $p < .001$; *set size three,* $F(2,\ 32) = 13.79$, $p < .001$; *and set size four,* $F(3,\ 48) = 5.73$, $p = .002$. To examine what was driving these interactions, we analysed the serial position effects for single-probe and whole-report tasks at each set size (Figure 4.6). There were significant serial position effects on whole-report tasks at all set sizes; *set size two:* $F(1,\ 16) = 9.2$, $p = .008$; *set size three:* $F(2,\ 32) = 11.68$, $p < .001$; *set size four:* $F(3,\ 48) = 11.5$, $p < .001$. There was a significant serial position effect on the single-probe task at set sizes two, $F(1,\ 16) = 15.07$, $p = .001$, and three, $F(2,\ 32) = 3.76$, $p = .034$. The serial position effect was not significant at set size four on the single-probe task, $F(3,\ 48) = 0.47$, $p = .705$.

We then compared the serial position effects in each recall task at each set size using Holm-Bonferroni corrected pairwise comparisons. At set size two, there was a primacy effect on the whole-report task, where the first item was remembered with greater precision than the second item ($p = .008$). This pattern was reversed in the single-probe task ($p = .001$). At set size three, the first item was remembered more precisely than the second item on the whole-report task ($p = .003$). No other comparisons were significant for either task ($p \geq 0.212$). The same pattern was observed at set size four, with the first item being remembered more precisely than the second item on the whole-report task ($p < .001$). No other comparisons were significant for either task ($p \geq 0.656$).

4.4.3 Discussion

This experiment examined the effect of moving from a whole-report to a partial-report task on the distribution of memory resources. The key finding was of a significant interaction between serial position and report type, such that imprecision significantly decreased with serial position in the partial-report task (a recency effect) but significantly increased

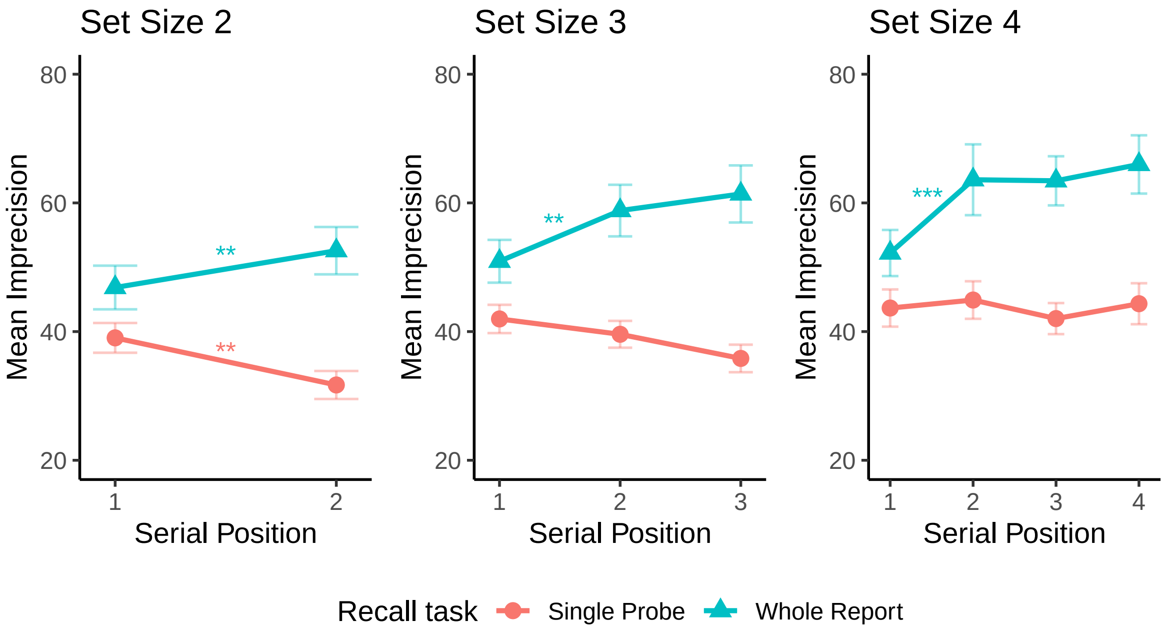

Figure 4.6: Mean imprecision for whole report (sequential presentation mode only) and single probe tasks as a function of serial position at each set size. Error bars represent the standard error of the mean.

with serial position in the whole-report task (a primacy effect). This recency effect was strongest at set size two, where the first presented item was recalled less precisely than the second presented item. The presence of a recency effect in this experiment suggests that the difference in serial position effects found in Experiments One and Two and those found by Gorgoraptis et al. (2011) and Zokaei et al. (2011) are a consequence of differences in the task used. The fact that changing the task from a whole-report to a single-report produces a very different pattern of data is consistent with the idea that the difference in the nature of the recall in the task (i.e., whether the task is whole-report or single-probe report) plays an important role in the distribution of resources.

4.5 General discussion

The current study explored how VSWM resources are distributed across sequences by examining the sources of recall error for sequences of spatial locations. When participants were asked to report all locations presented in a sequence, a primacy effect was observed for imprecision and misbinding, regardless of whether participants were free to move their eyes (Experiment One) or maintained fixation (Experiment Two). The whole-report task also required participants to make a sequence of goal-directed actions, as they were required to move the mouse to the correct location of item *N* while simultaneously maintaining the locations of items *N+1*, *N+2*, etc. Goal-directed actions are known to disrupt VSWM (Lawrence et al., 2001; McAteer et al., 2023; Pearson & Sahraie, 2003; Smyth & Scholey, 1994)[12] and increase imprecision as each action requires spatial updating that introduces noise into stored spatial representations (McAteer et al., 2023; Peterson et al., 2019)[13]. It therefore seems likely that the act of responding itself introduced additional noise into the representations of yet-to-be-reported items, resulting in a cumulative increase in imprecision across serial positions, and a primacy effect in the whole-report task. Consistent with this explanation, when four items were presented but only a single response was required in Experiment Three, the serial position effect was abolished (see Figure 4.6).

When a single-probe task was used (Experiment Three), a recency effect was observed. This recency effect is broadly consistent with previous work using a single-probe continuous report task in visual working memory (Gorgoraptis et al., 2011; Zokaei et al., 2011). One potential explanation for the existence of the recency effect is the dual-resource model, which proposes that encoding occurs via drawing on one resource pool to attend to an item before drawing on a second resource pool to retain the item following execution of a saccade towards that item (Udale et al., 2022). The implication of this model is that the final saccade target is represented more precisely in memory than preceding items. The recency effect observed in our Experiment Three was weaker than recency effects reported previously (Gorgoraptis et al., 2011; Udale et al., 2022; Zokaei et al., 2011). This difference may be due to the fact that we did not enforce any viewing strategy. In previous work, participants were required to maintain central fixation (Gorgoraptis et al., 2011) or were instructed make a series of saccades towards items (Udale et al., 2022). These viewing strategies are not reflective of natural viewing behaviour, indicating that the strength of the recency effect might also depend on viewing behaviour. Additionally,

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[12] McAteer et al. (2023) refers to the data presented in Chapter Five.

[13] McAteer et al. (2023) refers to the data presented in Chapter Five.

we found that imprecision was relatively stable across serial positions at set size four, which might indicate that participants learned that a maximum of four items would be presented. This learning might have resulted in resources being pre-allocated across four potential items before encoding. When fewer than four items were presented, the remaining resource was allocated to the final presented item. This flexibility in resource allocation reflects the dynamic nature of VSWM, and might represent an efficient strategy for task completion in single probe tasks in which it is not clear which item will be probed. Future work might examine this hypothesis across a larger number of set sizes, and in conditions where participants are instructed as to how many stimuli will be presented.

We also observed that VSWM precision was significantly reduced on the whole-report task compared with the single-probe task, consistent with the well-documented effect that performance on partial-report tasks is better than on whole-report tasks (Sperling, 1960). This effect was present for the first item, so cannot be fully explained by the response-induced noise account outlined above. An alternative explanation is that it reflects the use of different reference frames in whole-report and single-probe tasks. In the whole-report task, participants were required to recreate the full sequence of spatial locations at recall. The first item in the sequence was always recalled relative to central fixation, but subsequent items were recalled relative to the previously reported location. Participants may therefore have relied on global/relational information and a spatiotopic reference frame. Conversely, in the single-probe task, the sequence was almost irrelevant to task completion because recall of the probe item was always cued by the object colour not its place in the sequence, and initiated from the centre of the screen. The successful recall of the location in the single-probe task therefore relied on local information and a retinotopic reference frame. The maintenance of spatial locations is associated with activation in retinotopic spatial maps in visual areas and parietal cortex (Ester et al., 2009; Jerde et al., 2012; Pratte & Tong, 2014; Serences et al., 2009) consistent with the view that the default reference frame for representing spatial locations is retinotopic (Golomb & Kanwisher, 2012). Transformation from a retinotopic into a spatiotopic reference frame is noisy, leading to reduced memory performance (Golomb & Kanwisher, 2012; Shafer-

Skelton & Golomb, 2018). This noisy conversion explanation aligns with our observation that memory was less precise on the whole report task compared with the single probe task at all serial positions.

The flexibility in the use of retinotopic and spatiotopic reference frames highlights the flexibility in VSWM, where the nature of representation depends on task demands (Serences, 2016), which may include the nature of the recall task. However, it should be noted that our range of set-sizes (two to four) was somewhat smaller than those typically used to examine serial order effects (set sizes of one to seven) and it is possible that other or larger differences in the distribution of resources across items might emerge at larger set sizes. Additionally, it is possible that some subtle effects were missed in the analysis owing to the small sample sizes used. However, the overall trend of the data indicates that the distribution of resources depends on the nature of the recall task used, which was the key research question.

To summarise, we found evidence for a primacy effect in VSWM when participants were asked to recall all presented spatial locations in sequence (Experiments One and Two). These observations are not consistent with previous work using the continuous report task, which reported large recency effects (Gorgoraptis et al., 2011; Zokaei et al., 2011). However, when a single-probe task (Experiment Three) was used, a recency effect was observed, which is more consistent with previous work. We propose that the primacy effect in the whole-report task arises from the accumulation of noise caused by the execution of multiple spatially directed actions during recall, whereas the recency effect in the partial-report task reflects the redistribution of preallocated resources when an anticipated item is not presented. The fact that subtle differences in the nature of the recall task determines how resources are allocated demonstrates the flexible and dynamic nature of resource allocation in VSWM (Bays et al., 2009; Udale et al., 2022).

4.6 Supplementary Material

4.6.1 Experiment One (Free Viewing) Presentation Mode Analysis

The linear mixed effects model included fixed effects of set size and presentation mode, as well as the interaction between set size and presentation mode. We included participant ID as a random effect.[14] Effects in the sequential presentation mode were collapsed across serial positions.

For imprecision (Figure 4.7A), a significant effect of set size was observed; $F(3,\ 18) = 43.71$, $p < .001$. The effect of presentation mode [$F(1,\ 6) = 0.43$, $p = .536$] and the interaction between presentation mode and set size [$F(3,\ 18) = 1.71$, $p = .201$] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed a significant difference between set size one ($M = 24.86$, $SD = 10.6$) and set size two ($M = 46.89$, $SD = 12.12$); $p < .001$. No other comparisons were significant; $p \geq 0.079$.

For the probability of reporting the target location (Figure 4.7B), a significant effect of set size was found; $F(3,\ 18) = 6.11$, $p = .005$. The effect of presentation mode [$F(1,\ 6) = 0.66$, $p = .447$] and the interaction between set size and presentation mode [$F(3,\ 18) = 0.83$, $p = .494$] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed no significant differences between set sizes; $p \geq 0.066$.

For the probability of misbinding (Figure 4.7C), a significant effect of set size was found; $F(3,\ 18) = 6.36$, $p = .004$. The effect of presentation mode [$F(1,\ 6) = 0.04$, $p = .849$] and the interaction between set size and presentation mode [$F(3,\ 18) = 0.05$, $p = .986$] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed no significant differences between adjacent set sizes; $p \geq 0.067$.

For the probability of guessing (Figure 4.7D), no significant effects of set size [$F(3,\ 18) = 1.61$, $p = .222$], presentation mode [$F(1,\ 6) = 1.54$, $p = .261$], or the interaction between

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[14] The formula for the model was as follows for imprecision: imprecision ~ set size + presentation mode + set size*presentation mode + (1|ID)

set size and presentation mode [$F(3,\,18) = 1.09$, $p = .380$] were found.

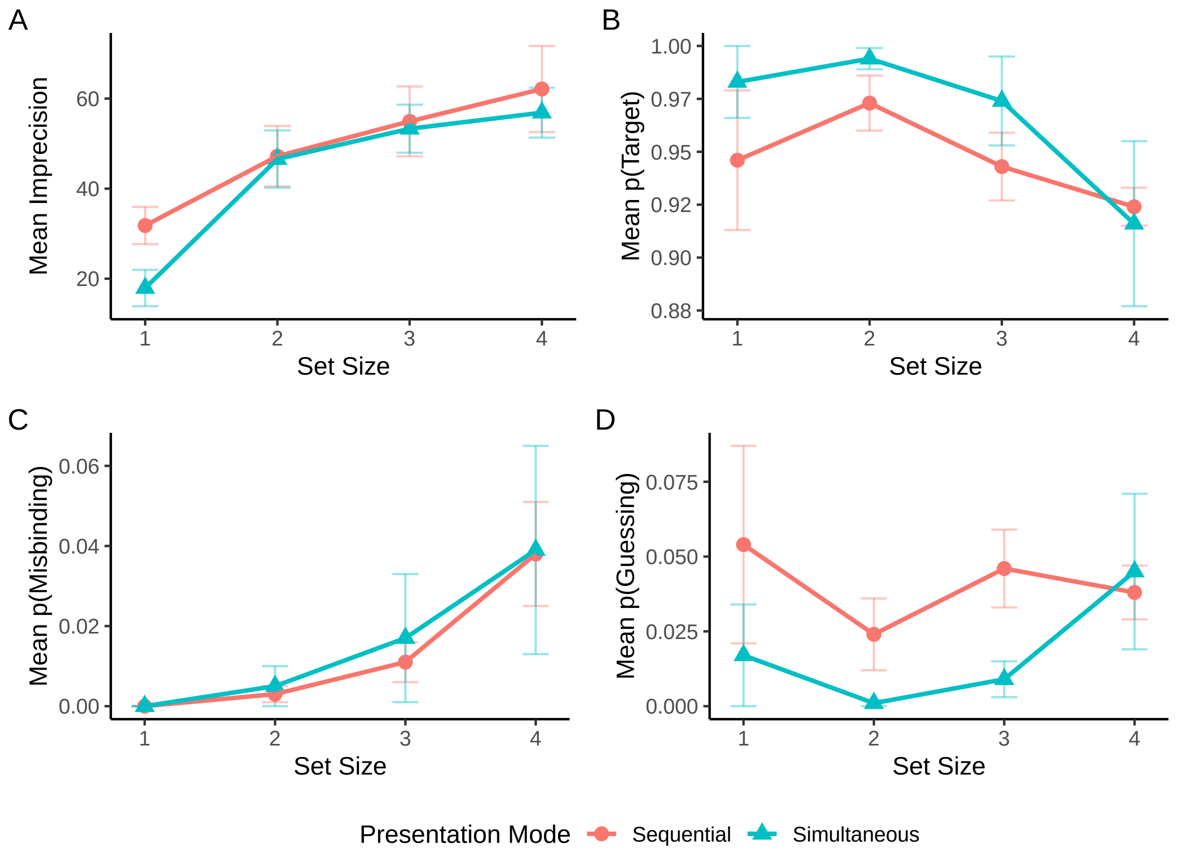

Figure 4.7: Mean imprecision (A), probability of reporting the target location (B), probability of misbinding (C), and probability of guessing (D) for each presentation mode as a function of set size. Effects in sequential presentation mode are collapsed across serial order. Error bars represent the standard error of the mean.

4.6.2 Experiment Two (Fixed Viewing) Presentation Mode Analysis

For imprecision (Figure 4.8A), a significant effect of set size was observed; $F(3,\,24) = 10.24$, $p < .001$. The effect of presentation mode [$F(1,\,8) = 0.64$, $p = .448$] and the interaction between presentation mode and set size [$F(3,\,24) = 2.95$, $p = .053$] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed no significant differences between adjacent set sizes; $p \geq 0.123$.

For the probability of reporting the target location (Figure 4.8B), a significant effect of set size was found; $F(3,\,24) = 12.26$, $p < .001$. The effect of presentation mode [$F(1,\,8)$

= 3.86, p = .085] and the interaction between set size and presentation mode [F(3, 24) = 0.97, p = .422] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed a significant difference between set size three (*M* = 0.98, *SD* = 0.02) and set size four (*M* = 0.89, *SD* = 0.09); $p < .001$. No other differences were significant; $p \geq 1.000$.

For the probability of misbinding (Figure 4.8C), a significant effect of set size was found; F(3, 24) = 7.94, $p < .001$. The effect of presentation mode [F(1, 8) = 0.16, p = .698] and the interaction between set size and presentation mode [F(3, 24) = 0.09, p = .963] were not significant. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed a significant difference between set size three [*M* = 0.01, *SD* = 0.02] and set size four [*M* = 0.06, *SD* = 0.06]; p = .005 . No other differences were significant; $p \geq 1.000$.

For the probability of guessing (Figure 4.8D), significant effects of set size [F(3, 24) = 4, p = .019] and presentation mode [F(1, 8) = 12.37, p = .008] were observed, such that guessing was significantly higher on sequential (*M* = 0.04, *SD* = 0.05) compared to simultaneous (*M* = 0, *SD* = 0.01) presented arrays. The interaction between set size and presentation mode was not significant; F(3, 24) = 2.27, p = .106. Bonferroni-Holm corrected pairwise comparisons between set sizes revealed a significant difference between set size three (*M* = 0.01, *SD* = 0.02) and set size four (*M* = 0.05, *SD* = 0.06); p = .047. No other differences were significant; $p \geq 1.000$.

4.6.3 Comparison between Experiment One and Experiment Two

We examined whether the instruction to maintain central fixation affected imprecision in VSWM using linear mixed effects model (Figure 4.9). Set size, presentation mode and viewing condition were included as fixed effects, and participant ID was included as a random effect[15].

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[15] The formula for the model was as follows: imprecision ~ set size + presentation mode + viewing condition + set size*presentation mode + set size*viewing condition + set size*presentation mode*viewing condition + (1|ID)

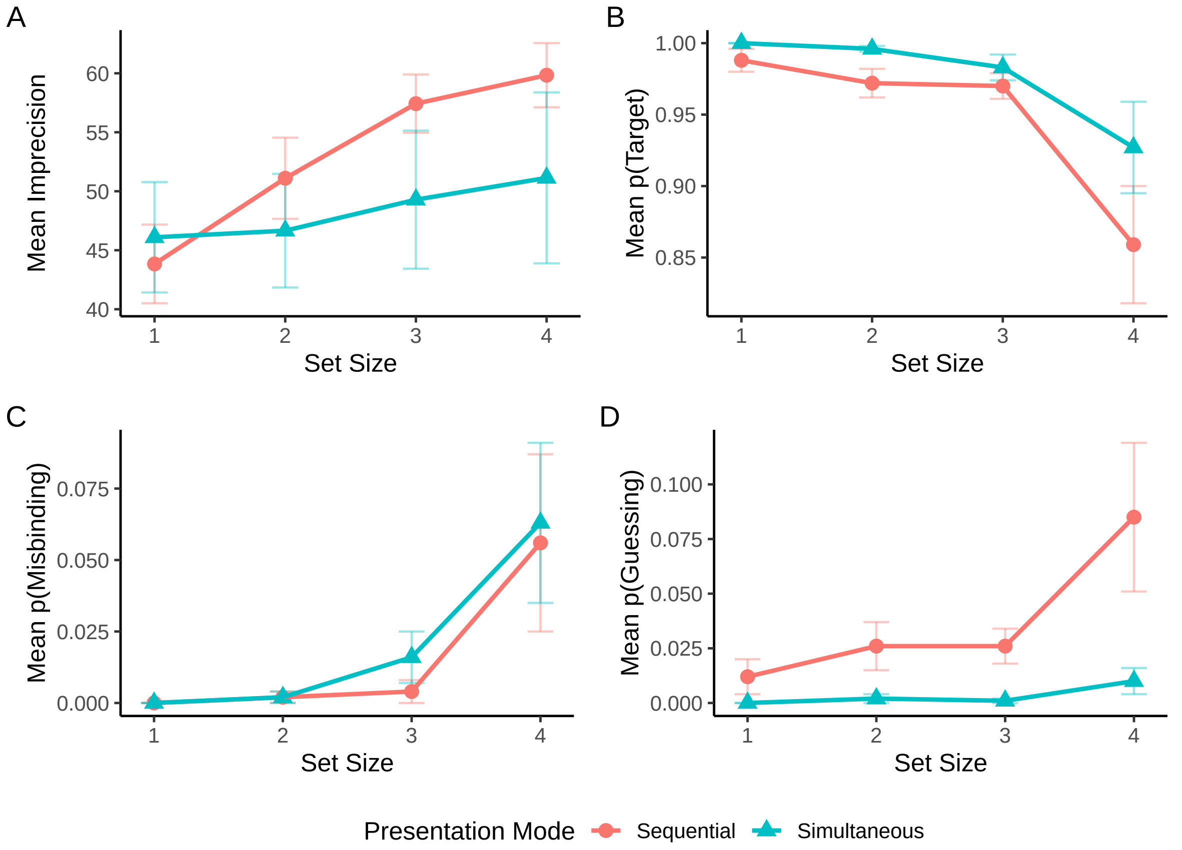

Figure 4.8: Mean imprecision (A), probability of reporting the target location (B), probability of misbinding (C), and probability of guessing (D) for each presentation mode as a function of set size. Effects in sequential presentation mode are collapsed across serial order. Error bars represent the standard error of the mean.

A significant interaction between viewing condition and set size was observed; $F(3,\ 42) = 8.64$, $p < .001$. Bonferroni-Holm corrected comparisons between free and fixed viewing at each set size revealed a significant difference between free viewing (M = 24.86, SD = 10.6) and fixed viewing (M = 44.97, SD = 8.64) at set size one; $p = .001$. No other differences were significant; $p \geq 0.467$.

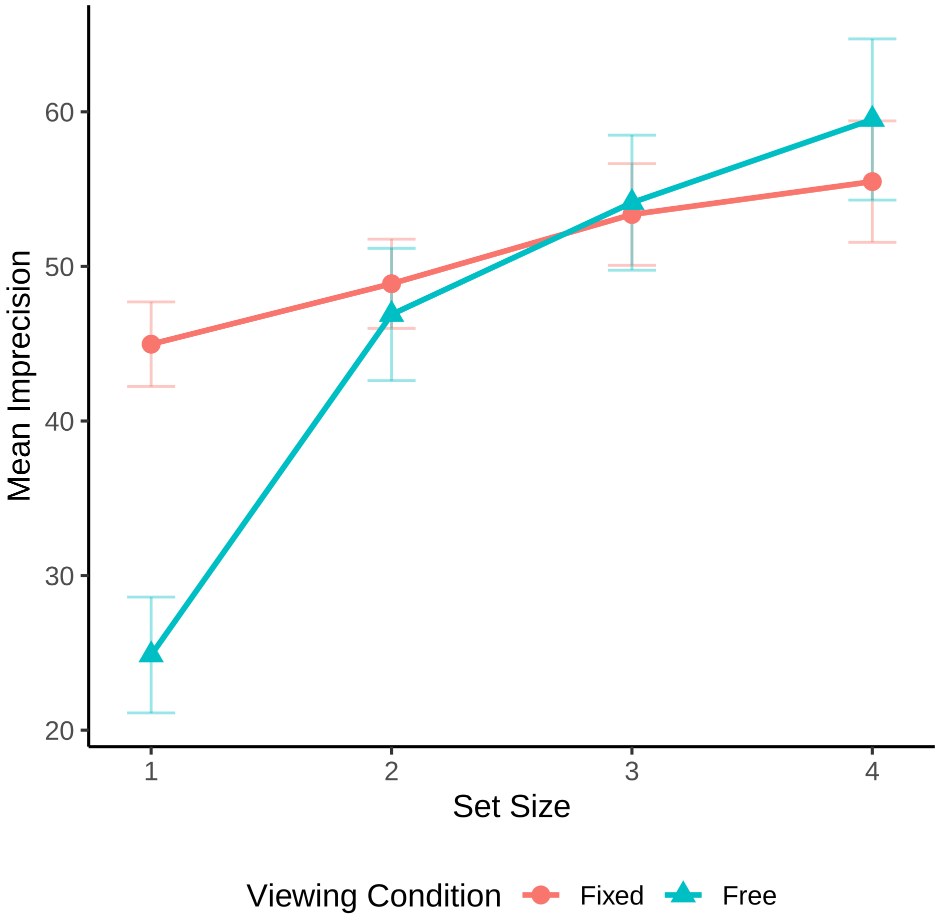

Figure 4.9: Mean imprecision as a function of set size in fixed viewing and free viewing. Error bars represent the standard error of the mean.

Preface to Chapter Five

Chapter Five aimed to examine how the oculomotor system might support maintenance of information within VSWM. The oculomotor system plays an important role in the maintenance of spatial locations in VSWM, but there is little consensus on its specific role. Studies comparing the involvement of the oculomotor system in spatial and visual memory may be problematic due to differences in the tasks used to measure VSWM (e.g. Pearson et al., 2014). The use of the continuous report task offers an ideal method of directly comparing the sources of recall error in spatial and visual memory, as only the feature to be recalled is varied between the two tasks. The following study aimed to compare the sources of recall error following covert and overt attentional delay-period interference in spatial and colour continuous report tasks.

The procedure in Chapter Five, in which a dual-task paradigm is used, differed from the preceding chapters. Although the dual-task paradigm is widely used to examine the role of the oculomotor system in VSWM maintenance (e.g. Pearson & Sahraie, 2003), the continuous report task has not been widely used in this paradigm. Some methodological decisions were therefore more difficult than in the preceding chapters. The three interference conditions were matched as closely as possible so that the only differences between the conditions were to do with the demands on covert and overt attention. Participants were asked to press the space bar to detect a target, which when combined with the eye movement data, resulted in a measure of how well they adhered to the task instructions. However, because I varied the set size and interference/secondary task conditions, and there were demands on both maintaining central fixation during different mnemonic stages, I decided to test 150 trials per condition across 3 sessions. I anticipated that around 20% of trials would be excluded due to eye movements, based on the preceding chapters. In addition to anticipating data loss due to eye movements, I increased the number of trials in anticipation that participants would have a lower than required hit rate in the interference conditions.

With respect to the structure of each testing session, I decided to block each session by interference task, and counterbalance the performance of these across participants. This decision was made in order to minimise the potential confusion that might have occurred across the covert and overt attention interference conditions, in which the only difference was whether to make saccades. Although this meant that the sessions were quite long (approximately 2-2.5 hours), participants were free to take self-paced breaks between blocks of trials to reduce potential effects of fatigue.

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Chapter 5

Oculomotor Rehearsal in Visuospatial Working Memory

The neural and cognitive mechanisms of spatial working memory are tightly coupled with the systems that control eye movements but the precise nature of this coupling is not well understood. It has been argued that the oculomotor system is selectively involved in rehearsal of spatial, but not visual material in visuospatial working memory. However, few studies have directly compared the effect of saccadic interference on visual and spatial memory, and there is little consensus on how the underlying working memory representation is affected by saccadic interference. In this study we aimed to examine how working memory for visual and spatial features is affected by overt and covert attentional interference across two experiments. Participants were shown a memory array, then asked to either maintain fixation, or to overtly or covertly shift attention in a detection task during the delay period. Using the continuous report task, we directly examined the precision of visual and spatial working memory representations and fit psychophysical functions to investigate the sources of recall error associated with different types of interference. These data were interpreted in terms of embodied theories of attention and memory and provide new insights into the nature of the interactions between cognitive and motor systems.

5.1 Introduction

Visuospatial working memory (VSWM) is the temporary store for the active maintenance of limited amounts of information about objects, with subcomponents for retaining information about their non-spatial features, such as colour, and spatial location (Baddeley & Hitch, 1974). Extensive work has shown that there is a tight coupling between VSWM and the oculomotor system during the encoding, maintenance, and retrieval phases (see recent reviews by Heuer et al., 2020; Olivers & Roelfsema, 2020; Van der Stigchel & Hollingworth, 2018). For example, several studies have reported enhanced encoding of visual features for memoranda that were the goal of saccadic eye movements (Bays & Husain, 2008; Hanning et al., 2016), and maintenance and retrieval of object features from VSWM is associated with eye movements towards the spatial location the object previously occupied (van Ede et al., 2019; Williams et al., 2013). The oculomotor system appears to play a similarly important role in the maintenance of spatial information (Pearson et al., 2014; Pearson & Sahraie, 2003; Tremblay, Saint-Aubin, et al., 2006). Indeed, performing saccades during the delay period has been shown to selectively impair memory for spatial information, with maintenance of non-spatial information, such as shape and size, being somewhat less affected by oculomotor interference (Ball et al., 2013; Postle et al., 2006). However, the extent to which the role of the oculomotor system in VSWM is specific to the rehearsal of spatial, as opposed to visual (non-spatial) features, and how these underlying representations are affected by saccadic disruption, remains unclear. This study attempts to address these questions by examining how saccadic and attentional disruption affects the precision of VSWM representations.

It has been argued that the oculomotor system aids rehearsal in VSWM through an active control process (Baddeley, 1986). This position has been supported by studies showing that performing eye movements during the retention interval reduces spatial working memory span (Baddeley, 1986; Pearson et al., 2014; Pearson & Sahraie, 2003; Postle et al., 2006). However, other forms of body movement, such as limb movement, also disrupt spatial span (Lawrence et al., 2001; Smyth et al., 1988; Smyth, 1996; Smyth

& Scholey, 1994), leading some researchers to argue that rehearsal in VSWM occurs via shifts in spatial attention towards locations held in VSWM (Awh et al., 1999, 2000, 1998). This theory of spatial attention rehearsal argues that, because shifts in spatial attention precede limb and eye movements, performance of these irrelevant behaviours interrupts the shifting of attention towards locations held in VSWM, thereby impairing VSWM maintenance (Awh et al., 1998; Awh & Jonides, 2001; Smyth, 1996; Williams et al., 2013). However, disruption to VSWM due to saccadic interference is greater than disruption caused by limb movement (Lawrence et al., 2004; Pearson & Sahraie, 2003) and by covert orienting (Lawrence et al., 2004; Lilienthal et al., 2018; Pearson & Sahraie, 2003). These findings suggest that oculomotor activity plays a role in VSWM rehearsal that is additional to and independent of covert shifts of attention. As a consequence, the idea that rehearsal takes place via shifts in attention alone has been challenged by several authors, who highlight a specific, functional role of the oculomotor system in the rehearsal of spatial information in VSWM (Belopolsky & Theeuwes, 2009a, 2009b; Postle et al., 2006).

The eye-abduction paradigm has been used to further challenge the argument that VSWM rehearsal takes place via shifts in attention alone. This paradigm involves presenting stimuli to the visual field outside of the oculomotor range, thereby preventing the programming and execution of saccades, without disrupting covert orientation of endogenous attention (Casteau & Smith, 2020; Smith et al., 2014, 2012). Using this paradigm, Ball et al. (2013) showed that disrupting saccade programming selectively decreased spatial span, with no significant effects on working memory for non-spatial features. Subsequently, Pearson et al. (2014) found that interference was greatest when eye-abduction was applied during the maintenance interval, considerably reduced when applied during encoding, and absent when during retrieval, consistent with the idea that the oculomotor system has a privileged role in the maintenance of spatial locations in VSWM. These studies, which allow for disentangling attentional mechanisms and oculomotor control processes, support the view that the oculomotor system has a functional role in the rehearsal of spatial information in VSWM, consistent with behavioural (Pearson & Sahraie, 2003; Postle et al., 2006; Tremblay, Saint-Aubin, et al., 2006) and neuropsychological evidence (Smith et al., 2021; Smith & Archibald, 2020). However, the reliance on the Corsi blocks task, which emphasises memory for both spatial location and temporal order rather than the quality of the information maintained in VSWM, means that they could not examine how or why disruption to the oculomotor system affected the representations held in VSWM. As a consequence, the precise nature of interference to spatial and non-spatial components of VSWM representations caused by disruption of the oculomotor system remains unclear.

One way to address the issue of how saccadic disruption affects the underlying representations is to use computational models (e.g. Bays et al., 2009; van den Berg & Ma, 2018; Zhang & Luck, 2008). Peterson et al. (2019) applied Zhang and Luck's (2008) model to investigate how saccadic and covert attentional interference disrupts VSWM in a location change detection task. Zhang and Luck's model (2008) fits a mixture of normal and uniform distributions to response data, giving an estimate of precision and guessing in VSWM. Peterson et al. (2019) found that VSWM was less precise when participants made a saccade to the periphery during the delay period but relatively unimpaired when participants covertly shifted attention to the periphery or maintained central fixation. The effect of saccadic interference was directionally specific: the loss in precision was greatest when changes occurred along the axis of the saccade, with no difference when the change in location occurred along the axis orthogonal to the direction of the saccade. The proposed mechanism for this change in precision was spatial remapping (Bays & Husain, 2007; Wolfe & Whitney, 2015), where the receptive fields of neurons in the visual system are shifted in preparation for a saccade. Within VSWM, this results in the representation of maintained information being remapped in the direction of the saccade (Peterson et al., 2019). This finding suggests that the oculomotor system plays a functional role in rehearsal of spatial information in VSWM by maintaining the precision of the representations of the spatial location of objects.

Although Peterson et al. (2019) have advanced understanding of the role of the oculomotor system in VSWM and discussed potential mechanisms underlying disruption of VSWM due to saccadic disruption, their methods and analyses were somewhat limited in their ability to allow detailed examination of *how* performing delay-period saccades change the VSWM representations. To probe precision, Peterson et al. (2019) varied the magnitude of the spatial change to be detected. However, because responses on this task are binary, the quality of the representation cannot be examined in depth. The degree of noise present within the representations must be inferred from a discrete response space, rather than the distribution of response error, thereby providing limited insight into the sources of recall error. One widely used alternative method is to use a continuous report task, where participants reproduce a feature of a probed stimulus along a continuous dimension, for example reporting the colour of the stimulus on a colour wheel (Wilken & Ma, 2004). This task permits a more complete insight into the underlying VSWM representation by characterising response error more thoroughly. Peterson et al. (2019) opted against using a continuous report task, arguing that, because it relies on manual responding, the delay-period interference tasks might have biased subsequent motor planning at response, which may have reduced their ability to isolate the effects of the interference tasks on VSWM. However, the primary function of VSWM is to guide subsequent behaviour and aid successful task completion (Baddeley, 2010; Manohar et al., 2017), so biases in motor planning during responding could be argued to reflect changes in the underlying VSWM representation.

Additionally, in Peterson et al.'s (2019) study, participants were required to remember information about only three stimuli. It has reliably been shown that VSWM performance is affected by the number of items retained, with precision in memory of non-spatial and spatial features decreasing monotonically as set size increases (Bays et al., 2009; Schneegans & Bays, 2016). Although saccadic and attentional interference decrease spatial span (Lawrence et al., 2004; Pearson & Sahraie, 2003), it is not clear whether the interference effects depend on how many items must be retained. Previous work has examined how working memory span or memory for a limited number of items is affected by different interference tasks (Lawrence et al., 2004; Pearson et al., 2014; Pearson & Sahraie, 2003; Peterson et al., 2019). However, examination over a range of set sizes allows more specific examination of the interference effects and how these might depend on how many objects are being retained in VSWM.

Finally, the application of Zhang and Luck's (2008) mixture model is problematic. This model has been criticised for presenting a simplistic overview of sources of error in VSWM because it assumes that all incorrect responses are guesses, occurring as a result of items not being maintained in VSWM (Bays et al., 2009; Ma, 2018). Bays et al.'s (2009) mixture model extends Zhang and Luck's (2008) model and accounts for the probability of reporting a non-target (misbinding), which can occur due to incorrectly binding non-spatial and spatial features together in VSWM. When the probability of misbinding is included in modelling, the amount of variance accounted for by guessing is significantly decreased (Bays et al., 2009), suggesting that it is an important source of error to consider in VSWM responses (Bays, 2016). From Peterson et al.'s (2019) method, misbinding errors could not be analysed because memory items were identical so there was no potential for misbinding errors to occur. Nonetheless, it may be premature to conclude that saccadic interference increases the probability of guessing without first examining whether misbinding errors are also affected.

5.1.1 Aim of current study

The current study aimed to address these criticisms and build on prior work (Pearson et al., 2014; Pearson & Sahraie, 2003; Peterson et al., 2019) to examine how the representations of spatial and non-spatial features in VSWM are affected by delay-period activation of the oculomotor system. We examined the effects of overt and covert shifts of attention on spatial and non-spatial memory representations using a continuous report task. Bays et al.'s (2009) mixture model was used to analyse the results. We carried out two experiments, one probing memory for location and the other memory for colour, to more directly examine how VSWM representations change due to saccadic disruption and to investigate the hypothesis that the oculomotor system plays a specific and critical role in rehearsal of spatial information in VSWM.

5.2 Experiment One

Experiment One attempted to examine the effects of delay-period saccadic interference (overt attentional shift) and covert shifts of attention on the representation of spatial information in VSWM. Given that delay-period saccades have been shown to interfere with working memory for spatial locations (e.g. Pearson & Sahraie, 2003; Peterson et al., 2019; Postle et al., 2006), and that shifting covert, endogenous attention is largely independent of the oculomotor system (Casteau & Smith, 2019, 2020; Smith & Schenk, 2012), we proposed the following hypotheses:

1. There will be a main effect of interference task type such that imprecision, misbinding, and guessing will be greatest when the oculomotor system is activated, i.e., in the overt attentional shift, compared to when central fixation is maintained. Although we expect that there will be disruption in the covert attentional shift condition, we expect that disruption in this condition will be smaller than that caused by overt shifts in attention because the oculomotor system is not being activated.

2. There will be a main effect of set size such that imprecision and misbinding will increase with set size, consistent with previous work (Bays et al., 2009; Schneegans & Bays, 2016).

3. The effect of overt attentional shifts on imprecision will be greater in this experiment compared to the effect of overt attentional shifts on imprecision in Experiment Two, which probed memory for colour, because the oculomotor system is selectively involved in memory for spatial locations (Ball et al., 2013; Pearson et al., 2014).

We also explored the interaction between set size and interference type, but made no specific predictions regarding this effect.

5.2.1 Method

5.2.1.1 Participants

An *a priori* power analysis was carried out using G*Power 3.1 (Faul et al., 2009) to determine how many participants are needed to carry out mixed ANOVA to detect a significant within-between interaction between task and interference task type on precision (Hypothesis 3). Based on unpublished pilot data, this interaction has an effect size of $\eta_p^2 = 0.13$ (Cohen's $f = 0.39$). Based on this, an alpha of .05, and 95% power, the power analysis suggested a total sample size of 24 participants, 12 per experiment. Data collection was finished when 12 usable data sets were obtained.

Undergraduate participants enrolled on Psychology courses at Durham University received participant pool credit for their time. We received ethical approval from Department of Psychology Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

5.2.1.2 Design

A within-subjects design was used. The independent variables were interference task type (three levels: overt attentional shift, covert attentional shift, and central fixation) and set size (three levels: one, two, and four items). The dependent variables were imprecision, and the probabilities of reporting the target, misbinding, and guessing.

Participants completed one practice block before beginning each interference task type condition. This practice block comprised 15 trials, five of each set size, to familiarise them with the task. The practice block was identical to the experimental blocks, with the exception that participants were shown their own response as well as the correct response on screen. They then completed 450 trials per interference task type condition, resulting in a total of 1350 trials for the experiment. Trials in each condition were randomised across 30 blocks. Within each interference interference task type condition, each set size was tested 150 times. The order of completing interference conditions was fully counterbalanced across participants, with the set sizes being randomised within each interference task type condition.

5.2.1.3 Stimuli and apparatus

The task was programmed using Matlab R2019a, using the psychophysics toolbox (Kleiner et al., 2007). The stimuli consisted of arrays comprising one, two, or four coloured dots (visual angle of each dot = 1°), and a fixation cross positioned at the centre of the screen (height of fixation cross in visual angle = 0.76°). The location of each dot was randomly sampled from 24 predefined locations equally spaced along circles with radii of 5, 7.5, and 10 degrees of visual angle from central fixation. This ensured that the locations of dots had no overlap. Colours of each dot were randomly chosen from a colour wheel, with at least 60° angular separation on the colour wheel between each colour. This ensured that each location and colour were sufficiently distinct and prevented verbal recoding and learning as much as possible. The visual mask comprised 800 coloured dots, with colours randomly chosen from the colour wheel, filling the annular space five to ten degrees of visual angle around central fixation.

The delay-period interference task was a detection task. Participants were shown chevrons (ˆ/v), with sideways chevrons (>/<) inserted into the sequence at a fixed interval after every four up- and down-facing chevrons. These were presented in black size 40 Arial font 10° of visual angle to the left or right of the centre of the screen in the overt and covert attentional shift conditions, or at the centre of the screen in the central fixation condition. Chevrons were presented at a rate of one every 250ms. Participants were required to press space bar to detect sideways chevrons in all conditions. In the overt and covert attentional shift conditions, the side of presentation flipped immediately after a sideways chevron was shown. In the overt attentional interference task type condition, participants were required to shift their gaze to fixate the chevrons. In the covert attentional interference task type condition, participants were required to orient attention to the contralateral channel and detect the sideways facing chevrons while maintaining fixation on the central fixation cross. In the central fixation condition, participants were required to detect sideways facing chevrons presented in the centre of the screen.

Participants' gaze was monitored using a tower-mounted EyeLink 1000 eye tracker (SR

Research). Stimuli were presented on a 20-inch CRT screen with a refresh rate of 85Hz. Participants sat 60cm from the computer screen, with the centre of screen at eye level.

5.2.1.4 Procedure

Participants were instructed to maintain fixation on the centre of the screen throughout presentation of the array. They were specifically informed that they should remember information about the coloured dots on screen. They were also instructed to either shift their gaze (overt attentional task type condition) or to maintain central fixation and detect chevrons appearing either to the left and right of the centre of the screen or at the centre of the screen throughout the delay period.

Trials began with the presentation of a fixation cross at the centre of the screen for 1000ms. The fixation cross was followed by a blank screen for 500ms. The fixation cross and the stimulus array, comprising one, two, or four coloured dots, were presented for 2000ms. After presentation of the array, the visual mask was presented for 100ms. Participants then performed the detection task for 5000ms. Following this delay period, one of the stimuli from the array was randomly chosen and presented in the centre of the screen. Participants were required to move the mouse to click the location on screen where it first appeared. After participants submitted their response, their response was shown on screen for 500ms. No other feedback was given in experimental trials. There was no time limit for responding, but participants were asked to respond as quickly and as accurately as possible. A 1500ms blank screen followed the response screen, before the beginning of the next trial. After each block of 15 trials, participants were permitted to take a self-paced break. An example trial is shown in Figure 5.1.

5.3 Experiment Two

Experiment Two attempted to examine whether there were analogous oculomotor interference effects in working memory for non-spatial features as in spatial working memory. We proposed the following hypotheses, based on the proposal that the oculomotor system

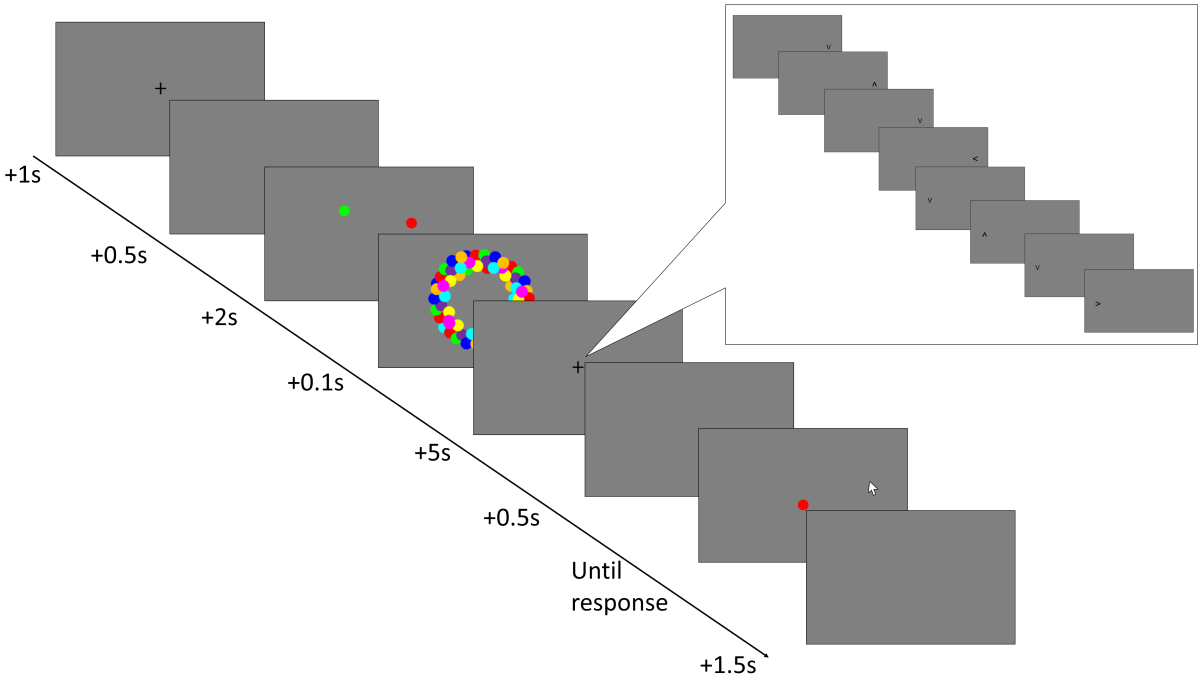

Figure 5.1: An example trial for each condition in Experiment One. Participants were shown an array of between one and four coloured dots. During the delay period, participants were required to complete a detection task at either central fixation or in peripheral vision by making saccades or covertly shifting attention. The detection task for saccadic and attentional interference conditions is shown in the bubble. After this delay, they were shown one of the coloured dots in the centre of the screen and asked to click on screen where that dot first appeared.

is selectively involved in maintenance of spatial information in VSWM (Pearson et al., 2014):

1. There will be a small effect of interference task type on misbinding due to participants performing a dual-task, with the possibility that misbinding will be highest for the overt attentional shift condition as activation of the oculomotor system may disrupt the memory of the spatial location, which has been proposed to aid maintenance of non-spatial features in VSWM (Schneegans & Bays, 2017). This interference of the spatial representations due to oculomotor activity may in turn disrupt memory for the colour-location binding. Furthermore, we predict that there may be a small effect of interference task type on guessing, where guessing will increase in the attentional shift conditions due to performing a dual-task. However, we predict that there will be no significant effect of interference task type on imprecision, and that the effect of interference task type on impreci-

sion will be smaller in this experiment compared to the effect of interference task type on imprecision in Experiment One, based on the proposal that the oculomotor system is selectively involved in maintenance of spatial locations in VSWM.

2. There will be a significant main effect of set size, such that imprecision and misbinding will increase with increases in the number of to-be-remembered items (Bays et al., 2009).

We also explored the interaction between set size and interference task type, but made no specific hypotheses regarding this effect.

5.3.1 Method

5.3.1.1 Participants

Based on the power analysis carried out to detect the interaction between task and interference type (Experiment One, Hypothesis 3), we required a sample of 12 participants for this experiment. Data collection was terminated when 12 usable datasets were obtained. Undergraduate participants received participant pool credit for their time. We received ethical approval from Department of Psychology Research Ethics Committee (reference: PSYCH-2019-10-28T15:23:58-lckd86).

5.3.1.2 Design

Design was the same as Experiment One.

5.3.1.3 Stimuli

Stimuli were the same as Experiment One, with the exception that, at recall, a colour wheel, with depth 2° of visual angle, was presented 11° to 13° of visual angle around central fixation.

5.3.1.4 Procedure

Procedure followed Experiment One, with the exception that, at recall, participants were shown the outline of one of the dots in their original location and were required to click the colour on the colour wheel that matched the colour originally presented at the probed location (see Figure 5.2).

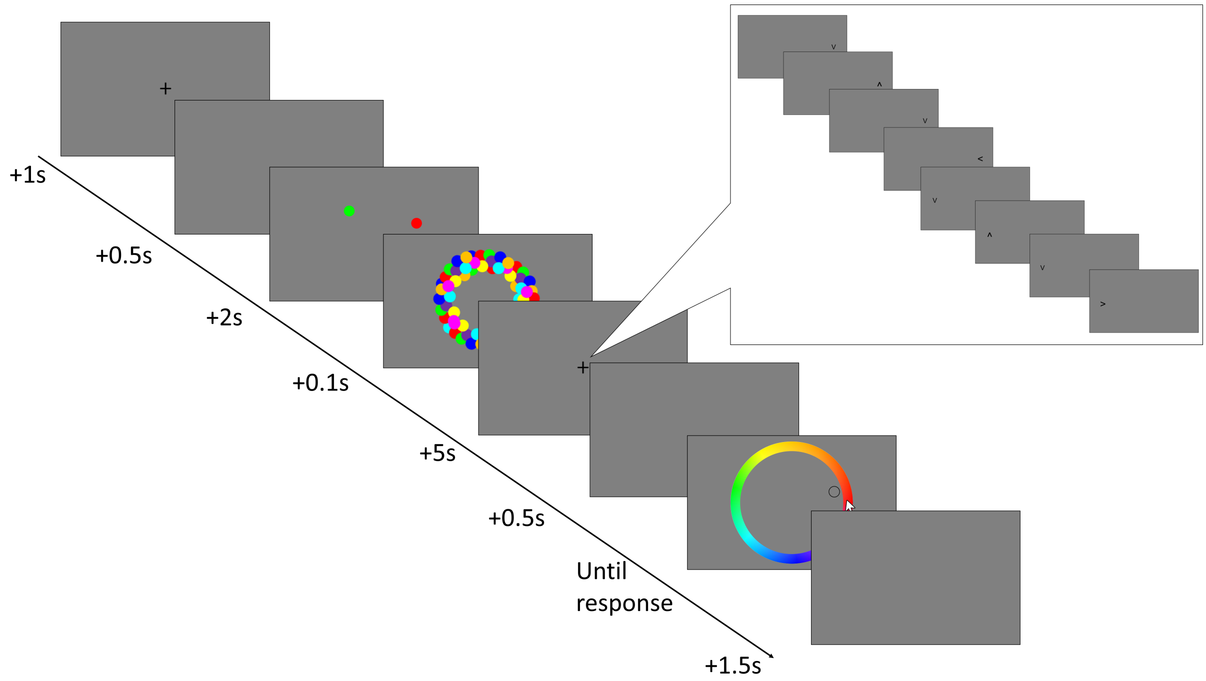

Figure 5.2: An example trial for each condition in Experiment Two. This is the same as Experiment 1 with the exception that participants were shown one of the dots in their original location and were asked to click on a colour wheel the original colour of the probe.

5.4 Statistical Analysis

For each experiment, we excluded any trials in which eye position was outside of an interest period with radius two degrees of visual angle around central fixation during the encoding period in all conditions, and during the delay period for the maintained fixation and covert attention interference task type conditions. Based on previous studies, around 20% of trials in our studies are excluded due to excessive eye movements. Additionally, participants were required to correctly detect more than 50% of the presented sideways-facing chevrons during the interference task. Therefore, a usable dataset was defined as one in which there were at least 120 trials per set size in each interference task after controlling for performance in the delay-period task and eye movements. This minimum number of trials is greater than the minimum number of trials required for the mixture modelling to be considered reliable (Bays et al., 2009).

We applied Bays et al.'s (2009) mixture modelling to the data for each experiment using the Matlab functions provided by Bays et al. (2009) and Grogan et al. (2020; Suchow et al., 2013). This modelling fits a mixture of normal and uniform distributions to the response data. The normal distributions are centred on the probed stimulus, representing the probability of reporting the target location, and the uniform distribution represents guessing, where all possible responses are equally likely. Additional normal distributions, centred on the non-probed stimuli, were also fit to the data to retrieve a measure of misbinding. The standard deviation of the normal distributions gives a measure of imprecision: the wider the distribution, the less precise (more variable) the response. The heights of each of the distributions represent response likelihood, between zero and one, for reporting the target feature, a non-target feature, and guessing. In Experiment One, the distributions were centred on the spatial location of the probed stimulus, therefore a bivariate Gaussian distribution was fit to the data (Grogan et al., 2020). In Experiment Two, the distributions were centred on the angle on the colour wheel of the probed stimulus, therefore a Von Mises distribution was fit to the data (Bays et al., 2009).

For each experiment, we analysed the imprecision, and the probabilities of reporting the target, misbinding and guessing using separate 3x3 repeated-measures ANOVA with factors of set size (three levels: one, two, four items) and interference task type (three levels: saccadic interference, covert attention, maintained fixation). If the assumption of sphericity was violated, Greenhouse-Geisser correction was applied. These analyses were carried out in R (R Core Team, 2019) using the `rstatix` package (Kassambara, 2019).

For a significant main effect of set size, we carried out pairwise comparisons, comparing set size one to set size two, and set size two to set size four. For a significant main effect of interference task type, we compared all interference tasks. To examine a significant interaction between set size and interference task type, we examined the differences between interference tasks at each set size. Holm-Bonferroni correction was applied to control for multiple comparisons.

We also directly compared the effects of interference task types between Experiments One and Two for imprecision to examine the hypothesis that the oculomotor system is specifically involved in rehearsal of spatial information in VSWM. The effects of interference type were collapsed across set sizes and analysed using 2x3 mixed ANOVA with between-subjects factor of task (two levels: spatial and colour) and within-subjects factor of interference task type (three levels: saccadic interference, covert attention, maintained fixation). If a significant interaction was observed, we examined the differences between each interference task condition for each task.

5.5 Results

5.5.1 Experiment One

Fifteen participants ($M_{\text{age}} = 19.33$ years, $SD_{\text{age}} = 1.18$, 12 females, 3 males, 13 right handed, 1 left handed, 1 ambidextrous, all confirmed normal or corrected-to-normal vision) volunteered and completed this experiment[16]. After acceptance, participants were unable to meet our original inclusion criteria. Due to differences in reaction times affecting the precision of when the press was detected, performance on the detection task was calculated by the total number of times the space bar was pressed, divided by the number of times a sideways-facing chevron was presented. Participants were unaware of this change in calculation and were instructed to perform the detection task as quickly and as accurately as possible. Additionally, participants were unable to meet our original target of at least 120 valid trials per set size in each condition, so this was relaxed to at least 50 valid trials per set size in each condition. This resulted in the exclusion of three datasets from analysis. Of the remaining 12 datasets, 30.58% of trials were excluded.

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[16] An additional six participants volunteered but withdrew during or after their first testing session. Their data were discarded upon their withdrawal from the study

5.5.1.1 Detection task analysis

We examined whether performance in the detection task varied according to the delay-period interference task type. Overall, the average performance on the detection task was 0.87 (*SD* = 0.07). Performance on the detection task did not differ across interference task types; $F(2,\ 22) = 1.76$, $p = .195$, $\eta_p^2 = 0.14$.

5.5.1.2 Mixture modelling

For imprecision (Figure 5.3A), a 3x3 repeated-measures ANOVA revealed a significant main effect of set size; $F(1.3,\ 14.25) = 15.27$, $p < .001$, $\eta_p^2 = 0.58$. Neither the main effect of interference task type [$F(2,\ 22) = 1.72$, $p = .202$, $\eta_p^2 = 0.14$] nor the interaction between interference task type and set size [$F(1.52,\ 16.7) = 0.79$, $p = .436$, $\eta_p^2 = 0.07$] were significant. Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size one ($M = 41.01$, *SD* = 12.08) and set size two ($M = 48.79$, *SD* = 16.24) was significant; $t(35) = -4.75$, $p < .001$. The difference between set size two and set size four ($M = 58.94$, *SD* = 27.2) was also significant; $t(35) = -3.52$, $p = .001$.

For the probability of reporting the target location (Figure 5.3B), repeated-measures ANOVA revealed significant main effects of set size [$F(1.12,\ 12.3) = 14.22$, $p = .002$, $\eta_p^2 = 0.56$] and of interference task type [$F(2,\ 22) = 4.93$, $p = .017$, $\eta_p^2 = 0.31$]. The interaction between interference task type and set size was not significant; $F(4,\ 44) = 0.91$, $p = .469$, $\eta_p^2 = 0.08$. For the main effect of set size, Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size one ($M = 0.96$, *SD* = 0.05) and set size two ($M = 0.89$, *SD* = 0.13) was significant; $t(35) = 4.64$, $p < .001$. The difference between set size two and set size four ($M = 0.8$, *SD* = 0.2) was also significant; $t(35) = 5.82$, $p < .001$. For the main effect of interference task type, the probability of reporting the target location was significantly lower in the overt attentional interference task ($M = 0.86$, *SD* = 0.17) compared to covert attentional interference task ($M = 0.89$, *SD* = 0.16; $t(35) = -2.76$, $p = .018$), and compared to when central fixation was maintained (M = 0.9, SD = 0.14; $t(35)$ = -3.15, p = .010). The difference between covert attentional interference task and central fixation was not significant; $t(35)$ = -1.18, p = .245.

For the probability of misbinding (Figure 5.3C), a repeated-measures ANOVA revealed a significant main effect of set size; $F(1, 11) = 4.95$, $p = .048$, $\eta_p^2 = 0.31$. That is, the difference between set size two (M = 0.04, SD = 0.06) and set size four (M = 0.07, SD = 0.1) was significant. Neither the main effect of interference task type [$F(2, 22) = 0.59$, $p = .565$, $\eta_p^2 = 0.05$] nor the interaction between interference task type and set size [$F(2, 22) = 1.26$, $p = .304$, $\eta_p^2 = 0.1$] were significant.

For the probability of guessing (Figure 5.3D), a repeated-measures ANOVA revealed significant main effects of set size [$F(1.22, 13.38) = 15.32$, $p = .001$, $\eta_p^2 = 0.58$] and interference task type [$F(2, 22) = 4.14$, $p = .030$, $\eta_p^2 = 0.27$]. The interaction between interference task type and set size was not significant; $F(1.53, 16.85) = 1.64$, $p = .224$, $\eta_p^2 = 0.13$. For the main effect of set size, Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size one (M = 0.04, SD = 0.05) and set size two (M = 0.07, SD = 0.08) was significant; $t(35)$ = -3.68, $p < .001$. The difference between set size two and set size four (M = 0.13, SD = 0.14) was also significant; $t(35)$ = -4.15, $p < .001$. For the main effect of interference type, the probability of guessing was significantly higher in the overt attentional interference task condition (M = 0.1, SD = 0.12) compared to covert attentional interference (M = 0.08, SD = 0.11; $t(35)$ = 2.57, p = .034), and compared to when central fixation was maintained (M = 0.06, SD = 0.08; $t(35)$ = 2.67, p = .034). The difference between the covert attentional interference task and central fixation was not significant; $t(35)$ = 1.31, p = .199.

5.5.1.3 Directional-specificity of localisation error (Exploratory analysis)

We also examined whether there was a directionally specific effect of interference task type on localisation error. Because responses were two dimensional, along the x- and y-axes, we analysed the error along these axes separately using a factor called axis of error. We carried out a 3 x 3 x 2 repeated measures analysis of variance with factors of interference

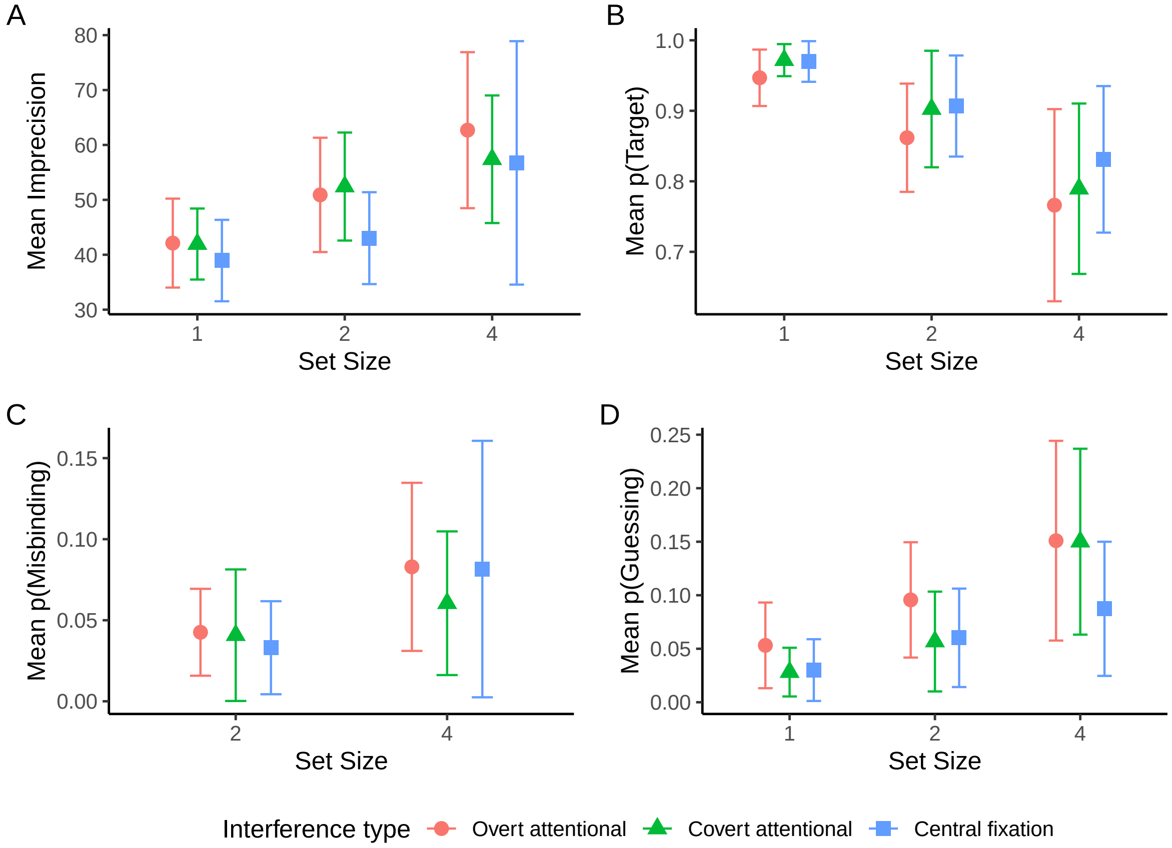

Figure 5.3: Mean imprecision (a), mean probability of reporting the target location (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) as a function of set size in each interference condition. Error bars represent 95% confidence intervals.

task type (3 levels: overt attentional, covert attentional interference, central fixation), set size (3 levels: one, two, and four items), and axis of error (2 levels: x-axis, y-axis). Significant effects of set size [$F(1.1,\ 12.07) = 15.86$, $p = .001$, $\eta_p^2 = 0.59$] and interference task type [$F(2,\ 22) = 5.48$, $p = .012$, $\eta_p^2 = 0.33$] were observed. A significant two-way interaction between axis of error and interference task type was also observed; $F(2,\ 22) = 5.19$, $p = .014$, $\eta_p^2 = 0.32$. Examination of this interaction revealed that localisation error along the x-axis ($M = 62.03$, $SD = 94.37$) was significantly greater than localisation error along the y-axis ($M = 55.98$, $SD = 93.85$) in the overt attentional shift condition; $t(35) = 4.26$, $p < .001$. The differences in localisation error along the x- and y-axes were not significant in the covert attention [$t(35) = 0.38$, $p = .703$] and central fixation conditions [$t(35) = 0.48$, $p = .634$]. No other effects were significant; $p \geq 0.054$. These results are illustrated in Figure 5.4.

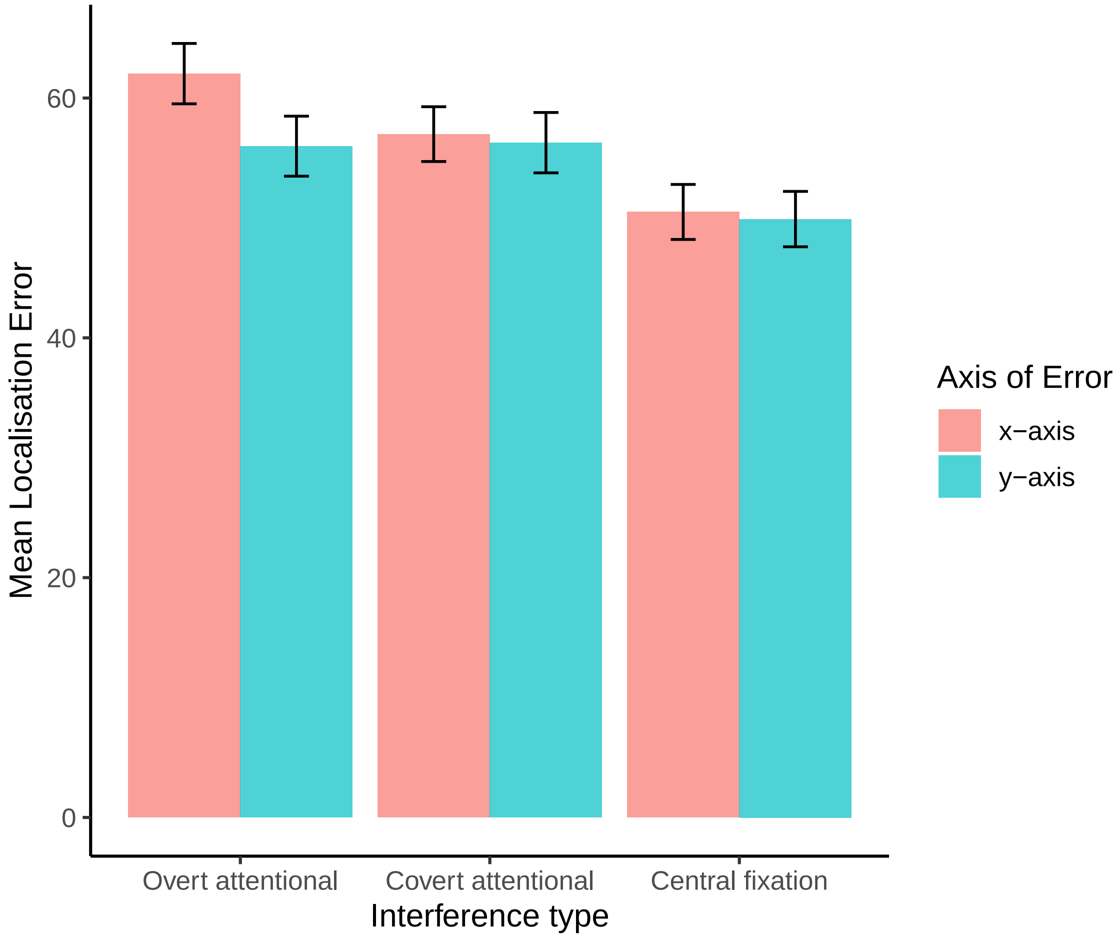

Figure 5.4: Mean localisation error for each axis of response in each interference condition. Error bars represent 95% confidence intervals.

5.5.1.4 Discussion

This experiment aimed to examine how overt and covert attentional interference tasks affected the representation of spatial information in VSWM. We found that the probability of guessing was highest when the oculomotor system was activated compared to when attention was covertly shifted and when central fixation was maintained. There was no significant difference in the probability of guessing between the covert attentional shift condition and maintaining central fixation. This result offered some support for Hypothesis 1. However, there was no significant effect of interference task type on imprecision or misbinding, which is inconsistent with the predictions outlined in Hypothesis 1. We also observed that imprecision and misbinding increased with increases in set size, consistent with the predictions of Hypothesis 2. The probability of guessing also increased with increases in set size, which was not predicted in any of our hypotheses. These findings of an effect of set size on imprecision, misbinding, and guessing are consistent with previous work supporting that VSWM is a flexible and dynamic resource (Bays et al., 2009). No significant interaction between interference task type and set size was found, indicating that the effect of interference task type does not differ as the number of memoranda differ.

The observation that guessing was highest following saccadic shifts compared to covert attentional shifts and maintaining central fixation is consistent with previous work (Peterson et al., 2019; Schut et al., 2017). However, the lack of an effect of interference type on imprecision is surprising, and not consistent with previous findings, which show a decrease in precision in VSWM following saccadic shifts (Peterson et al., 2019; Schut et al., 2017). The results of this experiment indicate that performing multiple task-irrelevant saccades does not impact the quality of the representation of spatial locations in VSWM; when participants are reporting an item that is represented in VSWM, they are relatively accurate. However, saccadic interference affects the probability of memory items being represented in VSWM. Specifically, it appears that producing a series of delay-period saccades results in the removal of information from VSWM.

We also explored whether there was a directionally specific effect of interference task type on response error. In line with previous work, response error was greatest along the axis of the saccade (Peterson et al., 2019). This result seems consistent with their proposal that spatial memory representations are updated when a saccade is executed, but that the updating process is noisy, leading to a loss of fidelity. Unlike Peterson et al. (2019), we observed no effect of saccades on precision per se. It is possible that a subtle, directional effect of saccadic interference on imprecision was hidden because the effects were collapsed across x- and y-axes to obtain a single measure of imprecision in spatial working memory. Nonetheless, our finding of a directionally specific increase in localisation error, which can be used as a proxy for precision, indicates a directionally specific loss in precision that is specific to activation of the oculomotor system. It is also possible that this difference reflects differences in the reference frame required for our task.

Specifically, our task required localisation of the memoranda, which may have engaged a more egocentric frame of reference, whereas that of Peterson et al. (2019) relied primarily on an allocentric frame to recall the relative positions of the stimuli.

5.5.2 Experiment Two

Seventeen participants ($M_{\text{age}} = 20.35$ years, $SD_{\text{age}} = 2.42$, 13 females, 4 males, 17 right handed, all confirmed normal or corrected-to-normal vision) volunteered and completed this experiment[17]. Five participants were excluded from analysis because they did not meet the revised inclusion criteria, as outlined in Experiment One. Of the remaining 12 datasets, 29.54% of trials were excluded.

5.5.2.1 Detection task analysis

We examined whether performance in the detection task varied according to the delay-period interference task type. Overall, average performance on the detection task was 0.86 ($SD = 0.07$) and this did not differ across interference task types; $F(1.15,\ 12.63) = 2.45$, $p = .140$, $\eta_p^2 = 0.18$.

5.5.2.2 Mixture modelling

Imprecision (Figure 5.5A) for colour data was calculated by transforming the concentration factor (κ) of the circular normal distribution to the circular standard deviation. A repeated-measures ANOVA revealed a significant main effect of set size; $F(2,\ 22) = 8$, $p = .002$, $\eta_p^2 = 0.42$. Neither the main effect of interference task type [$F(1.31,\ 14.4) = 3.02$, $p = .096$, $\eta_p^2 = 0.22$] nor the interaction between interference task type and set size [$F(2,\ 21.96) = 0.57$, $p = .572$, $\eta_p^2 = 0.05$] were significant. For the main effect of set size, Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size one ($M = 0.23$, $SD = 0.04$) and set size two ($M = 0.28$, $SD = 0.09$) was significant; $t(35) = -3.59$, $p = .002$. The difference between set size two and set size four ($M = 0.29$, $SD = 0.08$) was not significant; $t(35) = -1.04$, $p = .307$.

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[17] An additional five participants volunteered but withdrew during or after their first testing session. Their data were discarded upon their withdrawal from the study.

For the probability of reporting the target location (Figure 5.5B), a repeated-measures ANOVA revealed a significant main effect of set size; $F(1.12,\ 12.28) = 15.08$, $p = .002$, $\eta_p^2 = 0.58$. Neither the main effect of interference task type [$F(2,\ 22) = 0.51$, $p = .608$, $\eta_p^2 = 0.04$] nor the interaction between interference task type and set size [$F(2.13,\ 23.44) = 0.52$, $p = .615$, $\eta_p^2 = 0.04$] were significant. For the main effect of set size, Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size one ($M = 0.96$, $SD = 0.08$) and set size two ($M = 0.88$, $SD = 0.15$) was significant; $t(35) = 5.05$, $p < .001$. The difference between set size two and set size four ($M = 0.75$, $SD = 0.24$) was also significant; $t(35) = 6.29$, $p < .001$.

For the probability of misbinding (Figure 5.5C), a repeated-measures ANOVA revealed a significant main effect of set size; $F(1,\ 11) = 12.22$, $p = .005$, $\eta_p^2 = 0.53$. That is, the difference between set size two ($M = 0.08$, $SD = 0.11$) and set size four ($M = 0.14$, $SD = 0.18$) was significant. Neither the main effect of interference task type [$F(1.2,\ 13.16) = 0.3$, $p = .631$, $\eta_p^2 = 0.03$] nor the interaction between interference task type and set size [$F(1.1,\ 12.13) = 0.46$, $p = .531$, $\eta_p^2 = 0.04$] were significant.

For the probability of guessing (Figure 5.5D), a repeated-measures ANOVA revealed a significant main effect of set size; $F(1.15,\ 12.63) = 7.17$, $p = .017$, $\eta_p^2 = 0.39$. Neither the main effect of interference task type [$F(2,\ 22) = 0.89$, $p = .425$, $\eta_p^2 = 0.07$] nor the interaction between set size and interference task type [$F(1.24,\ 13.69) = 0.82$, $p = .408$, $\eta_p^2 = 0.07$] were significant. For the main effect of set size, Holm-Bonferroni corrected pairwise comparisons between set sizes revealed that the difference between set size two ($M = 0.04$, $SD = 0.06$) and set size four ($M = 0.11$, $SD = 0.16$) was significant; $t(35) = -2.91$, $p = .012$. The difference between set size one ($M = 0.04$, $SD = 0.08$) and set size two was not significant; $t(35) = 0.76$, $p = .454$.

A summary of the key effects in Experiments One and Two is presented in Table 5.1.

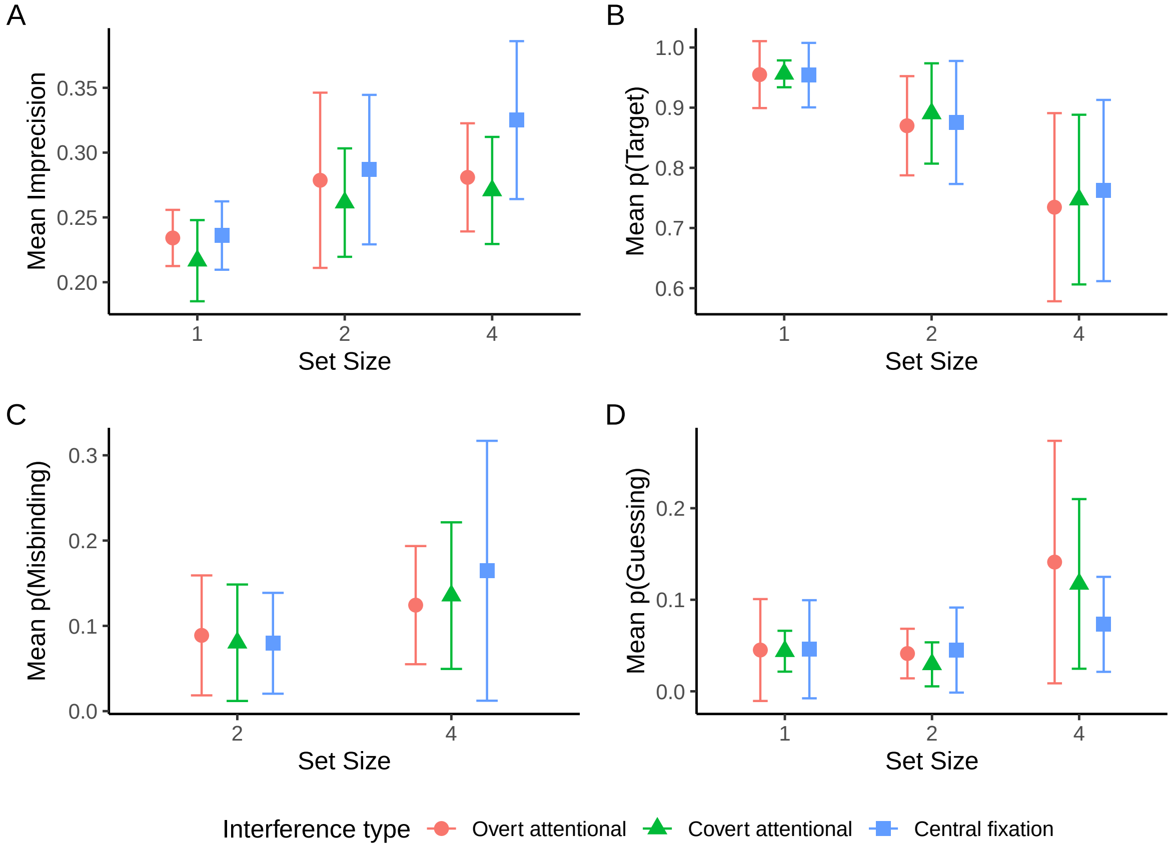

Figure 5.5: Mean imprecision (a), mean probability of reporting the target colour (b), mean probability of reporting a non-target (misbinding; c), and mean probability of guessing (d) as a function of set size in each interference condition. Error bars represent 95% confidence intervals.

5.5.2.3 Comparison between Experiment One and Experiment Two

We then examined whether the effects of the interference task types significantly differed from each other across experiments (i.e., whether there was a significant experiment x interference task type interaction). The imprecision data from Experiment One were transformed such that the area of the response space was equal to 360 to enable better comparison with the data from Experiment Two. Mixed-factor ANOVA revealed that the interaction between experiment and interference task type was not significant; $F(2,\ 44) = 2.67$, $p = .080$, $\eta_p^2 = 0.11$.

Table 5.1: Summary table of significance levels of each variable in each experiment.

Experiment	Dependent variable	Set size	Interference task type	Set size x interference task type interaction
Experiment One: Space	Imprecision	< .001***	.202	.436
	pTarget	.002**	.017*	.469
	pMisbinding	.048*	.565	.304
	pGuessing	.001***	.03*	.224
Experiment Two: Colour	Imprecision	.002**	.096	.572
	pTarget	.002**	.608	.615
	pMisbinding	.005**	.631	.531
	pGuessing	.017*	.425	.408

*Note: * indicates p<0.05, ** indicates p<0.01, *** indicates p<0.001*

5.5.2.4 Discussion

This experiment aimed to examine whether performing delay-period saccades impacted memory for colour in a similar way to the effects on memory for spatial locations. We found no significant effects of interference task type on any outcome variable, consistent with the predictions of Hypothesis 1. We observed reliable increases in imprecision and misbinding increased with increases in set size, consistent with the predictions outlined in Hypothesis 2. We also observed a significant effect of set size on guessing. These findings are consistent with previous work examining memory for colour (Bays et al., 2009). Additionally, there was no interaction between interference task type and experiment on imprecision (Experiment One, Hypothesis 3), indicating that the overt attentional interference task did not have a greater effect on the precision with which spatial locations are maintained in VSWM compared to the precision with which non-spatial features are maintained. This lack of an interaction between interference task type and experiment is perhaps unsurprising given the non-significant effect of interference task type on imprecision in Experiment One.

The lack of an effect of interference task type on misbinding was not consistent with the predictions of Hypothesis 1. The original rationale for this hypothesis arose from the fact that participants were required to compare the probed location with the stored location to retrieve the correct colour. This aspect of the design means any changes in precision of the representation of the probed location could lead to increased misbinding errors in the colour task (Hypothesis 1). However, performing delay-period saccades did not result in an increase in imprecision in memory for spatial location in Experiment One, and as a consequence there was no effect on the misbinding in the colour task.

To summarise the key findings from Experiment Two, no effect of interference task type was observed when examining any outcome variable. This is in contrast to Experiment One, where performing delay-period saccades resulted in an increase in guessing. This result confirms that saccadic disruption is not observed when probing non-spatial features in VSWM (Ball et al., 2013; Pearson et al., 2014; Pearson & Sahraie, 2003; Postle et al., 2006).

5.6 General Discussion

Previous work has shown that saccadic eye movements during the maintenance of spatial locations leads to an impairment of VSWM (Pearson & Sahraie, 2003; Peterson et al., 2019). This impairment is specific to spatial features and is greater than and independent of the interference caused by covert shifts of attention (Lawrence et al., 2004; Pearson et al., 2014). The current study investigated the mechanisms underlying this selective interference effect by examining how delay-period activation of the oculomotor system affected representations of spatial and non-spatial (visual) features in VSWM. Critically, saccadic eye movements resulted in an increase in the probability of guessing when spatial locations were probed (Experiment One) but not when colour memory was examined (Experiment Two). Covert shifts in attention had no effect on memory representations in either experiment. Furthermore, saccadic eye movements did not disrupt the precision with which spatial and visual features were maintained. However, in both experiments imprecision, misbinding and guessing increased with increases in set size.

These findings are broadly consistent with previous work showing that delay-period activation of the oculomotor system interferes with spatial but not visual working memory (Ball et al., 2013; Pearson et al., 2014). Our data cannot be explained by the removal of attention because our delay-period detection task required either a covert or overt shift of attention. If rehearsal in VSWM takes place via shifts in attention (Awh & Jonides, 2001), performance on the covert and overt attentional interference conditions would have been predicted to be relatively equal. In contrast, we observed that guessing responses were significantly higher in the overt than the covert attention interference task condition. Additionally, guessing in the covert attentional interference task condition was not significantly different from maintaining central fixation. This pattern of data indicates that it is activation of the oculomotor system and not shifts of attention alone that drives an increase in guessing. The increase in guessing in spatial memory found in Experiment One, but no increase in misbinding in Experiment Two, following saccadic movements is also consistent with Pearson and Sahraie (2003). When comparing the ratio of temporal errors with spatial errors across conditions, they showed significantly more spatial errors than temporal errors in conditions involving eye movements. Additionally, conditions involving eye movements produced significantly more spatial errors than shifts of covert attention alone (Pearson & Sahraie, 2003). Peterson et al. (2019) have also shown an increase in guessing following performance of delay-period saccades. Our findings and those of previous studies (Pearson & Sahraie, 2003; Peterson et al., 2019) therefore suggest that the mechanism by which delay-period saccades interfere with VSWM is by increasing guessing within spatial working memory.

Our exploratory analysis in Experiment One, examining the directional-specificity of interference task types on response error indicated that response error was greater along the axis of the saccade compared to the axis orthogonal to the saccade. This effect was not found when the oculomotor system was not activated, indicating that the effect is specific to the activation of the oculomotor system. This result lends support for the idea that performing saccades leads to noisy updating of the spatial maps that represent memory items (Peterson et al., 2019), with the caveat that we did not observe significant effects of saccadic interference on precision when collapsed across x- and y-axes.

Our data showed an increase in guessing with no corresponding increase in imprecision in Experiment One. One way to interpret the pattern of our data might be in terms of a slot model of VSWM (Zhang & Luck, 2008). According to a slot model, items are stored in a finite number of independent slots. Several recent studies have shown that the goal of an eye movement is automatically encoded into VSWM, irrespective of its task relevance (Schut et al., 2017; Tas et al., 2016). In the current task, memory items were encoded with the eyes fixated, then participants made saccades to the task-irrelevant locations. If these saccades led to the automatic encoding of the saccade targets, they would fill two of the available slots. This would result in VSWM representations being removed from two slots, which would manifest as an increase in guessing. Because the slots are independent, this removal would not affect the precision with which items in other slots are retained, consistent with the pattern of increased guessing in the absence of reduced precision.

However, there are reasons to be cautious in accepting this interpretation. Specifically, the slot model assumes that items are held as independent bound representations and that spatial and non-spatial features are held in the same representation. This model therefore predicts that there should be no misbinding of features. In contrast to this prediction, we found a reliable increase in misbinding with increases in set size, consistent with previous research in spatial (Schneegans & Bays, 2016) and visual working memory (Ma et al., 2014). Furthermore, contrary to the bound-representation assumption, we found that the overt attentional interference task interfered with spatial but not visual working memory, indicating that these features may be maintained somewhat independently. Indeed, these effects are more consistent with the resource model of VSWM (Bays et al., 2009), which proposes that precision is dependent on the proportion of resources dedicated to each item and that visual and spatial features are held independently (Bays, Wu, et al., 2011). We also observed a set size effect on precision for both spatial and visual memory, which is more consistent with resource than slot models.

The resource model appears to offer the best explanation for the majority of the results. However, it remains difficult to explain why guessing increased, without a corresponding increase in imprecision, in the overt attentional interference task condition in spatial working memory with this model. One speculative proposal is that VSWM items were encoded with a high degree of precision. When the saccade targets were encoded into VSWM during maintenance, resources were removed from VSWM items. However, this did not significantly affect the precision with which VSWM items were retained because the initial representation was encoded with such a high degree of precision. It may be that the effect of performing saccades on precision was limited due to the small range of set sizes used in this study. It is possible that as more items are to be retained and less resource is directed to each item, the effects of performing saccades would be greater on precision.

An alternative explanation might be that delay-period oculomotor activation disrupts the ability to discriminate signals from noise in spatial working memory. This would be problematic, because the resource model assumes that VSWM representations are noisy but have a high signal-to-noise ratio, resulting in responses falling around the probed item. Consistent with this, patients with Parkinson's disease show increased guessing responses with little difference in precision in orientation memory (Zokaei, McNeill, et al., 2014), which was attributed to reduced signal-to-noise ratio caused by dopamine depletion in Parkinson's disease. As has already been noted, saccadic eye-movements require the updating of the internal spatial maps that maintain representations of spatial locations. This updating is likely to be imperfect, which may plausibly result in a reduction of signal-to-noise in the maps. Reduced signal-to-noise would result in an inability to retrieve the correct information at recall, leading to increased guessing. However, because changing signal-to-noise does not affect the allocation of resource to the memoranda, precision of correctly recalled locations is unaffected, consistent with the data observed in Experiment One.

To summarise, we have demonstrated that interference in VSWM due to delay-period saccades are specific to spatial, but not visual, working memory, and that the disruptive effect arises from an increase in guessing rather than a reduction in the precision with which spatial locations are retained in VSWM. On first inspection the finding that disruption following saccades leads to increased guessing but not decreased precision appears to argue for a slot-based model of VSWM. However, we also observed increased misbinding and imprecision as set size increased and a dissociation in saccadic interference effects between spatial and colour working memory, which is more consistent with resource models. To reconcile the effect of guessing with the resource model, it was proposed that delay-period saccadic movements led to reduced signal-to-noise ratio in spatial working memory, thus increasing the probability that responses fell far from the location of the probed item.

Chapter 6

General Discussion

There is abundant evidence supporting the resource model of VSWM in visual features such as colour and orientation (see reviews by Fallon et al., 2016; Ma et al., 2014). However, the nature of representation of spatial locations in VSWM is less clear. Much of the research relies on binary response tasks, which means that the degree to which sources of error can be examined and understood is limited. A second issue is that the oculomotor system has a specific role, above that of covert shifts of attention, in the maintenance of spatial, but not visual information in VSWM (Ball et al., 2013; Pearson et al., 2014; Pearson & Sahraie, 2003; Postle et al., 2006). Any attempt to conceptualise spatial working memory in terms of resource allocation must therefore also consider the role of the oculomotor system in the allocation of resources to different items. The aims of this thesis were therefore:

1. to examine the representation of spatial locations, and distribution of resources, within VSWM; *and*
2. to examine the role of the oculomotor system in resource allocation in VSWM.

Throughout this thesis, spatial working memory is defined as memory for spatial locations. This definition is primarily concerned with the representation of locations in an egocentric reference frame because of the importance of VSWM in guiding and supporting upcoming goal-directed actions (Olivers & Roelfsema, 2020; Rösner et al., 2022). In contrast, visual working memory is defined as memory for non-spatial features concerned with object identity such as colour, orientation, and shape. These definitions of visual and spatial working memory used in this thesis reflect the fractionation between memory for spatial locations and object identity features both neurophysiologically (Courtney et al., 1996; Ren et al., 2019) and behaviourally (Darling et al., 2009; Darling et al., 2007) within the literature.

6.1 Key Findings

Chapter Two aimed to replicate and extend previous work applying the resource model to spatial working memory (Schneegans & Bays, 2016). In *Chapter Two*, the slot and resource models were compared in spatial working memory by examining the distributions of response errors across set sizes, ranging from one item to eight items. The resource model was found to provide a better fit to response errors in spatial working memory compared to the slot+averaging model, as the best fitting model contained variability in precision, misbinding, and guessing (Bays et al., 2009). Further, an exponential increase in response error with increases in set size was found. This pattern of data provides support to previous work in visual (Bays, Wu, et al., 2011; Bays et al., 2009; Gorgoraptis et al., 2011) and spatial working memory (Schneegans & Bays, 2016), as well as highlighting that the distribution of resources in spatial working memory is not linear.

Chapter Three examined how resource allocation in VSWM is affected by the positions of items in space. These data showed an eccentricity effect in spatial working memory, characterised by increasing imprecision and guessing with increases in eccentricity. The eccentricity effect was not replicated in colour memory, ruling out the possibility that the eccentricity effect in spatial working memory was a result of increased encoding noise. This pattern of data indicates that the mnemonic representation of spatial locations changes across the visual field, similar to perception and attention (Carrasco et al., 1995). This finding also provides strong behavioural evidence that VSWM resources are limited by the availability of cortical space in sensory regions, as predicted by the cortical maps hypothesis (Franconeri et al., 2013).

In *Chapter Four*, the serial order effect was examined to investigate how resources are distributed in time and space across sequences of spatial locations using a continuous report task and directly comparing performance on whole-report and partial-report tasks. Different serial position curves were observed depending on whether the task was a whole-report or partial-report task: a primacy effect was found when a whole-report task is used, whereas a recency effect was observed when a single-report task is used. These results highlight the flexibility in VSWM and emphasise the importance of the nature of the recall task when considering the distribution of resources in VSWM. Specifically, the recency curve in the partial-report task suggests dynamic allocation of VSWM resources depending on the number of to-be-remembered items that are presented on each trial. In contrast, in a whole-report task, the primacy effect arises as a result of spatial updating of maintained locations due to performing visually-guided actions in the recall of each item in a sequence. This spatial updating shows the relationship between the cortical maps in which locations in VSWM are maintained and the cortical maps that are used by the motor systems.

The role of the oculomotor system in VSWM was probed in *Chapter Five* by examining how different delay-period attentional tasks affected the sources of recall error in spatial and colour memory. It was observed that guessing, but not imprecision, was increased in spatial working memory following the performance of delay-period saccades. This effect was not replicated in visual working memory. These findings support the view that the oculomotor system plays a specific role in the maintenance of spatial locations in VSWM (Ball et al., 2013; Pearson et al., 2014; Pearson & Sahraie, 2003; Postle et al., 2006), and suggest that the mechanism by which delay-period saccades interferes with VSWM is by increasing guessing rather than by introducing additional noise into the representations within VSWM. This finding is consistent with the proposal that locations in VSWM are maintained as activity peaks within a cortical map, and provides additional evidence supporting that spatial working memory and action rely on a shared representation.

6.2 Spatial Locations are Maintained in a Cortical Map

The evidence presented in this thesis is consistent with the characterisation of VSWM as a finite but dynamic and flexible resource (Bays et al., 2009). However, the question of what this resource is, and how it is implemented cortically, remains. Cortical map architecture has been proposed as a potential format for VSWM resources within the brain (Franconeri et al., 2013). Topographic maps have been reported across a range of cognitive systems and behaviours, including the oculomotor system and attention (Bisley & Mirpour, 2019; Ikkai & Curtis, 2011), as well as in supporting arithmetic and reading (Dehaene & Cohen, 2007). A cortical map is defined as a representation containing activity peaks representing information in a coherent spatial organisation (Franconeri et al., 2013). Items within an information space, such as colour or spatial locations, compete with each other for representation as activity peaks within the map. These activity peaks represent the location of an item within the visual field. One example of cortical maps is within early visual cortex, in which there are retinotopic maps of space corresponding with percepts (Ress & Heeger, 2003). Another example of cortical maps is the representations of spatial locations in parietal cortex, which are used to guide actions such as eye movements (Ikkai & Curtis, 2011; Zimmermann et al., 2011).

The cortical maps hypothesis proposes that each position within the map represents a value in a specific information space. Items from different spaces are represented in different maps and do not compete. Consistent with this idea, working memory for visual features and memory for spatial locations are dissociated within VSWM, both neurophysiologically (Courtney et al., 1996; Sala et al., 2003) and behaviourally (Darling et al., 2009; Darling et al., 2007; Klauer & Zhao, 2004). For example, it has been shown that cortical areas such as posterior parietal cortex and dorsolateral prefrontal cortex are selectively involved in the maintenance of spatial locations (Alekseichuk et al., 2017; Ren et al., 2019). These areas are similar to those areas involved in the vision-for-action pathway (Goodale & Milner, 1992), emphasising the role of spatial working memory in visually-guided behaviour (Manohar et al., 2017). In contrast, the cortical areas involved in memory for non-spatial features, such as shape and orientation, are more similar to the cortical areas involved in the vision-for-perception pathway (Ren et al., 2019). In support of this view, it was observed that eccentricity effects are found in memory for spatial locations but not in memory for colour (*Chapter Three*), and that delay-period saccades interfere with memory for spatial locations but not memory for colour (*Chapter Five*). These findings indicate that resource allocation for spatial and colour memory may be underpinned by two separate sub-stores. In addition, the precision with which spatial locations are stored in VSWM depends on the amount of cortical "real estate" available (Franconeri et al., 2013). It was found that both the number of items (*Chapters Two, Three, Four* and *Five*) and the eccentricity of items (*Chapter Three*) affects the precision with which spatial locations are maintained in VSWM. These findings indicate that as more items are to be retained, there is less cortical space available to encode and maintain each item, so less VSWM resource can be directed to each item. As a result, the precision with which each item is maintained is decreased (Bays et al., 2009). The evidence throughout this thesis therefore supports the view that, within VSWM, spatial locations are maintained in a spatial cortical map, which is constrained by the amount of cortical space that is available for encoding and maintenance of to-be-remembered locations.

The cortical maps hypothesis also argues that cortical maps of space are topographically organised. Studies support that there is extensive overlap between the oculomotor system and spatial working memory both behaviourally (e.g. Ball et al., 2013; Pearson et al., 2014; Peterson et al., 2019) and neurophysiologically (e.g. Ikkai & Curtis, 2011). Moreover, the areas that are involved in spatial working memory contain topographic maps of space, for example posterior parietal cortex (Jerde et al., 2012). A key prediction of this hypothesis is that the precision with which representations are maintained in VSWM is constrained by the physiology of the cortical regions involved in maintaining the map. Indeed, evidence has shown support for this hypothesis. For example, Carrasco et al.

(2001) demonstrated that the horizontal-vertical anisotropy in perception (reduced perceptual performance for locations along the vertical meridian compared to iso-eccentric locations along the horizontal) is present in visual working memory (Carrasco et al., 2001). This anisotropy has been explained in terms of low-level physiological differences in the visual system, specifically with respect to the densities of retinal ganglion cells and cones, which is not radially symmetric across eccentricities in the visual field (Carrasco et al., 2001). Similar anisotropies can be seen in oculomotor behaviour, whereby large horizontal saccades have shorter latencies and higher accuracies compared to saccades along the vertical plane (Irving & Lillakas, 2019) and in spatial working memory, where spatial span and capacity is significantly reduced for locations presented along the vertical meridian compared to locations presented along the horizontal meridian (Smith, 2022).

However, the evidence from anisotropies in VSWM only indirectly supports the cortical maps hypothesis. The eccentricity effect observed in *Chapter Three* provides strong support for this view, showing that imprecision and guessing in spatial working memory increased with increasing eccentricity. The implication of this finding is that the distribution of VSWM is not equal across the visual field, but is constrained by the availability of cortical resources, which should follow the pattern of cortical magnification. That is, there are fewer cortical resources dedicated to processing each degree of visual angle as the visual field moves further into the periphery (Rovamo & Virsu, 1979; Virsu et al., 1987; Virsu & Rovamo, 1979), which manifests as decreased fidelity of the representation within VSWM, and some items not being encoded into VSWM, resulting in increased guessing.

Within the cortical map architecture, spatial locations are encoded and maintained as activity peaks (Ikkai & Curtis, 2011). It has been proposed that the oculomotor system plays a critical role in the maintenance of these peaks via feedback loops, where items are encoded as saccade targets in the priority map and rehearsed by covertly planning saccades to the memorised locations (Baddeley, 1986). Damage or interference with the oculomotor system results in decreased span due to disruption of these feedback loops (Pearson et al., 2014; Smith & Archibald, 2020). In *Chapter Five*, an increase in guessing following delay-period saccades was found in spatial memory, consistent with the differential involvement of the oculomotor system in visual and spatial working memory reported previously (Ball et al., 2013). The results of *Chapter Five* demonstrate unequivocally that saccade execution disrupts spatial working memory, independently of covert orienting of attention. The probability of guessing was significantly higher following saccade execution but there was no difference in the probability of guessing found between covert orienting and central fixation delay-period tasks. This comparison across three matched delay-period tasks, in which the demands of attentional orienting were equal, provides strong evidence against the hypothesis that oculomotor involvement in VSWM is epiphenomenal to shifts in attention (Awh et al., 2000; Awh & Jonides, 2001). Rather, this pattern of results was interpreted in terms of the oculomotor system being involved in maintaining a high signal-to-noise ratio for spatial locations in VSWM. Task-irrelevant delay-period saccades reduce this ratio, resulting in increased guessing because the signal cannot be discriminated from noise, therefore the representation cannot be recalled from the cortical map. Critically, there is no change in precision because the amount of noise within the representation is not affected.

The finding of increased guessing but no change in precision (*Chapter Five*) differs slightly from previous work showing a directionally-specific reduction in precision following performance of a delay-period saccade (Peterson et al., 2019). A key difference between *Chapter Five* and Peterson et al. (2019) is the task used to examine VSWM. Precision in the current studies was derived from a continuous distribution of recall error, whereas Peterson et al. (2019) derived their measure of precision from a binary response task in which the magnitude of change to be detected was varied. This difference between the tasks and measures of precision might have resulted in the different patterns of precision observed. In addition, a bivariate normal distribution assuming a circular standard deviation was applied to the data in *Chapter Five*, compared to the Gaussian probability density function used by Peterson et al. (2019), which might have also resulted in different measures of precision being obtained. Indeed, when the localisation error along x- and y-axes was examined, a directionally-specific effect of saccadic disruption was observed, similar to previous findings (Peterson et al., 2019), indicating that the circular standard deviation might have masked some of the effects observed in the measure of imprecision used. Nevertheless, the effects of delay-period saccadic interference are consistent with previous work demonstrating that VSWM relies on activation of the oculomotor system (Baddeley, 1986; Postle, 2006), especially during maintenance (Pearson et al., 2014; Pearson & Sahraie, 2003).

The cortical maps hypothesis argues that a region can be considered a map if it has a coherent spatial organisation (Franconeri et al., 2013). It has been proposed that the native co-ordinate system in VSWM is retinotopic, as memory for retinotopically mapped locations is more accurate compared to spatiotopically mapped locations (Golomb & Kanwisher, 2012; Shafer-Skelton & Golomb, 2018). The eccentricity effect observed in *Chapter Three* offered preliminary evidence for this retinotopic mapping. In addition, the flexibility of transforming between retinotopic and spatiotopic mapping was shown in *Chapter Four*. The different serial position curves shown between whole-report and partial-report tasks show that the reference frame of the cortical map in VSWM may depend on the nature of the recall task, highlighting the role of VSWM in guiding behaviour for upcoming task completion (Baddeley & Hitch, 1974; Manohar et al., 2017). Responses on the whole-report task were less precise than on the partial-report task, similar to the observation of decreased memory performance for spatiotopic locations (Golomb & Kanwisher, 2012; Shafer-Skelton & Golomb, 2018). The reference frame for the whole-report task was likely spatiotopic because participants were required to reproduce the full sequence of spatial locations, which were not always recalled from the centre of gaze. In contrast, in the partial-report task, recall of the single item was always from the centre of gaze, so transformation to a spatiotopic reference frame was not required. This transformation between reference frames is a noisy process, which would result in decreased precision for the locations that were transformed. In addition, the evidence supporting that the mapping within spatial working memory is retinotopic is consistent with work showing that spatial working memory is associated with activity in cortical regions that are retinotopically mapped (Ikkai & Curtis, 2011; Konen et al., 2013; Sereno et al., 2001).

As well as this transformation in the whole-report task, it is likely that the locations being maintained in VSWM were updated during the recall of each item. In the whole-report task, recall of each item required a goal-directed action, which is known to disrupt VSWM (Lawrence et al., 2004; Pearson & Sahraie, 2003) by increasing noise in the stored representation (Peterson et al., 2019). This spatial updating is a likely candidate for the primacy effect observed, where noise was accumulated within the VSWM representation of yet-to-be-recalled locations following each response. This noise accumulation is reflected in the primacy effect, characterised by increasing imprecision with each item to be maintained and recalled (*Chapter Four*). In contrast, when a single response was required in the partial-report task, no additional noise was present in the locations maintained in VSWM because only a single response from the centre of gaze was required. Indeed, for imprecision, the serial position effect was abolished at the maximum set size in the partial-report task, whereas a strong primacy effect was observed in the matched whole-report task condition, supporting this noise accumulation explanation. This pattern of results further highlights the overlap between action and VSWM (Pearson & Sahraie, 2003; Smith & Archibald, 2020), and show that the locations held in the cortical map of VSWM can be read out and updated by the cortical and subcortical maps that guide action, such as the superior colliculus (Ikkai & Curtis, 2011). This overlap also supports that the function of both VSWM (Baddeley & Hitch, 1974; Manohar et al., 2017) and cortical maps (Zelinsky & Bisley, 2015) is to support action and behaviour.

The data throughout this thesis suggests that the capacity of VSWM for spatial locations is flexible, with precision depending on the number (*Chapter Two*) and eccentricity of items (*Chapter Three*), as well as the nature of the recall task (*Chapter Four*). The oculomotor system plays an important role in the maintenance of the activity peaks within the cortical map, and therefore the accessibility of information in memory (*Chapter Five*).

One question that arises from the cortical maps architecture relates to where these cortical maps are represented in the brain. A prominent idea is the sensory recruitment hypothesis, which argues that VSWM maintenance occurs within early sensory cortex (Adam et al., 2022). Topographic maps have been shown throughout sensory (visual) and parietal cortex (Silver et al., 2005), and the eccentricity effect (*Chapter Three*) offers some support for topographic mapping in VSWM. This result suggests that there may be some overlap between the cortical areas involved in VSWM and perception, consistent with sensory recruitment hypothesis. Retinotopic maps have been observed in visual cortex (Wandell et al., 2007), ensuring that the fovea, and locations closest to the fovea, are represented with a high degree of precision. In VSWM, these locations might be considered to be the most relevant for upcoming task completion, and therefore it is advantageous to represent these locations more precisely within VSWM. This proposal might be considered somewhat similar to the finding that targets of upcoming saccades are represented more precisely in VSWM compared to non-targets (Bays & Husain, 2008; Udale et al., 2022), further highlighting the overlap between perception, oculomotor system, and VSWM (Ikkai & Curtis, 2011). The idea of sensory perception and spatial working memory sharing a cortical representation is a computationally efficient way to temporarily maintain information. Networks already specialised for encoding detailed sensory information are recruited to aid maintenance of this information without requiring additional specialisation of cortical networks. While the pattern of results in this thesis may indicate support for the sensory recruitment hypothesis, more research using neurophysiological methods is required to examine in more detail where cortical maps might be represented within the brain.

6.3 Evidence for a (Revised) Slot Model?

The findings outlined in the current thesis appear to fit best with the characterisation of VSWM as a finite but flexible resource (Bays et al., 2009). This resource might be implemented as a retinotopically-organised cortical map of space, wherein activation peaks are maintained via oculomotor activity. However, the contrasting view is that VSWM capacity is limited by the number of items that can be retained. It is therefore worthwhile to consider whether a (revised) slot+averaging model (Zhang & Luck, 2008) might also account for the pattern of data.

In *Chapter Two*, an exponential increase in localisation error with increases in set size might be considered consistent with a slot model. The small increases in error at set sizes lower than around four items would indicate an item limit of around four items in spatial working memory, consistent with previous work examining visual working memory (Zhang & Luck, 2008). The eccentricity effect (*Chapter Three*), can also be explained by a slot model. Because of the limited number of slots available, some spatial locations must be prioritised, especially at high set sizes. Balaban et al. (2019) showed that there are differences in accuracy across the visual field in the colour change detection task. They found that performance was greatest at the top two central locations, compared to the bottom of the visual field. However, differences between the best accuracy ($M = 0.82$) and lowest accuracy ($M = 0.72$) were small, and no inferential statistics were carried out to verify these conclusions. The primacy effect reported in *Chapter Four* can be explained in terms of slots being allocated to items on a first come-first serve basis, where later items are unable to displace the representations encoded into VSWM earlier in the sequence. Likewise, the increase in guessing following performing delay-period saccades could be interpreted in terms of the saccade targets being encoded into VSWM and displacing memoranda within VSWM.

Revisions in the form of different resolutions within slots depending on the location within the visual field and the nature of the recall task would be required in order for a slot model to fully account for the results presented in this thesis. These revisions are not easy to implement. How would the resolution of slots change across the visual field? What mechanism would be implemented to ensure that the nature of the recall task is taken into account? These revisions call for greater flexibility than the current iterations of the slot model assume, and would result in a slot model that would be almost identical to a resource model.

Furthermore, while it is possible that the pattern of data reported in this thesis might be consistent with a revised slot model, the overall pattern of results presented in this thesis pose a considerable challenge to key assumptions of the slot model. Model comparison in *Chapters Two* and *Three* showed that the best fitting mixture model includes misbinding errors in addition to precision and guessing (Bays et al., 2009) compared to including only precision and guessing (Zhang & Luck, 2008). The probability of guessing was relatively low in most participants and did not reliably increase with increases in set size, even at set size eight. An increase in guessing with set size was observed in *Chapters Three* and *Five*, but not in *Chapter Two*. In contrast, the effect of set size on misbinding was reliably observed in every chapter. If the slot model is correct, the probability of guessing should be around 0.5 at set size eight, which is double the estimate of typical VSWM capacity (Cowan, 2001; Luck & Vogel, 2013, 1997). The guessing rate was relatively low across all studies, indicating that all items were represented in VSWM to some degree.

Additionally, according to the slot model, visual and spatial features of items are not held in separate stores. Effects that are found in spatial memory, such as the eccentricity effect, should therefore be observed in colour memory. In contrast, the resource model (Bays et al., 2009) assumes that there are separate resources, which are responsible for the encoding and maintenance of each feature. These separate resources for each feature predicts that misbinding errors should occur in VSWM. Fractionation between colour and spatial working memory was observed in *Chapters Three* and *Five*, where the eccentricity effect and the disruptive effect of delay-period saccades were observed only for spatial locations in VSWM. These findings provide strong evidence against the assumption that items are held in bound representations within VSWM.

The slot model provides a parsimonious and highly interpretable model of VSWM capacity. However, in its current form it does not adequately account for the pattern of data observed in this thesis, as outlined by a mixture model including misbinding errors providing a mathematically better fit than a mixture model without misbinding errors in *Chapters Two* and *Three*. The revisions that would be required to explain the presented data would be extensive, calling into question its parsimony. Furthermore, these revisions would result in such a flexible slot model that it would be almost indistinguishable from the resource model. It therefore seems unlikely that a slot model, in any form, can explain the results presented in this thesis.

6.4 Limitations and Directions for Future Research

There are a few methodological limitations that must be considered in the interpretation of the results of this thesis. In *Chapters Three* and *Four*, the sample sizes in each experiment were quite small. *A priori* power analyses indicated that these sample sizes were sufficient to detect the indicated effects with at least 90% power. Sample sizes were increased slightly due to the data being noisy and due to data loss (see in particular Experiment Three, *Chapter Three*). In addition, some of the pilot data was deemed unreliable. This was particularly evident in the pilot study for *Chapter Four*, in which the serial position effect was not observed in the sample. Given how robust and highly replicable the serial position effect is in memory and perception (Logan, 2021), it was speculated that the pattern of results in the pilot study was observed due the task being run online, where participants may not have been fully engaged in the task. For this reason, the power analysis was based on Gorgoraptis et al. (2011). This study was chosen as an appropriate study on which to base the power analysis for *Chapter Four* because it was the most closely aligned study to the planned methodology, specifically with respect to the use of the continuous report task. However, it should be noted that this power analysis might be problematic because *Chapter Four* was concerned with memory of spatial locations of coloured dots, whereas Gorgoraptis et al. (2011) was concerned with the memory of the orientation of coloured bars. The probing of different memory features might recruit different cognitive systems (e.g. Ren et al., 2019), meaning that the power analysis should be interpreted with a degree of caution. For this reason, the power analysis in this study was used as an indicative, rather than definitive, minimum sample size.

In addition to increasing the sample sizes slightly beyond the minimum indicated by the power analyses, linear mixed effects models were used to analyse the data in these experiments (*Chapters Two* and *Three*). Using linear mixed effects models controls for the random variation in the data that is contributed by each participant, thereby providing more accurate estimates of the experimental effects. Despite the smaller sample sizes in these chapters, using linear mixed effects models increases the robustness of the results and decreased the probability of type I errors, leading to greater confidence that the results are a true reflection of the experimental effects of eccentricity and serial position.

A related limitation is that, throughout all of the experiments in which fixed viewing was enforced, data was lost. This might have been due to the removal of the central fixation cross in the first three empirical chapters. The fixation cross was not presented throughout encoding and maintenance periods in order to reduce the possibility that the fixation cross would be used as a landmark thereby enabling relative locations of items to be encoded into VSWM and improving VSWM performance (Jiang et al., 2000). This did appear to make it more difficult for participants to maintain fixation, with between approximately 8% and 30% of trials being excluded in each experiment where fixation was to be maintained. It should be noted that when the fixation cross was presented, this pattern did not change (*Chapter Five*). In addition, when fixed viewing and free viewing conditions were compared and when all trials were included in analysis (*Chapter Two*, supplementary materials), the overall pattern of the data did not change (e.g., *Chapter Four*). One possible interpretation of this lack of difference between free and fixed viewing conditions is that saccades, and thus the oculomotor system, might not play as important a role in encoding and the distribution of resources as previously thought (Ohl & Rolfs, 2017). However, in *Chapter Five* the task demands of attention and eye movements were precisely equated, and overt eye movements produced interference effects that were greater than that of covert orienting alone. These findings emphasise that the oculomotor system plays an important role, independent of covert attention, in the maintenance of spatial locations in VSWM.

Another potential limitation in this thesis is that it has not considered the role of individual differences in VSWM and performance in the continuous report task. It is possible that participants' performance might have improved due to practice, or due to the development of cognitive strategies across trials and blocks (Slana Ozimič et al., 2023). These effects were not captured by the data analysis process in this thesis, because trial-by-trial analysis was not conducted. It would be expected that participants would have shown a gradual increase in performance over time with practice, or a more rapid increase in performance with the use of a strategy. One cognitive strategy that may have been adapted in the tasks used in this thesis is that participants may have learned how the stimulus presentation area was restricted such that they strategically responded with locations within that area at recall. One way in which this strategy was corrected in the analysis was to use response resampling in the mixture modelling, which uses the participants own responses as a probability density function from which guessing responses are drawn. Using this response resampling in the model results in a more representative estimate of guessing, which reflects participants' knowledge of the task statistics. However, this measure does not necessarily provide support for the idea that participants were using cognitive strategies. In future, it is worthwhile to ask participants in a short questionnaire how they responded and to capture some metric of meta-cognition in the task in a manner similar to that used by Adam et al. (2017). Using such a measure in combination with trial-by-trial analysis would provide a greater insight into how performance might improve or degrade across testing sessions.

In addition to practice and the development of strategies, there are a number of other individual differences that might account for some of the findings reported. Experiential variables, which describe how participants feel while completing the task, are a particularly important category of individual differences. These variables include attentional disposition, fatigue, and informational chaos, and have been reported by participants to have affected performance on a change detection task (Oblak et al., 2022). Current theories of VSWM tend to focus on cognitive and neural explanations of task performance, but it is worthwhile considering how the participant's experience of the task might also limit or facilitate performance. For example, Oblak et al. (2022) reported that some participants did not fully understand the change detection task used, or were overwhelmed by the number of stimuli. These participants reported responding at random. In addition, some participants reported continuing with the task because of a sense of obligation, but were otherwise not motivated to continue. Again, these participants reported responding at random. The idea of a cognitive map, as proposed in the current thesis, which also considers individual differences in experience might better reflect how VSWM is used in behaviour and reflect the interactions between VSWM and other psychological processes to guide and influence our daily behaviour.

A further limitation in *Chapter Four* is that only a limited number of set sizes were examined. Previous studies using sequential presentation paradigms have used a wider range of set sizes (e.g. Gorgoraptis et al., 2011). It is possible that other or larger differences in the distribution of VSWM resources might emerge at larger set sizes. However, the use of the continuous report task to directly compare recall errors on the whole-report and partial-report tasks permitted a greater insight into the distribution of resources in a controlled manner whereby the only difference between tasks was the requirement to recall either the whole sequence or a single item. Future research might examine the differences between these two tasks across a larger range of set sizes to verify that the observations are true at typically supra-capacity set sizes. In addition, the hypothesis that VSWM resources are pre-allocated to the maximum number of items in a sequence could be explored by displaying valid and invalid cues before the sequence informing participants how many memoranda will be shown. In the valid cue condition, it would be hypothesised that the recency effect would be abolished due to the pre-allocation of the resources to the number of items in that sequence. In the invalid cue condition, the recency effect should increase as a function of the difference between the cued number of items and the actual number of items when the cued number is greater than the number of to-be-remembered items. This pattern would be hypothesised because the resources would be pre-allocated to a greater number of items than there are to be remembered, meaning that there would be greater proportion of resource directed towards the final (most task relevant) item. In contrast, when the cued number is less than the actual number of memoranda, an increase in guessing would be expected, which would increase as a function of the difference between the cued and actual number of memoranda, because there would be no resource available to encode the final item(s) after pre-allocation of the resource. Using this cueing paradigm would enable greater verification of the pre-allocation of resources in the partial recall task and give a greater insight into the flexibility of the allocation of VSWM resources.

In *Chapter Three* the sizes of stimuli and spacing between stimuli were not scaled as a function of eccentricity. When the size of stimuli is scaled according to the magnification factor (M-scaling), such that the cortical representation at each eccentricity is constant, the eccentricity effect is abolished in perceptual tasks, including in visual search (Carrasco & Frieder, 1997) and contrast sensitivity (Jigo et al., 2023). M-scaling is an especially important consideration for the measures of guessing and misbinding because, at the highest eccentricities where spacing was highest, it is unlikely that participants would unintentionally place a true guess response close to a non-target. In contrast, at the smallest eccentricity, stimuli were closer together, which might result in participants guessing, but the response landed close to one of the non-target locations on that trial. This response would be labelled as a misbinding response, thereby increasing the probability of misbinding and decreasing the probability of guessing for that condition. By scaling the stimuli according to the magnification factor, a greater degree of control over low-level visual features, such as retinal size of the stimuli, and the cortical representation of stimuli at each eccentricity is permitted. It follows that, if the cortical representation is equalised across eccentricities, the eccentricity effect should be reduced (Carrasco & Frieder, 1997). However, this neutralisation of the eccentricity effect by M-scaling is not always observed (Staugaard et al., 2016), which has been explained by attention being biased towards central stimuli (Wolfe et al., 1998). Future research might examine how M-scaling affects the eccentricity effect in spatial working memory to further investigate the effects of eccentricity on misbinding and guessing responses. In addition, M-scaling would allow for disentangling the contribution of visual factors and attentional factors in representing spatial locations within VSWM.

As well as using the selective interference paradigm (*Chapter Five*) to examine the contribution of the oculomotor system and attentional processes within VSWM, the eye-abduction paradigm can be used to more directly tease apart these contributions further (Craighero et al., 2004). Using this paradigm, it has been shown that the oculomotor system plays a specific functional role in the maintenance of spatial information in VSWM (Ball et al., 2013; Pearson et al., 2014). However, the extent to which the distribution of VSWM resources depends on the oculomotor system can be examined further by using the continuous report task and the eye-abduction paradigm. The eye-abduction paradigm prevents stimuli in the abducted hemifield from becoming the goal of a saccade by rotating the eye into the temporal hemifield, with no effect on visual acuity. The eye-abduction paradigm has been used to show that exogenous attention, but not endogenous attention, is restricted to the range of the oculomotor system (Smith et al., 2014). It seems likely that VSWM is constrained to the effective oculomotor range, given that patients with Progressive Supranuclear Palsy, a disease characterised by vertical paralysis of gaze, have significantly decreased spatial working memory capacity along the axis of paralysis compared to the non-paretic axis (Smith & Archibald, 2020). The key difference between the temporal and nasal hemifields in the continuous report task would be in imprecision and the probability of guessing. If the distribution of VSWM resources is constrained to the effective oculomotor range, it is hypothesised that the probability of guessing and imprecision would be increased in the temporal hemifield compared to the nasal hemifield because locations in the temporal hemifield cannot become the goal of a saccadic eye movement, therefore would not be represented in VSWM, or would receive a small share of VSWM resources for representation, thereby resulting in a noisy representation within VSWM. In contrast, if VSWM resources can be distributed beyond the oculomotor range, there should be no difference between temporal and nasal hemifields in the probability of guessing and precision. This research would extend the current proposal that spatial locations in VSWM are maintained in a cortical map by further examining the constraints of these cortical maps, and their interaction with the oculomotor system.

6.5 Conclusion

This thesis aimed to examine how spatial locations are represented in VSWM, and to investigate the role of the oculomotor system in the maintenance of information in VSWM. Across four studies, it was shown that precision in spatial working memory depends on the number (*Chapter Two*) and eccentricity of memoranda (*Chapter Three*), as well as the requirement to transform and update information within spatial working memory (*Chapter Four*).

These findings are consistent with the idea that spatial working memory is best characterised by a flexible resource (Bays et al., 2009). This resource is constrained by the amount of cortical space available, as proposed by the cortical maps hypothesis (Franconeri et al., 2013). The availability of cortical space is influenced by both the number and location of the memoranda across the visual field (*Chapter Three*). Within these cortical maps, spatial locations are represented by activity peaks that are maintained by the oculomotor system. This conclusion is supported by the finding that performance of delay-period saccades, but not covert shifts in attention, increased the probability of guessing, but not imprecision, in spatial working memory but not in colour working memory (*Chapter Five*). This finding was argued to reflect the role of the oculomotor system in the maintenance of high signal-to-noise ratio of the activity peaks within the cortical and subcortical maps that guide actions.

The results of this thesis, therefore, provide strong evidence that VSWM is best characterised as a limited but flexible resource (Bays et al., 2009), and that the oculomotor system plays a critical role in the maintenance of spatial, but not visual, information in VSWM. This VSWM resource might be implemented in brain areas that represent space, including primary visual cortex, parietal cortex, and frontal eye fields, as well as subcortical oculomotor regions such as superior colliculus, which relies on the oculomotor system to encode and maintain locations as activity peaks. A consequence of this cortical map architecture is that results appear to offer support for sensory recruitment hypothesis, given that position within the visual field appears to affect the representation in a similar way to perception (*Chapter Three*). Additionally, the results of this thesis emphasise the important functional relationships between VSWM and motor systems (*Chapters Four* and *Five*).

References

Adam, K. C. S., Rademaker, R. L., & Serences, J. T. (2022). Evidence for, and challenges to, sensory recruitment models of visual working memory. In *Visual Memory* (1st ed., pp. 5–25). Routledge. https://doi.org/10.4324/9781003158134-2

Adam, K. C. S., Vogel, E. K., & Awh, E. (2017). Clear evidence for item limits in visual working memory. *Cognitive Psychology*, *97*, 79–97. https://doi.org/10.1016/j.cogpsych.2017.07.001

Agam, Y., Bullock, D., & Sekuler, R. (2005). Imitating Unfamiliar Sequences of Connected Linear Motions. *Journal of Neurophysiology*, *94*(4), 2832–2843. https://doi.org/10.1152/jn.00366.2005

Agam, Y., Galperin, H., Gold, B. J., & Sekuler, R. (2007). Learning to imitate novel motion sequences. *Journal of Vision*, *7*(5), 1. https://doi.org/10.1167/7.5.1

Agam, Y., Huang, J., & Sekuler, R. (2010). Neural Correlates of Sequence Encoding in Visuomotor Learning. *Journal of Neurophysiology*, *103*(3), 1418–1424. https://doi.org/10.1152/jn.00662.2009

Alekseichuk, I., Pabel, S. C., Antal, A., & Paulus, W. (2017). P206 Cross-hemispheric frontoparietal desynchronization impairs the visual-spatial working memory in humans. *Clinical Neurophysiology*, *128*(3), e114. https://doi.org/10.1016/j.clinph.2016.10.323

Allen, K., Giofrè, D., Higgins, S., & Adams, J. (2020). Working memory predictors of written mathematics in 7- to 8-year-old children: *Quarterly Journal of Experimental Psychology*. https://doi.org/10.1177/1747021819871243

Allen, K., Higgins, S., & Adams, J. (2019). The Relationship between Visuospatial Working Memory and Mathematical Performance in School-Aged Children: A Systematic Review. *Educational Psychology Review*, *31*(3), 509–531. https://doi.org/10.1007/s10648-019-09470-8

Alloway, T. P., Kerr, I., & Langheinrich, T. (2010). The effect of articulatory suppression and manual tapping on serial recall. *European Journal of Cognitive Psychology*, *22*(2), 297–305. https://doi.org/10.1080/09541440902793731

Alvarez, G. A., & Cavanagh, P. (2004). The Capacity of Visual Short-Term Memory is Set Both by Visual Information Load and by Number of Objects. *Psychological Science*, *15*(2), 106–111. https://doi.org/10.1111/j.0963-7214.2004.01502006.x

Arai, K., McPeek, R. M., & Keller, E. L. (2004). Properties of saccadic responses in monkey when multiple competing visual stimuli are present. *Journal of Neurophysiology*, *91*(2), 890–900. https://doi.org/10.1152/jn.00818.2003

Arce, T., & McMullen, K. (2021). The Corsi Block-Tapping Test: Evaluating methodological practices with an eye towards modern digital frameworks. *Computers in Human Behavior Reports*, *4*, 100099. https://doi.org/10.1016/j.chbr.2021.100099

Ashkenazi, S., Rosenberg-Lee, M., Metcalfe, A. W. S., Swigart, A. G., & Menon, V. (2013). Visuo–spatial working memory is an important source of domain-general vulnerability in the development of arithmetic cognition. *Neuropsychologia*, *51*(11), 2305–2317. https://doi.org/10.1016/j.neuropsychologia.2013.06.031

Avons, S. E., & Trew, L. (2006). What kind of space is remembered in spatial span? *Cognitive Processing*, *7*(1), 157–159. https://doi.org/10.1007/s10339-006-0121-3

Awh, E., Anllo-Vento, L., & Hillyard, S. A. (2000). The role of spatial selective attention in working memory for locations: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *12*(5), 840–847. https://doi.org/10.1162/089892900562444

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual Working Memory Represents a Fixed Number of Items Regardless of Complexity. *Psychological Science*, *18*(7), 622–628.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, *5*(3), 119–126. https://doi.org/10.1016/S1364-6613(00)01593-X

Awh, E., Jonides, J., & Reuter-Lorenz, P. A. (1998). Rehearsal in Spatial Working Memory. *Journal of Experimental Psychology: Human Perception and Performance*, *24*(3), 780–790.

Awh, E., Jonides, J., Smith, E. E., Buxton, R. B., Frank, L. R., Love, T., Wong, E. C., & Gmeindl, L. (1999). Rehearsal in Spatial Working Memory: Evidence From Neuroimaging. *Psychological Science*, *10*(5), 433–437. https://doi.org/10.1111/1467-9280.00182

Baddeley, A. D. (2010). Working memory. *Current Biology*, *20*(4), R136–R140. https://doi.org/10.1016/j.cub.2009.12.014

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, *4*(11), 417–423. https://doi.org/10.1016/S1364-6613(00)01538-2

Baddeley, A. D. (2011). Working Memory: Theories, Models, and Controversies. *Annual Review of Psychology*, *63*(1), 1–29. https://doi.org/10.1146/annurev-psych-120710-100422

Baddeley, A. D. (1986). *Working memory.* Clarendon Press/Oxford University Press.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. A. Bower (Ed.), *Recent Advances in Learning and Motivation* (Vol. 8, pp. 47–89). Academic Press.

Baddeley, A. D., Hitch, G., & Allen, R. (2021). A Multicomponent Model of Working Memory. In R. H. Logie, V. Camos, & N. Cowan (Eds.), *Working Memory: The State of the Science* (pp. 10–43). Oxford University Press.

Baddeley, A. D., & Lieberman, K. (1980). Spatial working memory. In R. Nickerson (Ed.), *Attention and performance, VIII* (pp. 521–539). Erlbaum.

Balaban, H., Fukuda, K., & Luria, R. (2019). What can half a million change detection trials tell us about visual working memory? *Cognition*, *191*, 103984. https://doi.org/10.1016/j.cognition.2019.05.021

Ball, K., Pearson, D. G., & Smith, D. T. (2013). Oculomotor involvement in spatial working memory is task-specific. *Cognition*, *129*, 439–446.

Barton, B., Ester, E. F., & Awh, E. (2009). Discrete resource allocation in visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*. https://doi.org/10.1037/a0015792

Basso, A., Spinnler, H., Vallar, G., & Zanobio, M. E. (1982). Left hemisphere damage and selective impairment of auditory verbal short-term memory. A case study. *Neuropsychologia*, *20*(3), 263–274. https://doi.org/10.1016/0028-3932(82)90101-4

Bays, P. M. (n.d.). Analogue Report Toolbox. In *Cambridge Computational Cognition Group*. https://www.paulbays.com/toolbox/index.php.

Bays, P. M. (2016). Evaluating and excluding swap errors in analogue tests of working memory. *Scientific Reports*, *6*, 19203. https://doi.org/10.1038/srep19203

Bays, P. M. (2014). Noise in Neural Populations Accounts for Errors in Working Memory. *Journal of Neuroscience*, *34*(10), 3632–3645. https://doi.org/10.1523/JNEUROSCI.3204-13.2014

Bays, P. M. (2015). Spikes not slots: Noise in neural populations limits working memory. *Trends in Cognitive Sciences*, *19*(8), 431–438. https://doi.org/10.1016/j.tics.2015.06.004

Bays, P. M. (2018). Failure of self-consistency in the discrete resource model of visual working memory. *Cognitive Psychology*, *105*, 1–8. https://doi.org/10.1016/j.cogpsych.2018.05.002

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, *9*(10), 7.1–11. https://doi.org/10.1167/9.10.7

Bays, P. M., Gorgoraptis, N., Wee, N., Marshall, L., & Husain, M. (2011). Temporal dynamics of encoding, storage, and reallocation of visual working memory. *Journal of Vision*, *11*(10), 6–6. https://doi.org/10.1167/11.10.6

Bays, P. M., & Husain, M. (2007). Spatial remapping of the visual world across saccades. *Neuroreport*, *18*(12), 1207–1213. https://doi.org/10.1097/WNR.0b013e328244e6c3

Bays, P. M., & Husain, M. (2008). Dynamic Shifts of Limited Working Memory Resources in Human Vision. *Science*, *321*(5890), 851–854. https://doi.org/10.1126/science.1158023

Bays, P. M., Wu, E. Y., & Husain, M. (2011). Storage and binding of object features in visual working memory. *Neuropsychologia*, *49*(6), 1622–1631. https://doi.org/10.1016/j.neuropsychologia.2010.12.023

Belopolsky, A. V., & Theeuwes, J. (2009a). Inhibition of saccadic eye movements to locations in spatial working memory. *Attention, Perception, & Psychophysics*, *71*(3), 620–631. https://doi.org/10.3758/APP.71.3.620

Belopolsky, A. V., & Theeuwes, J. (2009b). No functional role of attention-based rehearsal in maintenance of spatial working memory representations. *Acta Psychologica*, *132*(2), 124–135. https://doi.org/10.1016/j.actpsy.2009.01.002

Berch, D. B., Krikorian, R., & Huha, E. M. (1998). The Corsi block-tapping task: Methodological and theoretical considerations. *Brain and Cognition*, *38*(3), 317–338. https://doi.org/10.1006/brcg.1998.1039

Berry, E. D. J., Allen, R. J., Waterman, A. H., & Logie, R. H. (2019). The Effect of a Verbal Concurrent Task on Visual Precision in Working Memory. *Experimental Psychology*, *66*(1), 77–85. https://doi.org/10.1027/1618-3169/a000428

Bisley, J. W., & Mirpour, K. (2019). The neural instantiation of a priority map. *Current Opinion in Psychology*, *29*, 108–112. https://doi.org/10.1016/j.copsyc.2019.01.002

Bochynska, A., & Laeng, B. (2015). Tracking down the path of memory: Eye scanpaths facilitate retrieval of visuospatial information. *Cognitive Processing*, *16*(1), 159–163. https://doi.org/10.1007/s10339-015-0690-0

Botta, F., Santangelo, V., Raffone, A., Lupiáñez, J., & Belardinelli, M. O. (2010). Exogenous and endogenous spatial attention effects on visuospatial working memory. *Quarterly Journal of Experimental Psychology*, *63*(8), 1590–1602. https://doi.org/10.1080/17470210903443836

Brandt, S. A., & Stark, L. W. (1997). Spontaneous Eye Movements During Visual Imagery Reflect the Content of the Visual Scene. *Journal of Cognitive Neuroscience*, *9*(1), 27–38. https://doi.org/10.1162/jocn.1997.9.1.27

Brooks, L. R. (1967). The suppression of visualisation by reading. *Quarterly Journal of Experimental Psychology*, *19A*, 289–299.

Buschman, T. J., Siegel, M., Roy, J. E., & Miller, E. K. (2011). Neural substrates of cognitive capacity limitations. *Proceedings of the National Academy of Sciences*, *108*(27), 11252–11255. https://doi.org/10.1073/pnas.1104666108

Campana, G., Cowey, A., Casco, C., Oudsen, I., & Walsh, V. (2007). Left frontal eye field remembers “where” but not “what.” *Neuropsychologia*, *45*(10), 2340–2345. https://doi.org/10.1016/j.neuropsychologia.2007.02.009

Carrasco, M., Evert, D. L., Chang, I., & Katz, S. M. (1995). The eccentricity effect: Target eccentricity affects performance on conjunction searches. *Perception & Psychophysics*, *57*(8), 1241–1261. https://doi.org/10.3758/BF03208380

Carrasco, M., & Frieder, K. S. (1997). Cortical Magnification Neutralizes the Eccentricity Effect in Visual Search. *Vision Research*, *37*(1), 63–82. https://doi.org/10.1016/S0042-6989(96)00102-2

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision*, *15*(1), 61–75. https://doi.org/10.1163/15685680152692015

Casteau, S., & Smith, D. T. (2019). Associations and Dissociations between Oculomotor Readiness and Covert Attention. *Vision*, *3*(2), 17. https://doi.org/10.3390/vision3020017

Casteau, S., & Smith, D. T. (2020). Covert attention beyond the range of eye-movements: Evidence for a dissociation between exogenous and endogenous orienting. *Cortex*, *122*, 170–186. https://doi.org/10.1016/j.cortex.2018.11.007

Chen, X., Li, B., & Liu, Y. (2017). The Impact of Object Complexity on Visual Working Memory Capacity. *Psychology*, *08*, 929. https://doi.org/10.4236/psych.2017.86060

Christophel, T. B., Hebart, M. N., & Haynes, J.-D. (2012). Decoding the Contents of Visual Short-Term Memory from Human Visual and Parietal Cortex. *Journal of Neuroscience*, *32*(38), 12983–12989. https://doi.org/10.1523/JNEUROSCI.0184-12.2012

Cocchini, G., Logie, R. H., Sala, S. D., MacPherson, S. E., & Baddeley, A. D. (2002). Concurrent performance of two memory tasks: Evidence for domain-specific working memory systems. *Memory & Cognition*, *30*(7), 1086–1095. https://doi.org/10.3758/BF03194326

Colom, R., Abad, F. J., Quiroga, M. Á., Shih, P. C., & Flores-Mendoza, C. (2008). Working memory and intelligence are highly related constructs, but why? *Intelligence*, *36*(6), 584–606. https://doi.org/10.1016/j.intell.2008.01.002

Colom, R., Escorial, S., Shih, P. C., & Privado, J. (2007). Fluid intelligence, memory span, and temperament difficulties predict academic performance of young adolescents. *Personality and Individual Differences*, *42*(8), 1503–1514. https://doi.org/10.1016/j.paid.2006.10.023

Corsi, P. M. (1972). *Human memory and the medial temporal region of the brain* [Unpublished Doctoral Thesis]. McGill University.

Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An Area Specialized for Spatial Working Memory in Human Frontal Cortex. *Science*, *279*(5355), 1347–1351. https://doi.org/10.1126/science.279.5355.1347

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and Spatial Visual Working Memory Activate Separate Neural Systems in Human Cortex. *Cerebral Cortex*, *6*(1), 39–49. https://doi.org/10.1093/cercor/6.1.39

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *The Behavioral and Brain Sciences*, *24*(1), 87-114; discussion 114-185.

Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye Position Affects Orienting of Visuospatial Attention. *Current Biology*, *14*(4), 331–333. https://doi.org/10.1016/j.cub.2004.01.054

Curcio, C. A., Sloan, K. R., Packer, O., Hendrickson, A. E., & Kalina, R. E. (1987). Distribution of Cones in Human and Monkey Retina: Individual Variability and Radial Asymmetry. *Science*, *236*(4801), 579–582. https://doi.org/10.1126/science.3576186

Curtis, C. E., Rao, V. Y., & D'Esposito, M. (2004). Maintenance of Spatial and Motor Codes during Oculomotor Delayed Response Tasks. *Journal of Neuroscience*, *24*(16), 3944–3952. https://doi.org/10.1523/JNEUROSCI.5640-03.2004

Czoschke, S., Henschke, S., & Lange, E. B. (2019). On-item fixations during serial encoding do not affect spatial working memory. *Attention, Perception, & Psychophysics*, *81*(8), 2766–2787. https://doi.org/10.3758/s13414-019-01786-5

D'Esposito, M., Aguirre, G. K., Zarahn, E., Ballard, D., Shin, R. K., & Lease, J. (1998). Functional MRI studies of spatial and nonspatial working memory. *Cognitive Brain Research*, *7*(1), 1–13. https://doi.org/10.1016/S0926-6410(98)00004-4

D'Esposito, M., & Postle, B. R. (2015). THE COGNITIVE NEUROSCIENCE OF WORKING MEMORY. *Annual Review of Psychology*, *66*, 115–142. https://doi.org/10.1146/annurev-psych-010814-015031

Dai, M., Li, Y., Gan, S., & Du, F. (2019). The reliability of estimating visual working memory capacity. *Scientific Reports*, *9*(1), 1–8. https://doi.org/10.1038/s41598-019-39044-1

Damiano, C., & Walther, D. B. (2019). Distinct roles of eye movements during memory encoding and retrieval. *Cognition*, *184*, 119–129. https://doi.org/10.1016/j.cognition.2018.12.014

Darling, S., Della Sala, S., & Logie, R. H. (2007). Behavioural evidence for separating components within visuo-spatial working memory. *Cognitive Processing*, *8*(3), 175–181. https://doi.org/10.1007/s10339-007-0171-1

Darling, S., Della Sala, S., Logie, R. H., & Cantagallo, A. (2006). Neuropsychological evidence for separating components of visuo-spatial working memory. *Journal of Neurology*, *253*(2), 176–180. https://doi.org/10.1007/s00415-005-0944-3

Darling, S., Sala, S. D., & Logie, R. H. (2009). Dissociation between appearance and location within visuo-spatial working memory. *The Quarterly Journal of Experimental Psychology*, *62*(3), 417–425. https://doi.org/10.1080/17470210802321984

Daucourt, M. C., Schatschneider, C., Connor, C. M., Al Otaiba, S., & Hart, S. A. (2018). Inhibition, Updating Working Memory, and Shifting Predict Reading Disability Symptoms in a Hybrid Model: Project KIDS. *Frontiers in Psychology*, *9*. https://doi.org/10.3389/fpsyg.2018.00238

de Brouwer, A. J., Flanagan, J. R., & Spering, M. (2021). Functional Use of Eye

Movements for an Acting System. *Trends in Cognitive Sciences*, *25*(3), 252–263. https://doi.org/10.1016/j.tics.2020.12.006

Dehaene, S., & Cohen, L. (2007). Cultural Recycling of Cortical Maps. *Neuron*, *56*(2), 384–398. https://doi.org/10.1016/j.neuron.2007.10.004

Della Sala, S., Gray, C., Baddeley, A., Allamano, N., & Wilson, L. (1999). Pattern span: A tool for unwelding visuo–spatial memory. *Neuropsychologia*, *37*(10), 1189–1199. https://doi.org/10.1016/S0028-3932(98)00159-6

Deubel, H. (1989). Sensory and motor aspects of saccade control. *European Archives of Psychiatry and Neurological Sciences*, *239*(1), 17–22. https://doi.org/10.1007/BF01739738

Donkin, C., Nosofsky, R. M., Gold, J. M., & Shiffrin, R. M. (2013). Discrete-Slots Models of Visual Working-Memory Response Times. *Psychological Review*, *120*(4), 873–902. https://doi.org/10.1037/a0034247

Emrich, S. M., Riggall, A. C., LaRocque, J. J., & Postle, B. R. (2013). Distributed Patterns of Activity in Sensory Cortex Reflect the Precision of Multiple Items Maintained in Visual Short-Term Memory. *Journal of Neuroscience*, *33*(15), 6516–6523. https://doi.org/10.1523/JNEUROSCI.5732-12.2013

Eng, H. Y., Chen, D., & Jiang, Y. (2005). Visual working memory for simple and complex visual stimuli. *Psychonomic Bulletin & Review*, *12*(6), 1127–1133. https://doi.org/10.3758/BF03206454

Eriksson, J., Vogel, E. K., Lansner, A., Bergström, F., & Nyberg, L. (2015). Neurocognitive Architecture of Working Memory. *Neuron*, *88*(1), 33–46. https://doi.org/10.1016/j.neuron.2015.09.020

Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially Global Representations in Human Primary Visual Cortex during Working Memory Maintenance. *Journal of Neuroscience*, *29*(48), 15258–15265. https://doi.org/10.1523/JNEUROSCI.4388-09.2009

Fallon, S. J., Zokaei, N., & Husain, M. (2016). Causes and consequences of limitations in visual working memory: Limitations in working memory. *Annals of the New York*

Academy of Sciences, *1369*(1), 40–54. https://doi.org/10.1111/nyas.12992

Fanari, R., Meloni, C., & Massidda, D. (2019). Visual and Spatial Working Memory Abilities Predict Early Math Skills: A Longitudinal Study. *Frontiers in Psychology*, *10*. https://doi.org/10.3389/fpsyg.2019.02460

Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149–1160. https://doi.org/10.3758/BRM.41.4.1149

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/BF03193146

Fehd, H. M., & Seiffert, A. E. (2008). Eye movements during multiple object tracking: Where do participants look? *Cognition*, *108*(1), 201–209. https://doi.org/10.1016/j.cognition.2007.11.008

Feldmann-Wüstefeld, T., Vogel, E. K., & Awh, E. (2018). Contralateral Delay Activity Indexes Working Memory Storage, Not the Current Focus of Spatial Attention. *Journal of Cognitive Neuroscience*, *30*(8), 1185–1196. https://doi.org/10.1162/jocn_a_01271

Ferreira, F., Apel, J., & Henderson, J. M. (2008). Taking a new look at looking at nothing. *Trends in Cognitive Sciences*, *12*(11), 405–410. https://doi.org/10.1016/j.tics.2008.07.007

Foster, J. J., Bsales, E. M., Jaffe, R. J., & Awh, E. (2017). Alpha-Band Activity Reveals Spontaneous Representations of Spatial Position in Visual Working Memory. *Current Biology: CB*, *27*(20), 3216–3223.e6. https://doi.org/10.1016/j.cub.2017.09.031

Foulsham, T., & Kingstone, A. (2013). Fixation-dependent memory for natural scenes: An experimental test of scanpath theory. *Journal of Experimental Psychology: General*, *142*(1), 41–56. https://doi.org/10.1037/a0028227

Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: Competitive content maps for attention and memory. *Trends in Cognitive Sciences*, *17*(3), 134–141. https://doi.org/10.1016/j.tics.2013.01.010

Fukuda, K., Awh, E., & Vogel, E. K. (2010). Discrete capacity limits in visual working memory. *Current Opinion in Neurobiology*, *20*(2), 177–182. https://doi.org/10.1016/j.conb.2010.03.005

Fukuda, K., Woodman, G. F., & Vogel, E. K. (2015). Individual differences in visual working memory capacity: Contributions of attentional control to storage. In P. Jolicoeur, C. Lefebvre, & J. Martinez-Trujillo (Eds.), *Mechanisms of Sensory Working Memory: Attention and Perfomance XXV* (pp. 105–119). Elsevier.

Gegenfurtner, K. R., Kiper, D. C., & Fenstemaker, S. B. (1996). Processing of color, form, and motion in macaque area V2. *Visual Neuroscience*, *13*, 161–172.

Godijn, R., & Theeuwes, J. (2012). Overt is no better than covert when rehearsing visuo-spatial information in working memory. *Memory & Cognition*, *40*(1), 52–61. https://doi.org/10.3758/s13421-011-0132-x

Godijn, R., & Theeuwes, J. (2004). The Relationship Between Inhibition of Return and Saccade Trajectory Deviations. *Journal of Experimental Psychology: Human Perception and Performance*, *30*(3), 538–554. https://doi.org/10.1037/0096-1523.30.3.538

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The Native Coordinate System of Spatial Attention Is Retinotopic. *Journal of Neuroscience*, *28*(42), 10654–10662. https://doi.org/10.1523/JNEUROSCI.2525-08.2008

Golomb, J. D., & Kanwisher, N. (2012). Retinotopic memory is more precise than spatiotopic memory. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(5), 1796–1801. https://doi.org/10.1073/pnas.1113168109

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*(1), 20–25. https://doi.org/10.1016/0166-2236(92)90344-8

Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic Updating of Working Memory Resources for Visual Objects. *The Journal of Neuroscience*, *31*(23), 8502–8511. https://doi.org/10.1523/JNEUROSCI.0208-11.2011

Griffin, I., & Nobre, A. (2003). Orienting Attention to Locations in Internal Representations. *Journal of Cognitive Neuroscience*, *15*, 1176–1194. https://doi.org/10.1162/

089892903322598139

Groeger, J. A., Field, D., & Hammond, S. M. (1999). Measuring memory span. *International Journal of Psychology*, *34*(5-6), 359–363. https://doi.org/10.1080/002075999399693

Grogan, J. P., Fallon, S. J., Zokaei, N., Husain, M., Coulthard, E. J., & Manohar, S. G. (2020). A new toolbox to distinguish the sources of spatial memory error. *Journal of Vision*, *20*(13), 6–6. https://doi.org/10.1167/jov.20.13.6

Grossi, D., Becker, J. T., Smith, C., & Trojano, L. (1993). Memory for visuospatial patterns in Alzheimer's disease. *Psychological Medicine*, *23*(1), 65–70. https://doi.org/10.1017/S003329170003885X

Guérard, K., & Tremblay, S. (2008). Revisiting evidence for modularity and functional equivalence across verbal and spatial domains in memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(3), 556–569. https://doi.org/10.1037/0278-7393.34.3.556

Haist, F., Shimamura, A. P., & Squire, L. R. (1992). On the relationship between recall and recognition memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *18*(4), 691–702. https://doi.org/10.1037/0278-7393.18.4.691

Hanley, J. R., Young, A. W., & Pearson, N. A. (1991). Impairment of the visuo-spatial sketch pad. *The Quarterly Journal of Experimental Psychology Section A*, *43*(1), 101–125. https://doi.org/10.1080/14640749108401001

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology*, *115*(2), 1071–1076. https://doi.org/10.1152/jn.00927.2015

Harrison, W. J., & Bays, P. M. (2018). Visual Working Memory Is Independent of the Cortical Spacing Between Memoranda. *The Journal of Neuroscience*, *38*(12), 3116–3123. https://doi.org/10.1523/JNEUROSCI.2645-17.2017

Hebb, D. O. (1968). Concerning imagery. *Psychological Review*, *75*(6), 466–477. https://doi.org/10.1037/h0026771

Hecker, R., & Mapperson, B. (1997). Dissociation of visual and spatial processing in working memory. *Neuropsychologia*, *35*(5), 599–603. https://doi.org/10.1016/S0028-3932(96)00106-6

Henderson, J. M., Williams, C. C., & Falk, R. J. (2005). Eye movements are functional during face learning. *Memory & Cognition*, *33*(1), 98–106. https://doi.org/10.3758/BF03195300

Heuer, A., Ohl, S., & Rolfs, M. (2020). Memory for action: A functional view of selection in visual working memory. *Visual Cognition*, *0*(0), 1–13. https://doi.org/10.1080/13506285.2020.1764156

Hollingworth, A., Richard, A. M., & Luck, S. J. (2008). Understanding the function of visual short-term memory: Transsaccadic memory, object correspondence, and gaze correction. *Journal of Experimental Psychology. General*, *137*(1), 163–181. https://doi.org/10.1037/0096-3445.137.1.163

Huang, L. (2010). Visual working memory is better characterized as a distributed resource rather than discrete slots. *Journal of Vision*, *10*(14), 8. https://doi.org/10.1167/10.14.8

Hurlstone, M. J., Hitch, G. J., & Baddeley, A. D. (2014). Memory for serial order across domains: An overview of the literature and directions for future research. *Psychological Bulletin*, *140*(2), 339–373. https://doi.org/10.1037/a0034221

Husain, M., Mannan, S., Hodgson, T., Wojciulik, E., Driver, J., & Kennard, C. (2001). Impaired spatial working memory across saccades contributes to abnormal search in parietal neglect. *Brain: A Journal of Neurology*, *124*(Pt 5), 941–952. https://doi.org/10.1093/brain/124.5.941

Huynh Cong, S., & Kerzel, D. (2021). Allocation of resources in working memory: Theoretical and empirical implications for visual search. *Psychonomic Bulletin & Review*, *28*(4), 1093–1111. https://doi.org/10.3758/s13423-021-01881-5

Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review*, *17*(5), 680–686. https://doi.org/10.3758/PBR.17.5.680

Ikkai, A., & Curtis, C. E. (2011). Common neural mechanisms supporting spatial working memory, attention and motor intention. *Neuropsychologia*, *49*(6), 1428–1434. https://doi.org/10.1016/j.neuropsychologia.2010.12.020

Inhoff, A. W., & Weger, U. (2005). Memory for word location during reading. *Memory & Cognition*, *33*(3), 447–461.

Irving, E. L., & Lillakas, L. (2019). Difference between vertical and horizontal saccades across the human lifespan. *Experimental Eye Research*, *183*, 38–45. https://doi.org/10.1016/j.exer.2018.08.020

Jerde, T. A., Merriam, E. P., Riggall, A. C., Hedges, J. H., & Curtis, C. E. (2012). Prioritized Maps of Space in Human Frontoparietal Cortex. *The Journal of Neuroscience*, *32*(48), 17382–17390. https://doi.org/10.1523/JNEUROSCI.3810-12.2012

Jiang, Y., Olson, I., & Chun, M. (2000). Organization of Visual Short-Term Memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *26*(3), 683–702. https://doi.org/10.1037/0278-7393.26.3.683

Jigo, M., Tavdy, D., Himmelberg, M. M., & Carrasco, M. (2023). Cortical magnification eliminates differences in contrast sensitivity across but not around the visual field. *eLife*, *12*, e84205. https://doi.org/10.7554/eLife.84205

Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced during encoding. *Journal of Experimental Psychology. Human Perception and Performance*, *38*(5), 1289–1314. https://doi.org/10.1037/a0026585

Jones, D., Farrand, P., Stuart, G., & Morris, N. (1995). Functional equivalence of verbal and spatial information in serial short-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *21*(4), 1008–1018.

Jonikaitis, D., & Moore, T. (2019). The interdependence of attention, working memory and gaze control: Behavior and neural circuitry. *Current Opinion in Psychology*, *29*, 126–134. https://doi.org/10.1016/j.copsyc.2019.01.012

Jost, K., & Mayr, U. (2016). Switching between filter settings reduces the efficient utilization of visual working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *16*(2), 207–218. https://doi.org/10.3758/s13415-015-0380-5

Jüttner, M., & Rentschler, I. (2000). Scale-invariant superiority of foveal vision in perceptual categorization. *The European Journal of Neuroscience*, *12*(1), 353–359. https://doi.org/10.1046/j.1460-9568.2000.00907.x

Kalogeropoulou, Z., Jagadeesh, A. V., Ohl, S., & Rolfs, M. (2017). Setting and changing feature priorities in visual short-term memory. *Psychonomic Bulletin & Review*, *24*(2), 453–458. https://doi.org/10.3758/s13423-016-1094-6

Kassambara, A. (2019). *Rstatix: Pipe-Friendly Framework for Basic Statistical Tests.*

Keshvari, S., van den Berg, R., & Ma, W. J. (2013). No Evidence for an Item Limit in Change Detection. *PLoS Computational Biology*, *9*(2), e1002927. https://doi.org/10.1371/journal.pcbi.1002927

Kessels, R. P. C., Zandvoort, M. J. E. van, Postma, A., Kappelle, L. J., & Haan, E. H. F. de. (2000). The Corsi Block-Tapping Task: Standardization and Normative Data. *Applied Neuropsychology*, *7*(4), 252–258. https://doi.org/10.1207/S15324826AN0704_8

Kinjo, H., Fooken, J., & Spering, M. (2020). Do eye movements enhance visual memory retrieval? *Vision Research*, *176*, 80–90. https://doi.org/10.1016/j.visres.2020.07.013

Kintsch, W. (1970). Models for free recall and recognition. In D. A. Norman (Ed.), *Models of human memory* (pp. 331–373). Academic Press.

Klauer, K. C., & Zhao, Z. (2004). Double Dissociations in Visual and Spatial Short-Term Memory. *Journal of Experimental Psychology: General*, *133*(3), 355–381. https://doi.org/10.1037/0096-3445.133.3.355

Kleiner, M., Brainard, D. H., & Pelli, D. (2007). *What's new in Psychtoolbox-3?*

Konen, C. S., Mruczek, R. E. B., Montoya, J. L., & Kastner, S. (2013). Functional organization of human posterior parietal cortex: Grasping- and reaching-related activations relative to topographically organized cortex. *Journal of Neurophysiology*, *109*(12), 2897–2908. https://doi.org/10.1152/jn.00657.2012

Konstantinou, N., Constantinidou, F., & Kanai, R. (2017). Discrete capacity limits and neuroanatomical correlates of visual short-term memory for objects and spatial locations. *Human Brain Mapping*, *38*(2), 767–778. https://doi.org/10.1002/hbm.23416

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package:

Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Laeng, B., & Teodorescu, D.-S. (2002). Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cognitive Science*, *26*(2), 207–231. https://doi.org/10.1207/s15516709cog2602_3

Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research*, *41*(25), 3559–3565. https://doi.org/10.1016/S0042-6989(01)00102-X

Land, M. F., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception*, *28*(11), 1311–1328. https://doi.org/10.1068/p2935

Lane, A. R., Smith, D. T., Schenk, T., & Ellison, A. (2012). The involvement of posterior parietal cortex and frontal eye fields in spatially primed visual search. *Brain Stimulation*, *5*(1), 11–17. https://doi.org/10.1016/j.brs.2011.01.005

Lange, E. B., & Engbert, R. (2013). Differentiating between Verbal and Spatial Encoding using Eye-Movement Recordings. *Quarterly Journal of Experimental Psychology*, *66*(9), 1840–1857. https://doi.org/10.1080/17470218.2013.772214

Lara, A. H., & Wallis, J. D. (2012). Capacity and precision in an animal model of visual short-term memory. *Journal of Vision*, *12*(3), 1–12. https://doi.org/10.1167/12.3.13

Lara, A. H., & Wallis, J. D. (2014). Executive control processes underlying multi-item working memory. *Nature Neuroscience*, *17*(6), 876–883. https://doi.org/10.1038/nn.3702

Lawrence, B. M., Myerson, J., & Abrams, R. A. (2004). Interference with spatial working memory: An eye movement is more than a shift of attention. *Psychonomic Bulletin & Review*, *11*(3), 488–494. https://doi.org/10.3758/BF03196600

Lawrence, B. M., Myerson, J., Oonk, H. M., & Abrams, R. A. (2001). The effects of eye and limb movements on working memory. *Memory*, *9*(4-6), 433–444. https://doi.org/10.1080/09658210143000047

Lecerf, T., & de Ribaupierre, A. (2005). Recognition in a visuospatial memory task:

The effect of presentation. *European Journal of Cognitive Psychology*, *17*(1), 47–75. https://doi.org/10.1080/09541440340000420

Lee, C., Rohrer, W. H., & Sparks, D. L. (1988). Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature*, *332*(6162), 357–360. https://doi.org/10.1038/332357a0

Lee, E.-Y., Cowan, N., Vogel, E. K., Rolan, T., Valle-Inclan, F., & Hackley, S. A. (2010). Visual working memory deficits in patients with Parkinson's disease are due to both reduced storage capacity and impaired ability to filter out irrelevant information. *Brain*, *133*(9), 2677–2689. https://doi.org/10.1093/brain/awq197

Lenth, R. V. (2022). *Emmeans: Estimated Marginal Means aka Least-Squares Means.*

Lilienthal, L., Myerson, J., Abrams, R. A., & Hale, S. (2018). Effects of environmental support on overt and covert visuospatial rehearsal. *Memory*, *26*(8), 1042–1052. https://doi.org/10.1080/09658211.2018.1462390

Logan, G. D. (2021). Serial order in perception, memory, and action. *Psychological Review*, *128*(1), 1–44. https://doi.org/10.1037/rev0000253

Logie, R. H., Zucco, G. M., & Baddeley, A. D. (1990). Interference with visual short-term memory. *Acta Psychologica*, *75*(1), 55–74. https://doi.org/10.1016/0001-6918(90)90066-O

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, *17*(8), 391–400. https://doi.org/10.1016/j.tics.2013.06.006

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–281. https://doi.org/10.1038/36846

Luria, R., Balaban, H., Awh, E., & Vogel, E. K. (2016). The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews*, *62*, 100–108. https://doi.org/10.1016/j.neubiorev.2016.01.003

Ma, W. J. (2018). Problematic usage of the Zhang and Luck mixture model. *bioRxiv*. https://doi.org/10.1101/268961

Ma, W. J., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory.

Nature Neuroscience, *17*(3), 347–356. https://doi.org/10.1038/nn.3655

Machizawa, M. G., & Driver, J. (2011). Principal component analysis of behavioural individual differences suggests that particular aspects of visual working memory may relate to specific aspects of attention. *Neuropsychologia*, *49*(6), 1518–1526. https://doi.org/10.1016/j.neuropsychologia.2010.11.032

Machizawa, M. G., Goh, C. C. W., & Driver, J. (2012). Human Visual Short-Term Memory Precision Can Be Varied at Will When the Number of Retained Items Is Low. *Psychological Science*, *23*, 554–559.

Mahmoudi, A., Takerkart, S., Regragui, F., Boussaoud, D., & Brovelli, A. (2012). Multivoxel Pattern Analysis for fMRI Data: A Review. *Computational and Mathematical Methods in Medicine*, *2012*, 961257. https://doi.org/10.1155/2012/961257

Mammarella, I. C., Borella, E., Pastore, M., & Pazzaglia, F. (2013). The structure of visuospatial memory in adulthood. *Learning and Individual Differences*, *25*, 99–110. https://doi.org/10.1016/j.lindif.2013.01.014

Mammarella, I. C., Pazzaglia, F., & Cornoldi, C. (2006). The assessment of imagery and visuo-spatial working memory functions in children and adults. In T. Vecchi & G. Bottini (Eds.), *Imagery and Spatial Cognition: Methods, models and cognitive assessment* (pp. 15–38). John Benjamins Publishing.

Mammarella, I. C., Pazzaglia, F., & Cornoldi, C. (2008). Evidence for different components in children's visuospatial working memory. *British Journal of Developmental Psychology*, *26*(3), 337–355. https://doi.org/10.1348/026151007X236061

Manohar, S. G., Pertzov, Y., & Husain, M. (2017). Short-term memory for spatial, sequential and duration information. *Current Opinion in Behavioral Sciences*, *17*, 20–26. https://doi.org/10.1016/j.cobeha.2017.05.023

Martarelli, C. S., & Mast, F. W. (2013). Eye movements during long-term pictorial recall. *Psychological Research*, *77*(3), 303–309. https://doi.org/10.1007/s00426-012-0439-7

Martín, L., Tapper, A., González, D. A., Leclerc, M., & Niechwiej-Szwedo, E. (2017). The effects of task-relevant saccadic eye movements performed during the encoding of a serial sequence on visuospatial memory performance. *Experimental Brain Research*, *235*, 1519–1529. https://doi.org/10.1007/s00221-017-4915-6

Masson, N., Andres, M., Carneiro Pereira, S., Vandenberghe, A., Pesenti, M., & Vannuscorps, G. (2021). Shifting attention in visuospatial short-term memory does not require oculomotor planning: Insight from congenital gaze paralysis. *Neuropsychologia*, 107998. https://doi.org/10.1016/j.neuropsychologia.2021.107998

Matthey, L., Bays, P. M., & Dayan, P. (2015). A Probabilistic Palimpsest Model of Visual Short-term Memory. *PLOS Computational Biology*, *11*(1), e1004003. https://doi.org/10.1371/journal.pcbi.1004003

McAteer, S. M., McGregor, A., & Smith, D. T. (2023). Oculomotor rehearsal in visuospatial working memory. *Attention, Perception, & Psychophysics*, *85*(1), 261–275. https://doi.org/10.3758/s13414-022-02601-4

McAteer, S. M., McGregor, A., & Smith, D. T. (2021, August). The precision of representations in visuospatial working memory depends on their location in the visual field. *43rd European Conference on Visual Perception*.

McCants, C. W., Katus, T., & Eimer, M. (2019). The capacity and resolution of spatial working memory and its role in the storage of non-spatial features. *Biological Psychology*, *140*, 108–118. https://doi.org/10.1016/j.biopsycho.2018.12.006

McCarthy, G., Puce, A., Constable, T., Krystal, J. H., Gore, J. C., & Goldman-Rakic, P. (1996). Activation of Human Prefrontal Cortex during Spatial and Nonspatial Working Memory Tasks Measured by Functional MRI. *Cerebral Cortex*, *6*(4), 600–611. https://doi.org/10.1093/cercor/6.4.600

Milner, B. (1971). Interhemispheric differences in the localization of psychological processes in man. *British Medical Bulletin*, *27*(3), 272–277.

Monaco, M., Costa, A., Caltagirone, C., & Carlesimo, G. A. (2013). Forward and backward span for verbal and visuo-spatial data: Standardization and normative data from an Italian adult population. *Neurological Sciences*, *34*(5), 749–754. https://doi.org/10.1007/s10072-012-1130-x

Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor Origins of Covert Spatial Attention. *Neuron*, *40*(4), 671–683. https://doi.org/10.1016/S0896-6273(03)00716-5

Morey, C. C. (2018). The case against specialized visual-spatial short-term memory. *Psychological Bulletin*, *144*(8), 849–883. https://doi.org/10.1037/bul0000155

Murdock, B. B. (1968). Serial order effects in short-term memory. *Journal of Experimental Psychology*, *76*(4, Pt.2), 1–15. https://doi.org/10.1037/h0025694

Nee, D. E., Brown, J. W., Askren, M. K., Berman, M. G., Demiralp, E., Krawitz, A., & Jonides, J. (2013). A meta-analysis of executive components of working memory. *Cerebral Cortex (New York, N.Y.: 1991)*, *23*(2), 264–282. https://doi.org/10.1093/cercor/bhs007

Nee, D. E., & D'Esposito, M. (2018). Working Memory. In *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience* (pp. 1–26). American Cancer Society. https://doi.org/10.1002/9781119170174.epcn112

Noton, D., & Stark, L. (1971). Scanpaths in saccadic eye movements while viewing and recognizing patterns. *Vision Research*, *11*(9), 929–IN8. https://doi.org/10.1016/0042-6989(71)90213-6

Nouwens, S., Groen, M. A., & Verhoeven, L. (2017). How working memory relates to children's reading comprehension: The importance of domain-specificity in storage and processing. *Reading and Writing*, *30*(1), 105–120. https://doi.org/10.1007/s11145-016-9665-5

Nystrom, L., Braver, T., Sabb, F., Delgado, M., & Cohen, J. (2000). Working Memory for Letters, Shapes, and Locations: fMRI Evidence against Stimulus-Based Regional Organization in Human Prefrontal Cortex. *NeuroImage*. https://doi.org/10.1006/nimg.2000.0572

Oblak, A., Slana Ozimič, A., Repovš, G., & Kordeš, U. (2022). What Individuals Experience During Visuo-Spatial Working Memory Task Performance: An Exploratory Phenomenological Study. *Frontiers in Psychology*, *13*, 811712. https://doi.org/10.3389/fpsyg.2022.811712

Ohl, S., & Rolfs, M. (2020). Bold moves: Inevitable saccadic selection in visual short-term memory. *Journal of Vision*, *20*(2), 11–11. https://doi.org/10.1167/jov.20.2.11

Ohl, S., & Rolfs, M. (2017). Saccadic Eye Movements Impose a Natural Bottleneck on

Visual Short-Term Memory. *Journal of Experimental Psychology-Learning Memory and Cognition*, *43*(5), 736–748. https://doi.org/10.1037/xlm0000338

Ohl, S., & Rolfs, M. (2018). Saccadic selection of stabilized items in visuospatial working memory. *Consciousness and Cognition*, *64*, 32–44. https://doi.org/10.1016/j.concog.2018.06.016

Olivers, C. N. L., & Roelfsema, P. R. (2020). Attention for action in visual working memory. *Cortex*, *131*, 179–194. https://doi.org/10.1016/j.cortex.2020.07.011

Olsen, R. K., Chiew, M., Buchsbaum, B. R., & Ryan, J. D. (2014). The relationship between delay period eye movements and visuospatial memory. *Journal of Vision*, *14*(1), 8–8. https://doi.org/10.1167/14.1.8

Olson, I. R., & Marshuetz, C. (2005). Remembering "what" brings along "where" in visual working memory. *Perception & Psychophysics*, *67*(2), 185–194. https://doi.org/10.3758/BF03206483

Ostendorf, F., Finke, C., & Ploner, C. J. (2004). Inhibition of visual discrimination during a memory-guided saccade task. *Journal of Neurophysiology*, *92*(1), 660–664. https://doi.org/10.1152/jn.01045.2003

Palmer, J. (1990). Attentional limits on the perception and memory of visual information. *Journal of Experimental Psychology. Human Perception and Performance*, *16*(2), 332–350. https://doi.org/10.1037//0096-1523.16.2.332

Paré, M., & Wurtz, R. H. (1997). Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *Journal of Neurophysiology*, *78*(6), 3493–3497. https://doi.org/10.1152/jn.1997.78.6.3493

Parmentier, F. B. R., & Jones, D. M. (2000). Functional characteristics of auditory temporal—spatial short-term memory: Evidence from serial order errors. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*(1), 222–238. https://doi.org/10.1037/0278-7393.26.1.222

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*(4), 369–378. https://doi.org/10.3758/BF03210419

Patt, V. M., Thomas, M. L., Minassian, A., Geyer, M. A., Brown, G. G., & Perry,

W. (2014). Disentangling working memory processes during spatial span assessment: A modeling analysis of preferred eye movement strategies. *Journal of Clinical and Experimental Neuropsychology*, *36*(2), 186–204. https://doi.org/10.1080/13803395.2013.877123

Pearson, D. G., Ball, K., & Smith, D. T. (2014). Oculomotor preparation as a rehearsal mechanism in spatial working memory. *Cognition*, *132*(3), 416–428. https://doi.org/10.1016/j.cognition.2014.05.006

Pearson, D. G., & Sahraie, A. (2003). Oculomotor Control and the Maintenance of Spatially and Temporally Distributed Events in Visuo-Spatial Working Memory. *The Quarterly Journal of Experimental Psychology Section A*, *56*(7), 1089–1111. https://doi.org/10.1080/02724980343000044

Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid forgetting prevented by retrospective attention cues. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(5), 1224–1231. https://doi.org/10.1037/a0030947

Pertzov, Y., Dong, M. Y., Peich, M.-C., & Husain, M. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, *7*(10), e48214. https://doi.org/10.1371/journal.pone.0048214

Pertzov, Y., & Husain, M. (2014). The privileged role of location in visual working memory. *Attention, Perception, & Psychophysics*, *76*(7), 1914–1924. https://doi.org/10.3758/s13414-013-0541-y

Peterson, M. S., Kelly, S. P., & Blumberg, E. J. (2019). Saccadic eye movements smear spatial working memory. *Journal of Experimental Psychology. Human Perception and Performance*, *45*(2), 255–263. https://doi.org/10.1037/xhp0000596

Pickering, S. J., Gathercole, S. E., Hall, M., & Lloyd, S. A. (2001). Development of memory for pattern and path: Further evidence for the fractionation of visuo-spatial memory. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *54*(2), 397–420. https://doi.org/10.1080/713755973

Pisella, L., Berberovic, N., & Mattingley, J. B. (2004). Impaired Working Memory for Location but not for Colour or Shape in Visual Neglect: A Comparison of Parietal and Non-Parietal Lesions. *Cortex*, *40*(2), 379–390. https://doi.org/10.1016/S0010-9452(08)70132-1

Poirier, M., Yearsley, J. M., Saint-Aubin, J., Fortin, C., Gallant, G., & Guitard, D. (2019). Dissociating visuo-spatial and verbal working memory: It's all in the features. *Memory & Cognition*, *47*(4), 603–618. https://doi.org/10.3758/s13421-018-0882-9

Postle, B. R. (2006). Working Memory as an Emergent Property of the Mind and Brain. *Neuroscience*, *139*(1), 23–38. https://doi.org/10.1016/j.neuroscience.2005.06.005

Postle, B. R., Idzikowski, C., Sala, S. D., Logie, R. H., & Baddeley, A. D. (2006). The selective disruption of spatial working memory by eye movements. *Quarterly Journal of Experimental Psychology*, *59*(1), 100–120. https://doi.org/10.1080/17470210500151410

Postma, A., & De Haan, E. H. (1996). What was where? Memory for object locations. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, *49*(1), 178–199. https://doi.org/10.1080/713755605

Pratte, M. S., Park, Y. E., Rademaker, R. L., & Tong, F. (2017). Accounting for stimulus-specific variation in precision reveals a discrete capacity limit in visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*, *43*(1), 6–17. https://doi.org/10.1037/xhp0000302

Pratte, M. S., & Tong, F. (2014). Spatial specificity of working memory representations in the early visual cortex. *Journal of Vision*, *14*(3), 22–22. https://doi.org/10.1167/14.3.22

R Core Team. (2019). *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing.

Ramaty, A., & Luria, R. (2018). Visual Working Memory Cannot Trade Quantity for Quality. *Frontiers in Psychology*, *9*. https://doi.org/10.3389/fpsyg.2018.00719

Ren, Z., Zhang, Y., He, H., Feng, Q., Bi, T., & Qiu, J. (2019). The Different Brain Mechanisms of Object and Spatial Working Memory: Voxel-Based Morphometry and Resting-State Functional Connectivity. *Frontiers in Human Neuroscience*, *13*. https://doi.org/10.3389/fnhum.2019.00248

Ress, D., & Heeger, D. J. (2003). Neuronal correlates of perception in early visual cortex. *Nature Neuroscience*, *6*(4), 414–420. https://doi.org/10.1038/nn1024

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1), 31–40. https://doi.org/10.1016/0028-3932(87)90041-8

Robison, M. K., Miller, A. L., & Unsworth, N. (2018). Individual differences in working memory capacity and filtering. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(7), 1038–1053. https://doi.org/10.1037/xhp0000513

Rosen, V. M., & Engle, R. W. (1997). Forward and backward serial recall. *Intelligence*, *25*(1), 37–47. https://doi.org/10.1016/S0160-2896(97)90006-4

Rösner, M., Sabo, M., Klatt, L.-I., Wascher, E., & Schneider, D. (2022). Preparing for the unknown: How working memory provides a link between perception and anticipated action. *NeuroImage*, *260*, 119466. https://doi.org/10.1016/j.neuroimage.2022.119466

Rothmayr, C., Baumann, O., Endestad, T., Rutschmann, R. M., Magnussen, S., & Greenlee, M. W. (2007). Dissociation of neural correlates of verbal and non-verbal visual working memory with different delays. *Behavioral and Brain Functions : BBF*, *3*, 56. https://doi.org/10.1186/1744-9081-3-56

Rouder, J. N., Morey, R. D., Morey, C. C., & Cowan, N. (2011). How to measure working memory capacity in the change detection paradigm. *Psychonomic Bulletin & Review*, *18*(2), 324–330. https://doi.org/10.3758/s13423-011-0055-3

Rovamo, J., & Virsu, V. (1979). An estimation and application of the human cortical magnification factor. *Experimental Brain Research*, *37*(3), 495–510. https://doi.org/10.1007/bf00236819

Rudkin, S. J., Pearson, D. G., & Logie, R. H. (2007). Executive processes in visual and spatial working memory tasks. *Quarterly Journal of Experimental Psychology*, *60*(1), 79–100. https://doi.org/10.1080/17470210600587976

Saint-Aubin, J., & Poirier, M. (2000). Immediate serial recall of words and nonwords: Tests of the retrieval-based hypothesis. *Psychonomic Bulletin & Review*, *7*(2), 332–340. https://doi.org/10.3758/BF03212990

Saint-Aubin, J., Tremblay, S., & Jalbert, A. (2007). Eye Movements and Serial Memory for Visual-Spatial Information. *Experimental Psychology*, *54*(4), 264–272. https://doi.org/10.1027/1618-3169.54.4.264

Sala, J., Rämä, P., & Courtney, S. M. (2003). Functional topography of a distributed neural system for spatial and nonspatial information maintenance in working memory. *Neuropsychologia*. https://doi.org/10.1016/S0028-3932(02)00166-5

Salahub, C., Lockhart, H. A., Dube, B., Al-Aidroos, N., & Emrich, S. M. (2019). Electrophysiological correlates of the flexible allocation of visual working memory resources. *Scientific Reports*, *9*(1), 19428. https://doi.org/10.1038/s41598-019-55948-4

Salway, A. F. S., & Logie, R. H. (1995). Visuospatial working memory, movement control and executive demands. *British Journal of Psychology*, *86*(2), 253–269. https://doi.org/10.1111/j.2044-8295.1995.tb02560.x

Sanada, M., Ikeda, K., & Hasegawa, T. (2015). Shape and spatial working memory capacities are mostly independent. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.00581

Schneegans, S., & Bays, P. M. (2017). Neural Architecture for Feature Binding in Visual Working Memory. *The Journal of Neuroscience*, *37*(14), 3913–3925. https://doi.org/10.1523/JNEUROSCI.3493-16.2017

Schneegans, S., & Bays, P. M. (2016). No fixed item limit in visuospatial working memory. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *83*, 181–193. https://doi.org/10.1016/j.cortex.2016.07.021

Schneegans, S., & Bays, P. M. (2019). New perspectives on binding in visual working memory. *British Journal of Psychology*, *110*(2), 207–244. https://doi.org/10.1111/bjop.12345

Schneegans, S., Taylor, R., & Bays, P. M. (2020). Stochastic sampling provides a unifying account of visual working memory limits. *Proceedings of the National Academy of Sciences*, *117*(34), 20959–20968. https://doi.org/10.1073/pnas.2004306117

Schneider, D., Barth, A., Haase, H., Hickey, C., & Wascher, E. (2018). Distractor inhibition contributes to retroactive attentional orienting within working memory: Evidence by lateralized alpha oscillations in the EEG. *bioRxiv*, 235069. https://doi.org/10.1101/235069

Scholz, A., Klichowicz, A., & Krems, J. F. (2018). Covert shifts of attention can account for the functional role of "eye movements to nothing." *Memory & Cognition*, *46*(2), 230–243. https://doi.org/10.3758/s13421-017-0760-x

Schut, M. J., Stoep, N. V. der, Postma, A., & Van der Stigchel, S. (2017). The cost of making an eye movement: A direct link between visual working memory and saccade execution. *Journal of Vision*, *17*(6), 15–15. https://doi.org/10.1167/17.6.15

Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, *128*, 53–67. https://doi.org/10.1016/j.visres.2016.09.010

Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-Specific Delay Activity in Human Primary Visual Cortex. *Psychological Science*, *20*(2), 207–214. https://doi.org/10.1111/j.1467-9280.2009.02276.x

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of Contralateral Space in Retinotopic Coordinates by a Parietal Cortical Area in Humans. *Science*, *294*(5545), 1350–1354. https://doi.org/10.1126/science.1063695

Shafer-Skelton, A., & Golomb, J. D. (2018). Memory for retinotopic locations is more accurate than memory for spatiotopic locations, even for visually guided reaching. *Psychonomic Bulletin & Review*, *25*(4), 1388–1398. https://doi.org/10.3758/s13423-017-1401-x

Shah, P., & Miyake, A. (1996). The separability of working memory resources for spatial thinking and language processing: An individual differences approach. *Journal of Experimental Psychology: General*, *125*(1), 4–27. https://doi.org/10.1037/0096-3445.125.1.4

Shao, N., Li, J., Shui, R., Zheng, X., Lu, J., & Shen, M. (2010). Saccades elicit obligatory allocation of visual working memory. *Memory & Cognition*, *38*(5), 629–640. https://doi.org/10.3758/MC.38.5.629

Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *The Quarterly Journal of Experimental Psychology*

Section A, *38*(3), 475–491. https://doi.org/10.1080/14640748608401609

Silver, M. A., Ress, D., & Heeger, D. J. (2005). Topographic Maps of Visual Spatial Attention in Human Parietal Cortex. *Journal of Neurophysiology*, *94*(2), 1358–1371. https://doi.org/10.1152/jn.01316.2004

Slana Ozimič, A., Oblak, A., Kordeš, U., Purg, N., Bon, J., & Repovš, G. (2023). The Diversity of Strategies Used in Working Memory for Colors, Orientations, and Positions: A Quantitative Approach to a First-Person Inquiry. *Cognitive Science*, *47*(8), e13333. https://doi.org/10.1111/cogs.13333

Smith, D. T. (2022). A horizontal–vertical anisotropy in spatial short-term memory. *Visual Cognition*, *30*(4), 245–253. https://doi.org/10.1080/13506285.2022.2042446

Smith, D. T., & Archibald, N. (2020). Spatial working memory in Progressive Supranuclear Palsy. *Cortex*, *122*, 115–122. https://doi.org/10.1016/j.cortex.2018.07.004

Smith, D. T., Ball, K., & Ellison, A. (2014). Covert visual search within and beyond the effective oculomotor range. *Vision Research*, *95*, 11–17. https://doi.org/10.1016/j.visres.2013.12.003

Smith, D. T., Ball, K., Ellison, A., & Schenk, T. (2010). Deficits of reflexive attention induced by abduction of the eye. *Neuropsychologia*, *48*(5), 1269–1276. https://doi.org/10.1016/j.neuropsychologia.2009.12.028

Smith, D. T., Casteau, S., & Archibald, N. (2021). Spatial attention and spatial short term memory in PSP and Parkinson's disease. *Cortex*, *137*, 49–60. https://doi.org/10.1016/j.cortex.2020.12.019

Smith, D. T., Jackson, S. R., & Rorden, C. (2009). Repetitive transcranial magnetic stimulation over frontal eye fields disrupts visually cued auditory attention. *Brain Stimulation.*, *2*(2), 81–87. https://doi.org/10.1016/j.brs.2008.07.005

Smith, D. T., Jackson, S. R., & Rorden, C. (2005). Transcranial magnetic stimulation of the left human frontal eye fields eliminates the cost of invalid endogenous cues. *Neuropsychologia*, *43*(9), 1288–1296. https://doi.org/10.1016/j.neuropsychologia.2004.12.003

Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia*, *50*(6), 1104–1114. https://doi.org/10.1016/j.neuropsychologia.2012.01.025

Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology. Human Perception and Performance*, *38*(6), 1438–1447. https://doi.org/10.1037/a0027794

Smith, E. E., & Jonides, J. (1997). Working Memory: A View from Neuroimaging. *Cognitive Psychology*, *33*(1), 5–42. https://doi.org/10.1006/cogp.1997.0658

Smith, E. E., & Jonides, J. (1998). Neuroimaging analyses of human working memory. *Proceedings of the National Academy of Sciences*, *95*(20), 12061–12068. https://doi.org/10.1073/pnas.95.20.12061

Smith, E. E., Jonides, J., Koeppe, R. A., Awh, E., Schumacher, E. H., & Minoshima, S. (1995). Spatial versus object working memory: PET investigations. *Journal of Cognitive Neuroscience*, *7*(3), 337–356.

Smith, P. L., Corbett, E. A., Lilburn, S. D., & Kyllingsbæk, S. (2018). The power law of visual working memory characterizes attention engagement. *Psychological Review*, *125*(3), 435–451. https://doi.org/10.1037/rev0000098

Smyth, M. M. (1996). Interference with Rehearsal in Spatial Working Memory in the Absence of Eye Movements. *The Quarterly Journal of Experimental Psychology Section A*, *49*(4), 940–949. https://doi.org/10.1080/713755669

Smyth, M. M., Pearson, N. A., & Pendleton, L. R. (1988). Movement and Working Memory: Patterns and Positions in Space. *The Quarterly Journal of Experimental Psychology Section A*, *40*(3), 497–514. https://doi.org/10.1080/02724988843000041

Smyth, M. M., & Scholey, K. A. (1994). Interference in immediate spatial memory. *Memory & Cognition*, *22*(1), 1–13. https://doi.org/10.3758/BF03202756

Smyth, M. M., & Scholey, K. A. (1996). Serial Order in Spatial Immediate Memory. *Quarterly Journal of Experimental Psychology Section A*, *49*(1), 159–177.

Sommer, M. A., & Wurtz, R. H. (2001). Frontal eye field sends delay activity related to movement, memory, and vision to the superior colliculus. *Journal of Neurophysiology*, *85*(4), 1673–1685. https://doi.org/10.1152/jn.2001.85.4.1673

Souza, A. S., Czoschke, S., & Lange, E. B. (2020). Gaze-based and attention-based rehearsal in spatial working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(5), 980–1003. https://doi.org/10.1037/xlm0000771

Souza, A. S., Rerko, L., & Oberauer, K. (2016). Getting more from visual working memory: Retro-cues enhance retrieval and protect from visual interference. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(6), 890–910. https://doi.org/10.1037/xhp0000192

Sparks, D. L., Holland, R., & Guthrie, B. L. (1976). Size and distribution of movement fields in the monkey superior colliculus. *Brain Research*, *113*(1), 21–34. https://doi.org/10.1016/0006-8993(76)90003-2

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*, 1–29. https://doi.org/10.1037/h0093759

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research*, *65*(4), 235–241. https://doi.org/10.1007/s004260100059

Sprague, T. C., Ester, E. F., & Serences, J. T. (2016). Restoring Latent Visual Working Memory Representations in Human Cortex. *Neuron*, *91*(3), 694–707. https://doi.org/10.1016/j.neuron.2016.07.006

Sprague, T. C., Ester, E. F., & Serences, J. T. (2014). Reconstructions of Information in Visual Spatial Working Memory Degrade with Memory Load. *Current Biology*, *24*(18), 2174–2180. https://doi.org/10.1016/j.cub.2014.07.066

Standage, D., & Paré, M. (2018). Slot-like capacity and resource-like coding in a neural model of multiple-item working memory. *Journal of Neurophysiology*, *120*(4), 1945–1961. https://doi.org/10.1152/jn.00778.2017

Staugaard, C. F., Petersen, A., & Vangkilde, S. (2016). Eccentricity effects in vision and attention. *Neuropsychologia*, *92*, 69–78. https://doi.org/10.1016/j.neuropsychologia.2016.06.020

Suchow, J. W., Brady, T. F., Fougnie, D., & Alvarez, G. A. (2013). Modeling visual working memory with the MemToolbox. *Journal of Vision*, *13*(10). https://doi.org/10.1167/13.10.9

Swanson, H. L., & Beebe-Frankenberger, M. (2004). The Relationship Between Working Memory and Mathematical Problem Solving in Children at Risk and Not at Risk for Serious Math Difficulties. *Journal of Educational Psychology*, *96*(3), 471–491. https://doi.org/10.1037/0022-0663.96.3.471

Tamber-Rosenau, B. J., Fintzi, A. R., & Marois, R. (2015). Crowding in Visual Working Memory Reveals Its Spatial Resolution and the Nature of Its Representations. *Psychological Science*, *26*(9), 1511–1521. https://doi.org/10.1177/0956797615592394

Tas, A. C., Luck, S. J., & Hollingworth, A. (2016). The Relationship between Visual Attention and Visual Working Memory Encoding: A Dissociation between Covert and Overt Orienting. *Journal of Experimental Psychology. Human Perception and Performance*, *42*(8), 1121–1138. https://doi.org/10.1037/xhp0000212

Taylor, R., Thomson, H., Sutton, D., & Donkin, C. (2017). Does working memory have a single capacity limit? *Journal of Memory and Language*, *93*, 67–81. https://doi.org/10.1016/j.jml.2016.09.004

Taylor, T. L., & Klein, R. M. (2000). Visual and motor effects in inhibition of return. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(5), 1639–1656. https://doi.org/10.1037/0096-1523.26.5.1639

Theeuwes, J., Olivers, C. N. L., & Chizk, C. L. (2005). Remembering a Location Makes the Eyes Curve Away. *Psychological Science*, *16*(3), 196–199. https://doi.org/10.1111/j.0956-7976.2005.00803.x

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*(6984), 751–754. https://doi.org/10.1038/nature02466

Todd, J. J., & Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective & Behavioral Neuroscience*, *5*(2), 144–155.

Tremblay, S., Parmentier, F. B. R., Guérard, K., Nicholls, A. P., & Jones, D. M. (2006).

A spatial modality effect in serial memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*(5), 1208–1215. https://doi.org/10.1037/0278-7393.32.5.1208

Tremblay, S., Saint-Aubin, J., & Jalbert, A. (2006). Rehearsal in serial memory for visual-spatial information: Evidence from eye movements. *Psychonomic Bulletin & Review*, *13*(3), 452–457. https://doi.org/10.3758/BF03193869

Tresch, M. C., Sinnamon, H. M., & Seamon, J. G. (1993). Double dissociation of spatial and object visual memory: Evidence from selective interference in intact human subjects. *Neuropsychologia*, *31*(3), 211–219. https://doi.org/10.1016/0028-3932(93)90085-e

Tulving, E., & Watkins, M. J. (1973). Continuity between Recall and Recognition. *The American Journal of Psychology*, *86*(4), 739–748. https://doi.org/10.2307/1422081

Udale, R., Tran, M. T., Manohar, S., & Husain, M. (2022). Dynamic in-flight shifts of working memory resources across saccades. *Journal of Experimental Psychology. Human Perception and Performance*, *48*(1), 21–36. https://doi.org/10.1037/xhp0000960

Unsworth, N., Fukuda, K., Awh, E., & Vogel, E. K. (2014). Working Memory and Fluid Intelligence: Capacity, Attention Control, and Secondary Memory Retrieval. *Cognitive Psychology*, *71*, 1–26. https://doi.org/10.1016/j.cogpsych.2014.01.003

Vallar, G., & Baddeley, A. D. (1984). Phonological short-term store, phonological processing and sentence comprehension: A neuropsychological case study. *Cognitive Neuropsychology*, *1*(2), 121–141. https://doi.org/10.1080/02643298408252018

van den Berg, R., & Ma, W. J. (2018). A resource-rational theory of set size effects in human visual working memory. *eLife*, *7*, e34963. https://doi.org/10.7554/eLife.34963

van den Berg, R., Shin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *Proceedings of the National Academy of Sciences*, *109*(22), 8780–8785. https://doi.org/10.1073/pnas.1117465109

Van der Stigchel, S., & Hollingworth, A. (2018). Visuospatial Working Memory as a Fundamental Component of the Eye Movement System. *Current Directions in Psy-*

chological Science, *27*(2), 136–143. https://doi.org/10.1177/0963721417741710

van Ede, F., Chekroud, S. R., & Nobre, A. C. (2019). Human gaze tracks attentional focusing in memorized visual space. *Nature Human Behaviour*, *3*(5), 462–470. https://doi.org/10.1038/s41562-019-0549-y

Vandierendonck, A., Kemps, E., Fastame, M. C., & Szmalec, A. (2004). Working memory components of the Corsi blocks task. *British Journal of Psychology*, *95*(1), 57–79. https://doi.org/10.1348/000712604322779460

Vergauwe, E., Barrouillet, P., & Camos, V. (2009). Visual and spatial working memory are not that dissociated after all: A time-based resource-sharing account. *Journal of Experimental Psychology. Learning, Memory, and Cognition*. https://doi.org/10.1037/a0015859

Villena-González, M., Rubio-Venegas, I., & López, V. (2020). Data from brain activity during visual working memory replicates the correlation between contralateral delay activity and memory capacity. *Data in Brief*, *28*, 105042. https://doi.org/10.1016/j.dib.2019.105042

Virsu, V., Näsänen, R., & Osmoviita, K. (1987). Cortical magnification and peripheral vision. *JOSA A*, *4*(8), 1568–1578. https://doi.org/10.1364/JOSAA.4.001568

Virsu, V., & Rovamo, J. (1979). Visual resolution, contrast sensitivity, and the cortical magnification factor. *Experimental Brain Research*, *37*(3), 475–494. https://doi.org/10.1007/bf00236818

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*(6984), 748–751. https://doi.org/10.1038/nature02447

Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(1), 92–114. https://doi.org/10.1037/0096-1523.27.1.92

Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual Field Maps in Human Cortex. *Neuron*, *56*(2), 366–383. https://doi.org/10.1016/j.neuron.2007.10.012

Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology. General*, *131*(1), 48–64. https://doi.org/10.1037//0096-3445.131.1.48

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, *4*(12), 11. https://doi.org/10.1167/4.12.11

Williams, M., Pouget, P., Boucher, L., & Woodman, G. F. (2013). Visual-spatial attention aids the maintenance of object representations in visual working memory. *Memory & Cognition*, *41*(5), 698–715. https://doi.org/10.3758/s13421-013-0296-7

Wolfe, B. A., & Whitney, D. (2015). Saccadic remapping of object-selective information. *Attention, Perception & Psychophysics*, *77*(7), 2260–2269. https://doi.org/10.3758/s13414-015-0944-z

Wolfe, J. M., O'Neill, P., & Bennett, S. C. (1998). Why are there eccentricity effects in visual search? Visual and attentional hypotheses. *Perception & Psychophysics*, *60*(1), 140–156. https://doi.org/10.3758/BF03211924

Wynn, J. S., Olsen, R. K., Binns, M. A., Buchsbaum, B. R., & Ryan, J. D. (2018). Fixation reinstatement supports visuospatial memory in older adults. *Journal of Experimental Psychology. Human Perception and Performance*, *44*(7), 1119–1127. https://doi.org/10.1037/xhp0000522

Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*(7080), 91–95. https://doi.org/10.1038/nature04262

Xu, Z., Adam, K. C. S., Fang, X., & Vogel, E. K. (2018). The reliability and stability of visual working memory capacity. *Behavior Research Methods*, *50*(2), 576–588. https://doi.org/10.3758/s13428-017-0886-6

Yörük, H., Santacroce, L. A., & Tamber-Rosenau, B. J. (2020). Reevaluating the sensory recruitment model by manipulating crowding in visual working memory representations. *Psychonomic Bulletin & Review*, *27*(6), 1383–1396. https://doi.org/10.3758/s13423-020-01757-0

Zelinsky, G. J., & Bisley, J. W. (2015). The what, where, and why of priority maps and their interactions with visual working memory. *Annals of the New York Academy of Sciences*, *1339*(1), 154–164. https://doi.org/10.1111/nyas.12606

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*(7192), 233–235. https://doi.org/10.1038/nature06860

Zhang, W., & Luck, S. J. (2011). The Number and Quality of Representations in Working Memory. *Psychological Science*, *22*(11), 1434–1441. https://doi.org/10.1177/0956797611417006

Zhao, M., Gersch, T. M., Schnitzer, B. S., Dosher, B. A., & Kowler, E. (2012). Eye movements and attention: The role of pre-saccadic shifts of attention in perception, memory and the control of saccades. *Vision Research*, *74*, 40–60. https://doi.org/10.1016/j.visres.2012.06.017

Zhou, Y., Curtis, C. E., Sreenivasan, K. K., & Fougnie, D. (2022). Common Neural Mechanisms Control Attention and Working Memory. *Journal of Neuroscience*, *42*(37), 7110–7120. https://doi.org/10.1523/JNEUROSCI.0443-22.2022

Zimmermann, E., Burr, D., & Morrone, M. C. (2011). Spatiotopic visual maps revealed by saccadic adaptation in humans. *Current Biology: CB*, *21*(16), 1380–1384. https://doi.org/10.1016/j.cub.2011.06.014

Zokaei, N., Burnett Heyes, S., Gorgoraptis, N., Budhdeo, S., & Husain, M. (2015). Working memory recall precision is a more sensitive index than span. *Journal of Neuropsychology*, *9*(2), 319–329. https://doi.org/10.1111/jnp.12052

Zokaei, N., Gorgoraptis, N., Bahrami, B., Bays, P. M., & Husain, M. (2011). Precision of working memory for visual motion sequences and transparent motion surfaces. *Journal of Vision*, *11*(14), 2–2. https://doi.org/10.1167/11.14.2

Zokaei, N., & Husain, M. (2019). Working Memory in Alzheimer's Disease and Parkinson's Disease. In T. Hodgson (Ed.), *Processes of Visuospatial Attention and Working Memory* (Vol. 41, pp. 325–344). Springer International Publishing. https://doi.org/10.1007/7854_2019_103

Zokaei, N., McNeill, A., Proukakis, C., Beavan, M., Jarman, P., Korlipara, P., Hughes, D., Mehta, A., Hu, M. T. M., Schapira, A. H. V., & Husain, M. (2014). Visual short-term memory deficits associated with GBA mutation and Parkinson’s disease. *Brain*, *137*(8), 2303–2311. https://doi.org/10.1093/brain/awu143

Zokaei, N., Ning, S., Manohar, S., Feredoes, E., & Husain, M. (2014). Flexibility of representational states in working memory. *Frontiers in Human Neuroscience*, *8*. https://doi.org/10.3389/fnhum.2014.00853