

Influence of spatiotemporal stimulus structure on memory-guided saccade sequences

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ABSTRACT

Saccades - rapid eye movements that place targets of interest on the fovea - are used as a tool to measure cognitive processes such as visual working memory. The goal of this study was to identify the influence of spatiotemporal structure, set size, and order of presentation on performance in memory-guided saccade sequences. Fourteen participants were presented with visual stimuli that differed in spatiotemporal structure (Sequential, Spatial, or Random) and set size (3-6) which they had to reproduce with sequential saccades. Results were analyzed with respect to % correct target recall, absolute error, and relative error. There was a significant influence of structure on errors (random>spatial > sequential), set size on correct recall and errors, primacy on correct recall, and interaction effects. These results indicate that spatiotemporal structure is beneficial for memory 'chunking' in saccade sequence planning, however, this has complex interactions with set size, order, and the way saccade errors are measured.

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CHAPTER I: GENERAL INTRODUCTION

Working memory is a cognitive system used for the temporary storage and manipulation of information for use in an ongoing task (Baddeley, 1992; Baddeley & Hitch, 1974; Luck & Vogel, 2013). Working memory is used for many important processes such as learning, problem-solving, decision making and comprehension (Baddeley, 1992; Murray, Jaramillo, & Wang, 2017; Vogel, McCollough, & Machizawa, 2005). Vision also involves a working memory component referred to as visual working memory (VWM) (Luck & Vogel, 2013). Perception of a visual scene involves rapid eye movements called saccades which change the eyes' point of fixation. During a saccade there is little to no perception of visual information, thus, in order to have a continuous representation of visual information, there must be a role for memory to bridge the spatial and temporal changes (Irwin, 1992; Luck & Vogel, 2013; Prime, Tsotsos, Keith, & Crawford, 2007). VWM has been shown to have a role in bridging these spatiotemporal gaps (Atsma, Maij, Koppen, Irwin, & Medendorp, 2016; Irwin, 1992). Given the fact that we are constantly receiving an abundance of visual information, the brain must also make use of strategies to help increase VWM capacity in order to process as much information as possible – these strategies are often broadly referred to as chunking (Atkinson, Baddeley, & Allen, 2017; Bor, Duncan, Wiseman, & Owen, 2003; Mathy & Feldman, 2012; Schmidt et al., 2007). Previous studies have shown that people can use the spatiotemporal structure of a sequence of visual stimuli to increase VWM capacity (Bor et al., 2003; De Lillo, Kirby, & Poole, 2016). Given the complex nature of visual stimuli, in this project, we aim to study not only how spatiotemporal structure influences VWM but also how it interacts with other features such as set size and presentation order.

Vision and Saccades

One of our most widely used senses is the sense of vision. Vision is the ability to detect electromagnetic energy. In order to visually perceive the world, humans use several types of eye movements such as saccades, smooth pursuit and vergence in order to construct an image of a scene (Leigh & Zee, 2015). Of these movements, saccades are rapid eye movements that change the eyes' point of fixation. Saccades move the eyes so that the point of interest will be centred on the fovea, the centre of highest visual acuity in the human eye. As mentioned previously, during the actual movement of the eyes in a saccade, there is little to no perception of visual information. In fact, if a target were to move during the saccade, it would be missed and a corrective saccade would need to be made in order to fixate the target again, this is why saccades are often characterized as ballistic. The time it takes to initiate a saccade toward a visual target – the saccade latency – is approximately 200 milliseconds (Carpenter 1988). This rapid latency time and the ballistic nature of saccades allow them to be an important research tool to characterize higher-order cognitive processes such as attention and memory.

Saccades have been widely used in neuroscience as a way to measure cognitive processes because they are relatively simple to measure in laboratory settings, their dynamic properties have been well-defined and their neural substrates have been extensively studied (Leigh & Kennard, 2004). Saccades can be measured using eye-tracking equipment such as the EyeLink II (SR Research), used in this study. The fixation point of the eyes can be delineated using properties of saccades such as their peak velocity, amplitude, and acceleration. To determine whether a person intentionally moved their eyes toward a target a common criteria used is that the saccade preceding the fixation must reach a peak velocity of at least $30^{\circ}/\text{sec}$ and/or an acceleration of at least $8000^{\circ}/\text{sec}^2$ and a fixation must last at least 100 milliseconds (Hodgson, Winand, Henderson, & Kennard, 1999; Nuthmann, Vitu, Engbert, & Kliegl, 2016; Wu, Chua, & Yen, 2016). These are

important in research because the oculomotor system has properties that allow saccades to reflect underlying neurological mechanisms (Abrams, Meyer, & Kornblum, 1989; Robinson, 1981). For example, Hodgson et al., (1999) studied eye movement behaviour in Parkinson's disease patients. Their study found that these subjects made several low-amplitude saccades before reaching the final target position. Such behaviour is uncharacteristic of healthy humans and thus the researchers were able to make conclusions about the symptoms of Parkinson's disease based on eye movement properties.

Memory-Guided Saccades

Memory-guided saccades are saccades that are made in response to a remembered target. In order to make a movement toward a previously presented target, the brain must memorize information about that target for a short period of time. Involving a short – term memory aspect in generating saccades makes memory-guided saccade tasks an excellent tool for researching human memory capabilities. Memory in the human brain occurs in several different forms. Long-term memory refers to the ability to remember information for long periods of time; days, weeks or a lifetime (Brady, Konkle, Alvarez, & Oliva, 2008). Short-term memory refers to our ability to retain information for a few seconds to minutes. Working memory is a form of short-term memory where the information is maintained for a short period of time in order to complete an ongoing task. When saccades take place, there is a temporary suppression of visual processing. This should disrupt our perception however, visual working memory (VWM) bridges the gaps in time and space (Luck & Vogel, 2013)

There are several brain regions that are involved in the process of generating memory-guided saccade sequences. The preparation and triggering of any intentional saccades are attributed to the frontal eye field (FEF) in the frontal lobe of the brain, this includes memory-guided saccades which are produced in response to a target that is no longer present (Bullard, Griss, Greene, &

Gekker, 2012; Charles Pierrot-Deseilligny, Milea, & Müri, 2004). The supplementary eye field (SEF) and dorsolateral prefrontal cortex (dlPFC) have also been indicated in memory-guided sequential saccades (R. M. Müri, Rösler, & Hess, 1994; Reuter, Elsner, Möllers, & Kathmann, 2016). The SEF seems to be involved in the planning and control of sequential movements of saccades whereas the dlPFC is more involved in keeping the spatial locations of targets in working memory. The lateral intraparietal area (LIP) has also been shown to have involvement in the generation of visual attention, providing a salience map that can be used to direct memory-guided saccades (Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002; Goldberg, Bisley, Powell, & Gottlieb, 2006)

Visual Working Memory (VWM)

There are two main theories of visual working memory that are currently used in literature. One is the discrete or slot-based model and the other is the continuous resource model (Barton, Ester, & Awh, 2009; Paul M. Bays & Husain, 2008; Huang, 2010; Luck & Vogel, 2013). The discrete model describes VWM as a finite number of slots and when these slots are filled there is no information stored about any additional items. According to the discrete model, working memory has a limited capacity and several studies have suggested that this capacity is approximately 3-4 items (Adam, Vogel, & Awh, 2017; Anderson & MacAskill, 2013; Awh, Barton, & Vogel, 2014; Paul M. Bays, 2018a; Huang & Awh, 2018; Mathy & Feldman, 2012). Continuous resources models describe VWM as a pool that can be flexibly divided, however, with an increasing number of items to remember, fewer resources are allocated and therefore precision will decrease (Paul M. Bays, 2018a). There is evidence in the literature supporting both theories of VWM.

Zhang & Luck, 2008 conducted an experiment where human participants had to remember the colour of a previously presented probe by clicking its colour on a colour wheel. If participants had kept this information in working memory, the colour they select should resemble the colour of the original probe. If this information is not stored, the participants should be choosing random colours resulting in a uniform error. Their study found that participants were able to store precise information for a small number of items, which is in line with the discrete model. A study conducted by Huang (2010) however, showed evidence in support of the resource-based model. Participants were asked to memorize six out of eight possible colours presented on a screen and the number of correct responses was counted. According to the discrete model, the number of correct responses should be mostly consistent, due to a maximum capacity. According to the resource model, the memory should be shared amongst all six colours, resulting in imprecise responses but not completely random guessing. The results of the study showed that participants did not have a consistent number of correct responses, thus better fitting the continuous resource model.

Neurophysiology of Visual Working Memory

There are several techniques used in the field to measure visual working memory, each with their respective strengths and weaknesses. To comprehend the neural functions underlying visual working memory, neurophysiological approaches have an advantage in that they can record direct neuronal activity, as opposed to purely behavioural studies where inferences then must be made about the neuronal activity. Neurophysiological techniques can be used to study the connectivity, excitability, and plasticity of the brain. This can in turn aid with understanding how the brain functions in healthy, aging and diseased states. Several neurophysiological techniques including electrophysiological recordings, functional magnetic resonance imaging (fMRI),

electroencephalography (EEG) and transcranial magnetic stimulation (TMS) have been used to help better understand brain activity linked to VWM.

The emergence of new and improved neurophysiological techniques has made it possible to discover brain activity patterns that can be correlated with VWM. Electrophysiology studies, being one of the most robust approaches to neurophysiology have shown that when an item has to be maintained in VWM, there is a sustained increase in neural firing that is referred to as the delay activity (Joaquin M. Fuster & Alexander, 1971). Fuster and Alexander used electrophysiology to explore the electrical activity in neurons of the prefrontal cortex and the nucleus medialis dorsalis during a delayed response task. These areas had been understood to be involved in short-term memory but how they were involved was still not known at the time. The authors hypothesized that if these regions were involved in a transient memory process, then the spike discharge of these neurons should vary during the delayed response trials. The experiment was conducted using a single-unit recording setup for action potentials with five adult rhesus monkeys. A metal microelectrode was used to record the action potential activity extracellularly from the two aforementioned regions. The animals were sitting in front of a transparent plastic window with a view of a compartment containing the test objects. Two identical white wooden blocks are in front of each hand. A piece of apple is placed on one of two sides in full view of the animal for a brief amount of time, then hidden. After a period of delay, the blocks are revealed again, however, the apple is in a hidden compartment, If the animal reaches to the correct block where the apple previously was, they will retrieve the reward. Their results showed that there was increased spike activity during the delay period in both regions compared to other periods. Thus, they were able to discover an increase in neuronal activity associated with the information being held in temporary memory storage for prospective utilization – working memory.

Subsequent electrophysiology studies have shown that there are three major brain regions that seem to have neurons that show delay activity (Mccollough, Machizawa, & Vogel, 2007). These three regions are the prefrontal cortex (J M Fuster, 1973; Miller, Erickson, & Desimone, 1996), posterior parietal cortex (Gnadt & Andersen, 1988; Pesaran, Pezaris, Sahani, Mitra, & Andersen, 2002) and inferior temporal cortex (J M Fuster & Jervey, 1982). In 1973, Fuster conducted an experiment to better understand the role of prefrontal cortex in working memory. The author attributed three processes in short-term memory to the three periods in a delayed-response task, where the cue, delay and response period correspond to acquisition, retention and corollary use of information, respectively. The goal of the experiment was to see if prefrontal cortex neurons exhibit changes in activity that temporally correlate with the three periods. They were particularly interested in determining whether the neuron activity differed between the delay period and the intertrial period because the animal's environment would be the same in both conditions. Six adult male monkeys were used in the study. The task is identical to a previous experiment (Joaquin M. Fuster & Alexander, 1971) where the animal had to maintain the location of a reward in memory, and reach to its previously presented location in order to receive the reward. This study also utilized the single-unit recording method. Their results showed that the majority of units in the prefrontal cortex showed the highest activity at the end of the cue period or the beginning of the delay period. Interestingly, it has been found that the increased activity is highly dependent on whether the cue is important to remember because it means there is an upcoming action. It was concluded that this pattern of activity in the prefrontal cortex implies that its role could be related to sensorial and mnemonic attention, which would be needed for short-term memory.

The posterior parietal cortex has been shown to have involvement in visual working memory where brain regions like the lateral intraparietal area had spatially tuned increases in neuronal firing rate during a working memory task (Gnadt & Andersen, 1988). Pesaran and colleagues (2002) describe the spatially tuned activity as memory fields, similar to the receptive fields of the sensory system. The goal of their study was to understand the temporal structure of neuronal activity in the posterior parietal cortex. Neural activation that is temporally correlated becomes reverberations which seem to be implicated in cognitive processing. The authors used a memory-saccade task where an animal makes a saccade to a memorized location in one of eight directions. This study recorded local field potentials (LFPs) from the posterior parietal cortex (PPC), specifically the lateral intraparietal area (LIP) of two adult male Rhesus monkeys. Their results showed that 70% of neurons that they recorded from showed significant memory period activity. LFPs were analyzed and results showed that in the preferred direction, there was an increase in gamma-band power (25-90 Hz) sustained during the memory period. The increase in gamma-band power may be evidence for dynamic memory fields. Spectral analysis of spike activity from a representative cell with memory activity showed that there was a significant peak in the spectrum in the gamma band. The study was also able to show that oscillations in the gamma-band power corresponding to the spike activity may be evidence for showing that reverberant circuits are a basis for working memory.

The inferior temporal cortex (ITC) is known to be involved in high-level visual processing, particularly object recognition (Logothetis, Pauls, & Poggio, 1995). Object recognition is important for visual search since one has to find an object of interest from a scene that may already have many objects. Visual search involves the combination of memory and attention because there should be a stored representation of the object and way to select for that object (Chelazzi, Miller,

Duncan, & Desimone, 1993). Chelazzi and colleagues were interested in researching whether the neural activity in the inferior temporal cortex could exhibit changes based on whether the object representation was for memory or attention. The task for this experiment required animals to fixate at a dot on a computer screen, a cue picture would appear shortly, then two cues would be shown on screen again as a choice. One of the cues was previously presented and the animal was required to make a saccadic eye movement toward the side which had the previously presented cue. The recordings from ITC revealed that activity related to the cue was maintained throughout the delay period, which showed the delay activity that is characteristic of holding information in visual working memory. The ITC neurons also responded with higher activity for information about the target. Overall the authors were able to show that the internal representation of the cue and the selection of the target can be revealed through the neuronal activity.

Transcranial magnetic stimulation (TMS) studies have been particularly useful because TMS is one of the few techniques that can be used non-invasively on humans to make causal inferences about the involvement of a brain region in a behavioural outcome. TMS has been used in clinical research of neurological disorders and has been used to successfully treat symptoms of Parkinson's disease, schizophrenia, and depression (Dougall, Maayan, Soares-Weiser, McDermott, & McIntosh, 2015; George, 2010). In terms of visual working memory, Rademaker et al. (2017) conducted an experiment that examined how TMS impacted visual working memory precision and guess rate. The authors used TMS because it can allow for the active alteration of brain processing during memory. This study used a combination of functional and anatomical MRI with neuro-navigation for TMS. TMS was administered at 10 Hertz in triple pulses over early visual areas. The task involved a memory array with four locations that had a circular grating, the orientation of the four gratings were randomly chosen. This was followed by a two-second period

where the TMS pulses were given, then a cue would indicate which of the four locations were probed for recall. Following a short blank, a test grating would appear that they could adjust the orientation using button presses, to match the cued location. TMS pulses had two timings within the retention interval – early (exactly at the start) and late (900 milliseconds). Their results revealed that recall was slightly worse in trials where TMS was applied early compared to late. Improvements could also be seen as reduced response variability close to areas targeted by TMS, meaning that memory precision was improved locally due to TMS. The reduced recall in early pulses were due to increased guess rates. Overall, their results revealed that visual cortical TMS can be used to influence working memory, specifically, it can enhance memory representations. Seeing these effects warrants further research continuing to use non-invasive tools such as TMS and transcranial direct current stimulation (TDCS) to understand brain activity but also modulate detrimental brain activity as a means for treatment of impairments.

Taken together, it is of note that many brain areas involved in visual working memory processes are also involved in the saccadic system. FEF, SEF, dlPFC, and LIP, for example, are all involved in many overlapping processes with regards to VWM and saccades. Previous studies have provided evidence to support that there is overlap between these systems (Hollingworth & Luck, 2009; Schneegans, Spencer, Schöner, Hwang, & Hollingworth, 2014; Wong & Peterson, 2013). For example, Srimal & Curtis (2008) used a memory-guided saccade task and spatial item recognition task to compare spatial working memory and prospective saccade memory. They found the same pattern of activation in the parietal cortex and frontal eye fields contralateral to the cued visual field which suggests that even when there is no intention to make a saccade, holding information in working memory activates saccade planning areas in the brain.

Strategies for VWM: Chunking and Spatiotemporal Structure

The performance of human subjects in memory-guided saccade tasks has been shown to correlate with visual working memory capabilities, as mentioned previously. It is well documented that the brain uses several strategies to remember information, considering the enormous amount of input it receives. Some of these strategies include chunking as well as primacy and recency (Botvinick et al., 2009). Chunking of information is a common method employed by people to remember events. For example, when remembering a phone number, it is usually chunked into three groups (123-456-7890) as opposed to all single digits (1-2-3-4-5-6-7-8-9-0). Chunking involves grouping information together in a meaningful way to reduce the amount of encoding required or in other words, it can increase visual working memory capacity (Bullard et al., 2012; Portrat, Guida, Phénix, & Lemaire, 2016). Although it is known that the brain “chunks” information, the way in which it does so is not very clear (Mathy & Feldman, 2012). Our ability to increase visual working memory capacity, whether it be through chunking or other mechanisms, greatly depends on the visual and temporal information available (Cowan, 2000).

Goals and Rationale

This study was designed to determine the role of visuospatial and temporal information on performance in memory-guided sequential saccade tasks. Having targets appear sequentially allowed for testing aspects of temporal memory such as the order of presentation, in addition to spatial properties. The task is similar to classical Corsi block tapping tests where participants are required to point to a remembered sequence of blocks that an experimenter has already pointed to (Corsi, 1972; Vecchi & Richardson, 2001), however, because the goal of this study is to understand visual working memory and the influence of spatiotemporal structure on eye movements, participants were making saccades to a remembered sequence of targets. This behavioural study uses a combination of three spatiotemporal conditions to assess their influence on visual working

memory capacity in humans. The three conditions examined were structure, set size and order of presentation. In each condition, participants were required to recall a series of three to six targets presented in sequential order. Thus, the influence of spatial and temporal cues on the ability of a subject to recall the targets accurately was determined.

Memory capacity can be described and measured in several ways such as the number of items that can be remembered, whether temporal information can be recalled accurately, and whether spatial information can be recalled accurately. This study examines whether having spatial and temporal structure in a target sequence aids the capacity to remember that sequence and how it interacts with additional features including set size and presentation order. The results of this experiment will elucidate whether the spatiotemporal information presented is more or less cognitively taxing on the brain and whether this manifests in terms of performance in the task. This behavioural research is important for a better understanding of the role of memory in cognitive processing. Memory is a cognitive function used constantly by humans to accomplish countless tasks such as learning new information or remembering geographic locations. Memory is also one of the most common cognitive functions affected by aging and disorders of the brain such as stroke. Brain imaging studies could help elucidate neuronal circuitry behind memory-guided saccade sequence tasks which can, in turn, improve our understanding of this behaviour in healthy individuals as well as individuals who have impaired abilities.

Predictions and Hypotheses

There were three different structures presented to participants: sequential, spatial and random. Sequential sequences consisted of stimuli that formed a contiguous spatial path and presentation order followed the minimum-step route from one end to the other. Spatial sequences formed a contiguous spatial path, but stimuli were presented in random order. In random sequences, stimuli were presented at random locations in random order. With the support of

previous research, it is hypothesized that participants will have greater ability to recall stimuli with a sequential structure (Bor et al., 2003; De Lillo et al., 2016; Fagot & De Lillo, 2011; R.M. Müri, Faller, & Rösler, 1997). Bor et al. (2003) suggest that structured sequences may be easier to recall due to chunking effects. When comparing spatial and random structures, it is expected that performance in spatial sequences will be better due to recognizable shapes facilitating chunking. With regards to temporal information, humans are generally poor at recalling the order in which items were presented and recall declines further when more items are required to be recalled (R.M. Müri et al., 1997). Therefore, performance in the random structure condition should be lowest as it does not have spatial or temporal order.

The second condition being examined in this study was set size. This refers to the number of targets a participant was required to remember in any given trial. In this experiment, the set size of a trial was a minimum of three targets and up to a maximum of six targets. As mentioned earlier, the average number of items that can be held in working memory is three to four items (Adam et al., 2017; Ester, Fukuda, Vogel, & Awh, 2014; Mathy & Feldman, 2012). Therefore, it is hypothesized that participants should not be able to perform saccade sequences above four targets according to the discrete model or there should be a decrease in performance as the set size increases, according to the resource model.

The third condition being tested was presentation order. Müri et al., (1997) showed that chronological reproduction of sequences decreased as the number of targets presented in a sequence increased. Similarly, since this experiment involves the sequential presentation of targets, it is hypothesized that participants will have the highest accuracy recalling targets that are late in a sequence due to recency effects. Botvinick et al., (2009) describe that items that appear late in a sequence are remembered more easily, called recency effects.

There have been many previous studies that give insight into how each of these three variables may impact VWM. However, there aren't many studies that examine how these factors may interact with each other. Our visual world is naturally complex, with mixtures of these three factors and more that can influence how humans program saccade sequences. For example, it is expected that in conditions with larger set sizes, the structure may have a more significant influence as the presence of spatiotemporal structure could help reduce VWM load.

CHAPTER II: MANUSCRIPT

Title: Influence of spatiotemporal stimulus structure on memory-guided saccade sequences

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ABSTRACT

Saccades - rapid eye movements that place targets of interest on the fovea - are often used as a tool to measure underlying cognitive processes such as visual working memory. The goal of this study was to identify the influence of spatiotemporal structure, set size, and order of presentation in a stimulus display on performance in memory-guided saccade sequences. Fourteen participants were presented with sequences of transient visual stimuli that differed with respect to spatiotemporal structure (Sequential: spatially contiguous order, Spatial: spatially continuous and random order, or Random: spatiotemporally random) and set size (3-6) and then had to reproduce this with a series of saccades. Results were analyzed with respect to % correct target recall, absolute error from the target, and error relative to the previous saccade endpoint. There was a significant influence of spatiotemporal structure on absolute and relative errors (random>spatial>sequential), increased set size on correct recall and absolute error, and primacy of order in correct recall. There were also interactions between the effects of path type and set size (especially on the absolute error in the spatial condition) and order on absolute error. These results indicate that, whereas spatiotemporal stimulus structure is beneficial for memory 'chunking' in saccade sequence planning, this has complex interactions with stimulus set size, order, and the way in which one measures the resulting saccade errors.

INTRODUCTION

Saccades are rapid eye movements that bring regions of interest onto the fovea, which is the location of highest visual acuity on the retina (Leigh & Kennard, 2004; Martin, Tapper, Gonzalez, Leclerc, & Niechwiej-Szwedo, 2017; McSorley, Gilchrist, & McCloy, 2019). Humans make four to five saccades every second during visual interactions with the environment (Lévy-Bencheton, Khan, Pélisson, Tiliakete, & Pisella, 2016), often to a pre-planned sequence of multiple targets (Zimmermann, Morrone, & Burr, 2015). It is thought that working memory contributes to saccade sequence planning (Lévy-Bencheton et al., 2016; Luck & Vogel, 2013; McSorley et al., 2019), and conversely, those saccade signals are used to update memory of target location and identity (Irwin, 1992; Prime et al., 2007). Compared to saccades to a single remembered target (Brown et al., 2004; C Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991), the use of visual memory to control saccadic sequences is not well understood (McSorley et al., 2019). Memory-guided saccade performance has been shown to be highly impacted by the set size of a stimulus sequence, order of the sequence presentation and clustering effects (R.M. Müri et al., 1997). In the current study, we consider all three of these factors, and more importantly, the ways in which they interact to influence saccade performance along with several different spatial measures.

Visual Working Memory Capacity

Visual working memory (VWM) refers to the temporary maintenance of visual information in memory for use in an ongoing task (Baddeley & Hitch, 1974; Luck & Vogel, 2013). Although there have been numerous studies on VWM, there is still no consensus on the underpinnings of human VWM capacity limits. There are two main theories of visual working memory capacity that are currently used in literature. One is the discrete or slot-based model and the other is the continuous resource model (Barton et al., 2009; Paul M. Bays & Husain, 2008; Huang, 2010; Luck

& Vogel, 2013). The discrete model describes VWM as a finite number of slots and when these slots are filled, there is no information stored about any additional items. According to the discrete model, visual working memory capacity is approximately 3-4 items (Adam et al., 2017; Anderson & MacAskill, 2013; Awh et al., 2014; Paul M. Bays, 2018b; Huang & Awh, 2018; Mathy & Feldman, 2012). Continuous resources models define VWM as a pool of resources that can be flexibly divided, however, with an increasing number of items to remember, fewer resources are allocated and therefore precision will decrease (Paul M. Bays, 2018a). VWM also interacts with other factors related to saccade programming: saccades themselves may reduce VWM capacity (Martin et al., 2017), whereas attentional cues can interact with VWM constraints to enhance saccade performance (Yoo, Klyszejko, Curtis, & Ma, 2018). In our study, we use several measures of task performance which can help delineate the nature of capacity limits on VWM and the influence of multiple factors on VWM capacity.

Influence of Structure

The performance of human subjects in memory-guided saccade tasks has also been shown to correlate with visual working memory capabilities. It is well documented that the brain uses several strategies to remember information, considering the enormous amount of input it receives. Some of these strategies include chunking, primacy and recency (Botvinick et al., 2009). Chunking of information is a common method utilized by people to remember events. Chunking involves grouping information together in a meaningful way to reduce the amount of encoding required, or in other words, increase short term memory capacity (Portrat et al., 2016). Although it is known that the brain “chunks” information, the way in which it does so is not very clear (Mathy & Feldman, 2012). Our ability to increase short-term memory capacity, whether it be through chunking or other mechanisms, greatly depends on the visual and temporal information available (Cowan, 2000).

Studies using memory-guided sequential saccade tasks are a convenient way to explore the influence of structure on VWM since the number of targets and spatial locations of targets can be manipulated in ways that can test the limits of VWM capacity. Previous studies have shown that people can use the spatiotemporal structure of a sequence of visual stimuli to increase VWM capacity (Bor et al., 2003; De Lillo et al., 2016). Sequences that have structured pathways have been associated with greater recall ability (Bor et al., 2003; De Lillo et al., 2016; Fagot & De Lillo, 2011; R.M. Müri et al., 1997). Sequential structure conditions were those that had regular spatial arrangement conducive to chunking. De Lillo et al. (2016) had visual stimuli that could be presented in two different ways: structured or unstructured. The stimuli were three clusters of three squares and one by one, the squares would blink in a black colour to indicate the order and location of the targets to be remembered. In structured sequences, the squares were presented such that the three squares of one cluster blinked before moving on to the next cluster. In unstructured sequences, consecutive squares would blink in a different cluster each time. Their results showed that more items were recalled correctly if they were in the structured sequences which could be a result of properties such as clustering, proximity or continuity that allow them to have stronger memory representations.

Influence of Order

Serial position effects have also been observed in previous studies where saccade targets presented later in a sequence were more difficult to recall (R.M. Müri et al., 1997). Primacy and recency are also temporal effects that have been observed in previous studies. Primacy refers to stronger memory for items presented early in the sequence and recency refers to stronger memory for items presented later in a sequence (Botvinick et al., 2009). A study conducted by Parmentier and colleagues (2006) looked at serial position effects in visual stimuli sequences of different

spatial-temporal structures. They found a recency effect in recall performance in the control condition and scallop effect (both recency and primacy) in the converging and diverging conditions. This interaction effect shows that the relationship between multiple features should be considered when exploring the limitations of visual working memory capacity.

Previous studies have revealed various features such as structure, set size and order may individually impact VWM. However, there aren't many studies that examine how these factors may interact with each other especially in saccade sequences. It is rarely the case that our visual world has only one feature, we actually see several features at once. Therefore, it is expected that there will be conditions where one or more of the independent variables have a significant influence on VWM. It is known that saccade sequences are influenced by structure because organized structures may improve target predictability or mental imagery of the target sequence (De Lillo et al., 2016). The set size effect is well known in several contexts, the more items there are to remember, the more load there will be on VWM. Whether VWM is a finite or flexible resource, there are clear limitations. Temporally, there is also evidence to show that when recalling a sequence of items, recall performance can be dependent on strategies that may prefer early, late or middle items within a sequence. However, with the presence of several features, it is not well understood how the brain employs strategies to deal with increasing VWM load. The results of our current study reveal that the use of strategy to reduce VWM load is only seen in some cases where one feature such as structure or set size was at an upper limit. The use of strategy to reduce cognitive load works in complex ways that need to be further explored.

Present Study

In summary, a considerable amount is known about working memory and the way it influences the programming of saccade sequences, but less is known about how these factors interact, as they must in real-world circumstances. The current study was designed to test whether having spatial and temporal structure in a target sequence aids the capacity to remember that sequence and how it interacts with additional features including set size and presentation order. There were three different spatiotemporal structures presented to participants: sequential, spatial and random. Sequential sequences consisted of stimuli that formed a contiguous spatial path and presentation order followed the minimum-step route from one end to the other. Spatial sequences formed a contiguous spatial path, but stimuli were presented in random order. In random sequences, stimuli were presented at random locations in random order. Based on previous literature that recall performance would increase when presented with stimulus sequences that have spatiotemporal structure (Bor et al., 2003; De Lillo et al., 2016) it is also expected in this study that recall performance will be highest in the sequential condition, followed by spatial only and finally the random condition. However, this will also depend on the presence of additional cues such as set size and presentation order that will either aid or disrupt the chunking process. Specifically, it can be hypothesized that the benefit of structure will be more evident in the conditions where set size is larger as it will place a larger burden on VWM load. In sequential structure conditions, it can also be hypothesized that there may not be a primacy or recency effect because if chunking is happening, there is a greater chance that participants will remember groups of targets rather than individual ones.

METHODS

Participants

14 individuals participated in this study; nine females and five males between the ages of 21 – 34 (13 right-handed and one left-handed participant). Initially, data was collected from 16 participants, however, one participant could not complete the entire session and one participant was not able to maintain fixation for the appropriate amount of time, therefore, their results were not included in further analyses. All had normal or corrected-to-normal vision and no known neuromuscular deficits. All participants were naive with respect to the purpose of the experiment. This experiment was preapproved by the York Human Participants Review Subcommittee. All subjects were asked for informed consent in order to participate and given monetary compensation for their time.

Apparatus

Participants were seated in complete darkness in front of a table with their right hand resting on a start button located directly in front of them on the table surface (Fig. 1A). A personalized bite bar made of dental impression compound (Kerr Corporation, Orange, CA) was used to ensure that there was as little movement as possible by the participants. The heights of the seat and bite bar were adjusted so that the participant's eye level was aligned with the central target of the screen. The visual stimuli were presented on a 21" Dell Trinitron CRT monitor (2048x1536 pixels at 80 Hertz) which was 52 cm in front of the participant. A 5x5 placeholder array encompassing 20x20 visual degrees of space was presented on the computer screen and all targets appeared within the placeholder circles. All stimuli were presented on the screen except for an auditory cue that guided participants when to saccade to the target. Eye movements were only measured from the right eye using the EyeLink II System (SR Research, Ontario, Canada) and OptoTrak (NDI Digital).

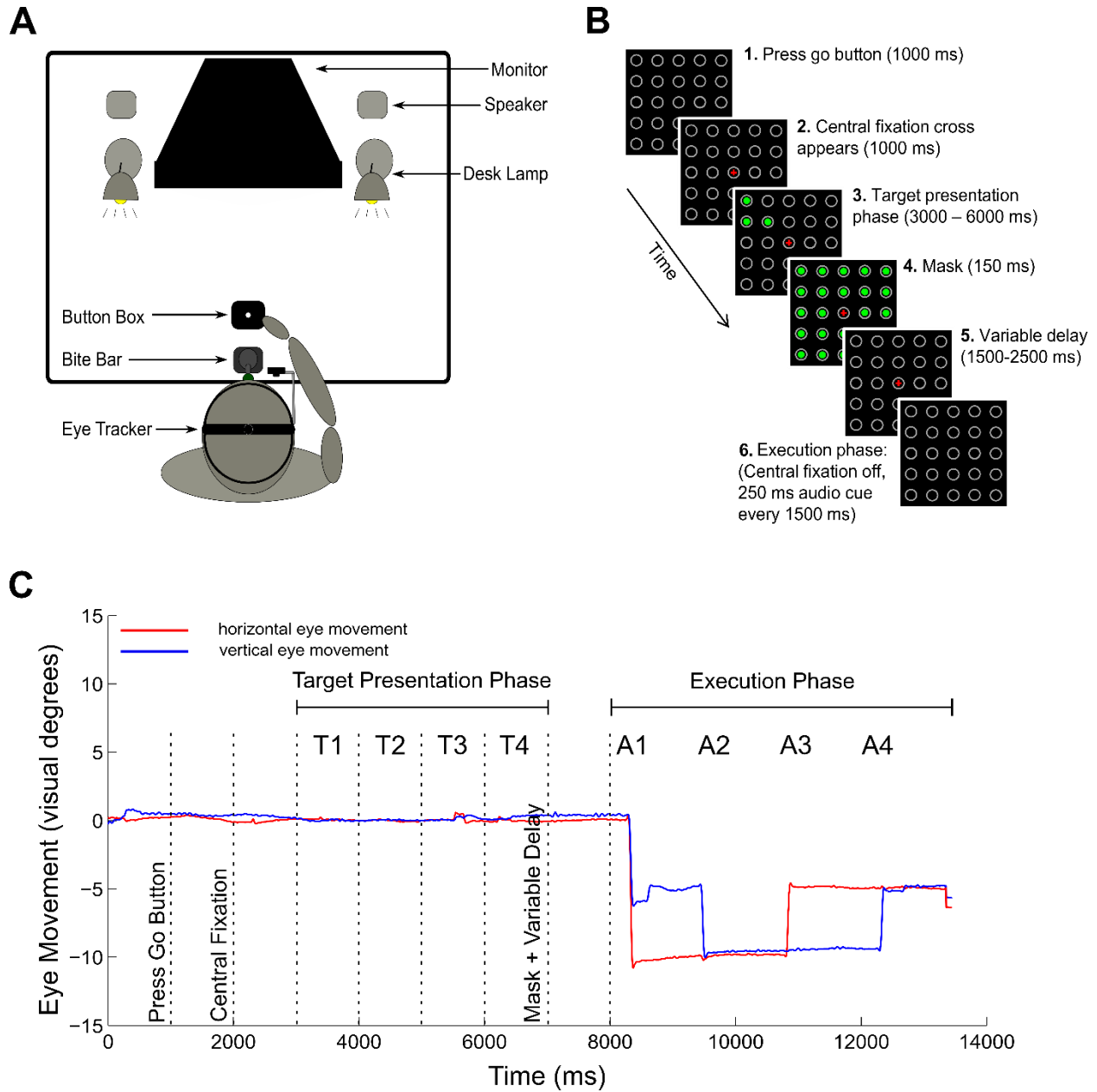


Figure 1. (A) Experiment setup – not drawn to scale. (B) Experimental paradigm – timing and order of on-screen stimuli for one example trial. (C) Eye movement data from one subject overlaid with the timing and events of a single trial.

Task and Stimuli

The subject was seated with their right hand resting on a box containing the start/end button and their left hand resting on their lap. The experiment started with a nine-dot calibration procedure where each participant was asked to look at the first, third and fifth target in the first, third and fifth rows on the screen, while the lights were still on in the experiment room. All eye movements were made in complete darkness following this step. At the start of each trial, a red-coloured fixation cross (4x4 mm) appeared in the centre of the stimuli array, at which subjects were to maintain fixation (Fig. 1B). After one second, the target presentation phase began. Central fixation was required during the entire target presentation phase, so the red central fixation cross remained illuminated. While maintaining central fixation, green-coloured target dots (4x4 mm) were presented in a sequential manner; participants could only be using peripheral vision to view these items.

Sequences had a set size ranging from three to six targets; all presented in one-second intervals. Any given sequence could also vary in terms of three possible sequence structures. Sequences could have a: 1) Sequential structure - stimuli formed a contiguous spatial path, and presentation order followed the minimum-step route from one end to the other (Fig. 2A), 2) Spatial structure - stimuli formed a contiguous spatial path but were presented in random order (Fig. 2B), or 3) Random structure - stimuli were presented at random locations and in random order (Fig. 2C). With three sequence structures (Sequential, Spatial and Random) and four set sizes (three, four, five, six) there were a total of 12 trial combinations. Sequences were presented in random locations of the screen and trial types were presented in random order.

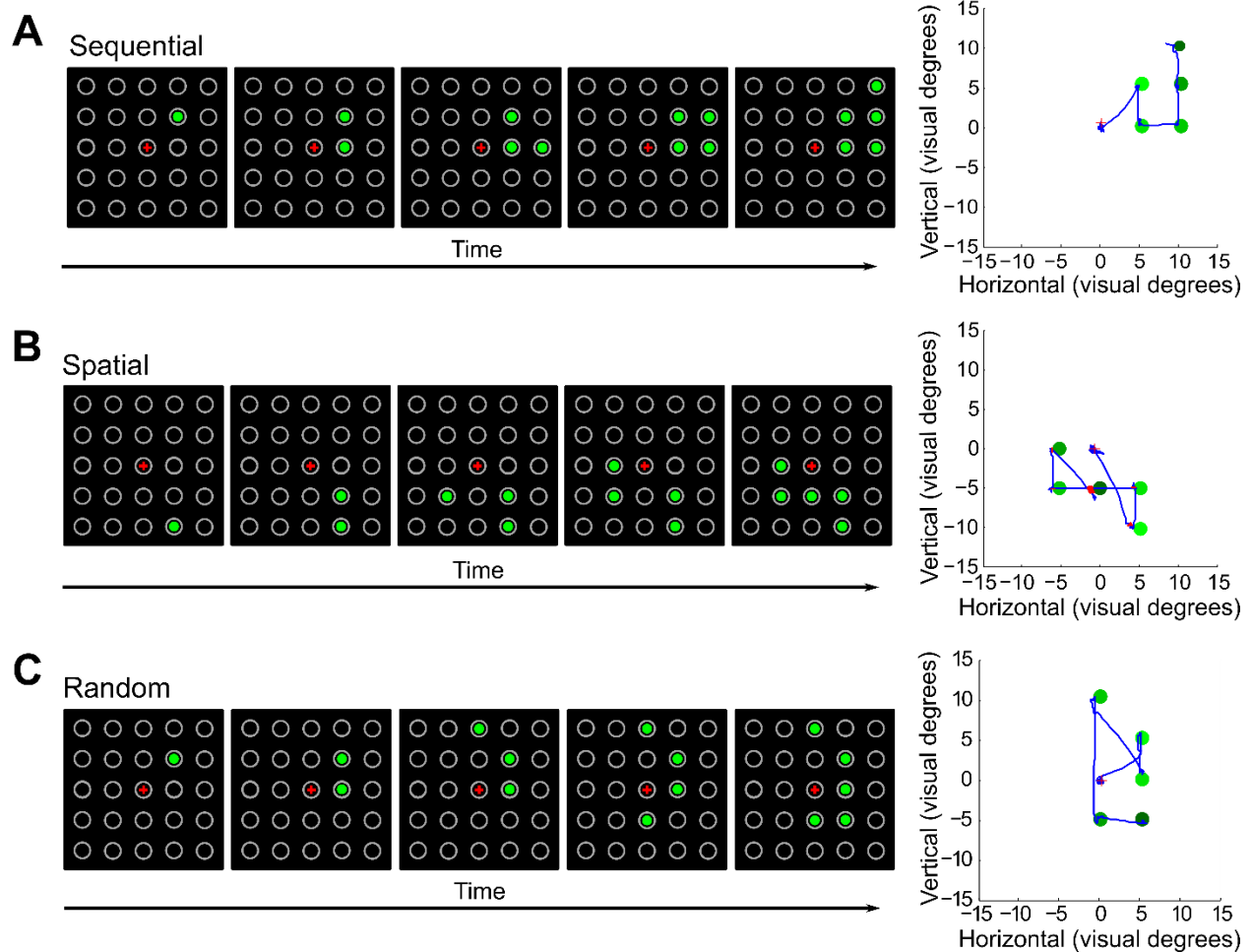


Figure 2. Sample trial for each structure type on the left with saccade data from a representative subject on the right. 25 grey placeholder circles remained on screen throughout the experiment and all targets appeared within them. Lightest green represents the first target in a sequence and each subsequent target is a darker green colour. Blue lines are eye movement tracings starting at the central fixation point to the end of the trial. **(A)** Sequential structure - stimuli formed a contiguous spatial path, and presentation order followed the minimum-step route from one end to the other. **(B)** Spatial structure - stimuli formed a contiguous spatial path but were presented in random order. **(C)** Random structure - stimuli were presented at random locations and in random order.

After the target presentation phase was completed, all items on the monitor illuminated for 150 ms to mask any after images. Following the mask, the central fixation cross disappeared, which served as the go signal for participants to make sequential saccades to each remembered target. There was a random delay varying from 1.5 to 2.5 seconds between the appearance of the mask and the go signal to reduce any anticipation effects. Following the execution of the saccades, the participant was instructed to press the button again to end the trial. There was a 250 ms auditory cue played in 1500 ms intervals matching the number of targets to help pace the participant's eye movements. Figure 1C shows an example of eye movement data from an example trial. The experiment was self-paced, so the participant initiated the next trial themselves with a press of the button. Every three trials, two desk lights (40W incandescent light bulbs) placed on either side of the LED stimuli monitor illuminated for one second to prevent any dark adaptation, then the next trial would begin.

Design

The experiment consisted of 144 trials in total; 12 repetitions of the 12 trial combinations (three structures x four set sizes). These were presented randomly and interleaved within four blocks. Trials were divided into three blocks of 37 trials each and a fourth block consisting of 33 trials. Each block of the experiment lasted approximately 12 minutes. The full experiment including eye-tracking setup and a nine-point calibration lasted for approximately 50-60 minutes per person.

Data Analysis

Data collected from the EyeLink software was analyzed in MatLab (MathWorks). A custom program code was written for this experiment that allowed for the automatic marking of fixation points. Based on values that have been previously used in literature, this automatic program marked intentional fixations as the first time point 250 ms after a saccade reaching a peak

velocity of at least 40°/sec which had no eye movement for at least 250 ms (Hodgson, Winand, Henderson, & Kennard, 1999; Nuthmann, Vitu, Engbert, & Kliegl, 2016; Wu, Chua, & Yen, 2016). Each subsequent fixation in a sequence was marked following a refractory period of 250 ms. Exclusion criteria were determined to mark appropriate fixation points. The first exclusion criterion was that central fixation had to be maintained at least 90% of the entire time the central fixation light was illuminated, excluding any time where there was blinking. The second criterion was to make sure the participant was not anticipating their first eye movement; therefore, the first saccade had to be initiated after the go signal. Failure to meet these two requirements resulted in the removal of that trial from further analyses.

Analysis of Memory Performance and Movement Performance

Eye movement endpoints were classified as correct if the Euclidean distance between the eye endpoint and the actual target location was not more than 2.5°. Distances above 2.5° were defined as erroneous. Figure 3A shows the saccade endpoints before any exclusion criteria were applied and it was visible that participants were accurate and precise in their saccades overall. Eye movements that were more than two standard deviations away from the mean for each participant were removed as outliers. Memory performance was used as a qualitative measure to determine how many trials a participant recalled correctly. For a trial to be correct, the participant had to recall all targets of the sequence in the correct location and order they were presented in. If a single target was missed or the saccades were made in the incorrect order, the entire trial was incorrect (Fig 3B). The memory performance was calculated as the percentage of correct trials in each of the twelve conditions.

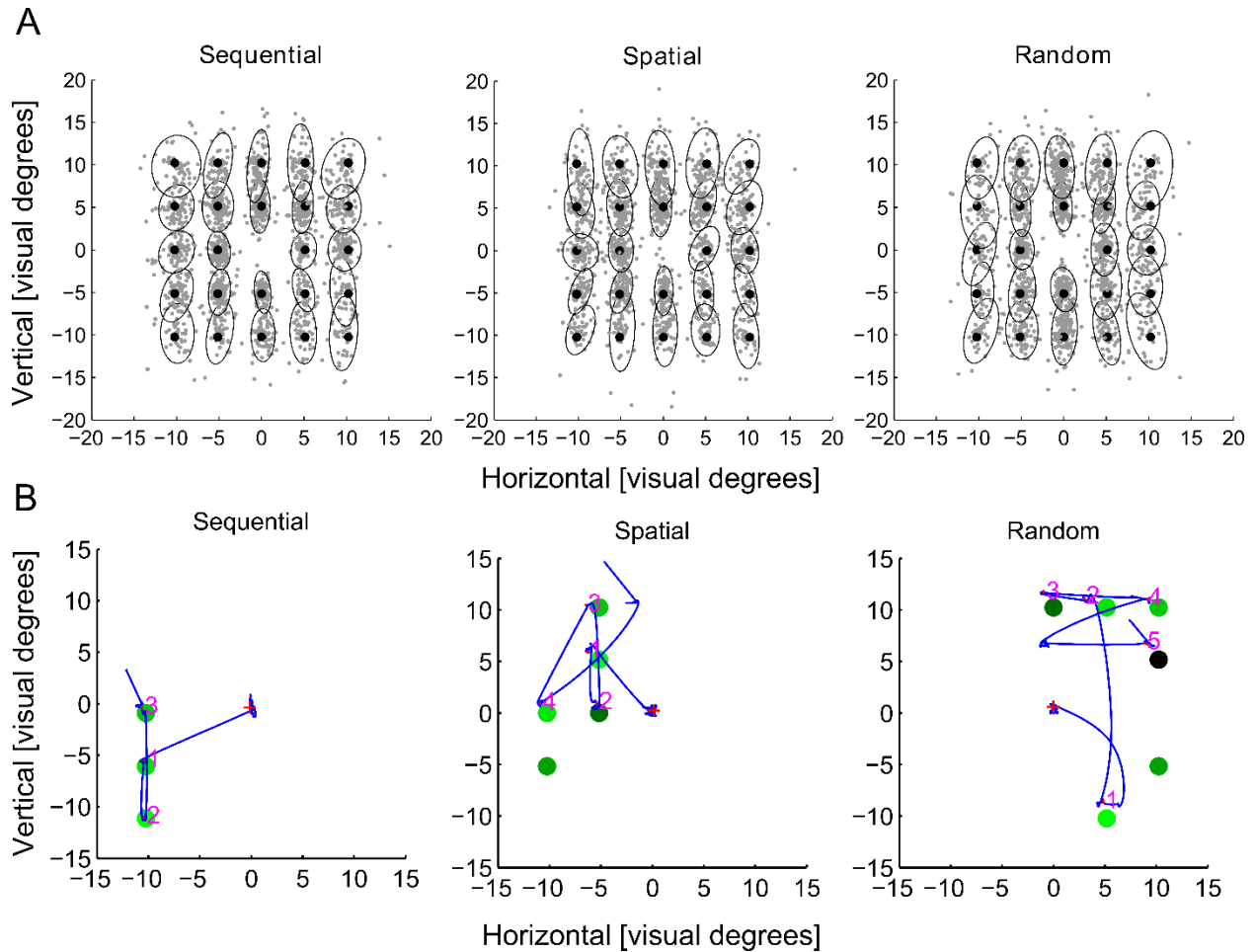


Figure 3. (A) Raw data - Saccade endpoints from all participants ($n = 14$) before exclusion criteria were applied. Black dots represent all 24 possible target locations. Small grey dots represent saccade endpoints. (B) Examples of incorrect trials. The left panel shows an example of the participant making saccades in the incorrect order. The middle panel shows an example of a missed target. The right panel shows an example of a missed target and incorrect order. Lightest green represents the first target in a sequence and each subsequent target is a darker green colour. Blue lines are eye movement tracings starting at the central fixation point to the end of the trial.

To analyze movement performance the same criteria were used to determine correct trials as in memory performance, however, the average error in visual degrees per trial was calculated instead of the percentage of correct trials. Additionally, a third measure for relative error was calculated by subtracting the previous target error from the current one.

All analyses were conducted using repeated-measures ANOVA. All results are reported with p-values corrected for multiple comparisons using Bonferroni posthoc correction. All data used in the following analyses were tested for normality using the Shapiro-Wilks test, Q-Q plots, Skewness and Kurtosis values. They were also tested for sphericity using Mauchly's test, appropriate corrections were used if data did not pass Mauchly's test. All analyses were conducted in SPSS (IBM).

RESULTS

A total of 2016 trials were recorded from 14 participants, i.e., 144 / subject. Of these, 64% met our inclusion criteria. After applying our exclusion criteria, each participant performed 22.79 ± 2.60 sequential trials, 21.21 ± 2.24 spatial trials, and 19.57 ± 1.41 random trials (mean \pm SEM across participants). Of these, 18.86 ± 2.05 had a set size of 3, 17.29 ± 1.72 had a set size of 4, 14.29 ± 1.52 had a set size of 5, and 12.14 ± 1.29 had a set size of 6 (mean \pm SEM across participants). Overall performance of analyzed trials (mean \pm SEM across participants) was $44 \pm 4\%$ (measured as % correct trials), $1.58 \pm 0.54^\circ$ (measured as absolute errors) and $0.76 \pm 0.29^\circ$ (measured as errors relative to previous saccade end-point). However, these numbers were influenced by path type, set size, order, and their interactions, as described in the following sections.

Main Effects

Structure

The effect of structure on the three measures of visual working memory performance can be seen in Figure 4. When examining memory performance (the percent of trials that were correctly recalled), the two-way repeated-measures ANOVA for structure and set size revealed that there was no significant main effect of structure (Fig. 4A). The absolute error was calculated as the Euclidean distance between each target location and the location that the participant's eye landed. In terms of absolute error (Fig. 4B), there was a significant main effect of structure ($F_{(2, 26)} = 6.55$, $p < .01$, $\eta_p^2 = 0.34$) where sequential structures had a lower error than random structures which was statistically significant ($p < .01$). Relative error (Fig. 4C), was calculated by subtracting the previous absolute error from the current one such that any cumulative error effects were removed. There was a significant main effect of structure on relative error ($F_{(2, 26)} = 24.91$, $p < .01$, $\eta_p^2 = 0.66$). All three structures were statistically significant from each other, with the relative error

being the smallest in the sequential condition, followed by spatial conditions then random conditions with the largest relative error ($p < .001$ for sequential and spatial, sequential and random; $p < .05$ for spatial and random).

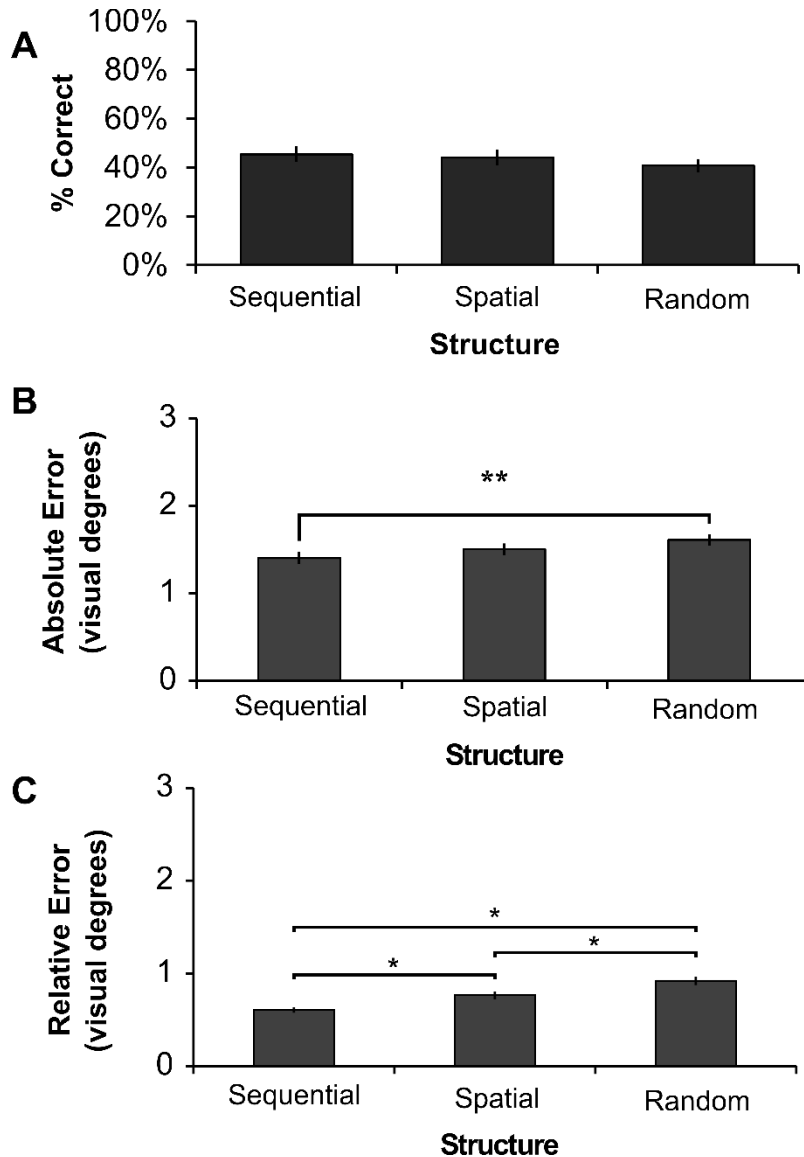


Figure 4. Influence of structure on visual working memory (A) Average memory performance \pm standard error of the mean (SEM) as the percent of total trials that were correct. (B) Average absolute error \pm SEM in visual degrees. (C) Average relative error \pm SEM in visual degrees.

Set Size

This experiment had four possible set sizes per sequence: three, four, five or six targets. Visual working memory performance based on the set size of the sequence can be seen in Figure 5. We found significant main effects of set size for memory performance ($F_{(3, 39)} = 10.38, p < .0001, \eta_p^2 = 0.44$), absolute error ($F_{(3, 39)} = 7.17, p < .001, \eta_p^2 = 0.36$) and relative error with Greenhouse-Geisser correction ($F_{(2.039, 26.505)} = 4.01, p < .05, \eta_p^2 = 0.24$). In terms of memory performance, the highest performance was seen in set sizes of three targets followed by a decrease in performance as the set size increased to four, five and six targets. These trends can be seen in Fig. 5A. For absolute error, the opposite trend can be seen where absolute error increases as set size increased (Fig. 5B). For relative error, although there was a significant main effect of set size, there were no significant simple effects. Overall, however, it can be seen in Fig. 5C that relative error also increases as the set size of the sequence increases.

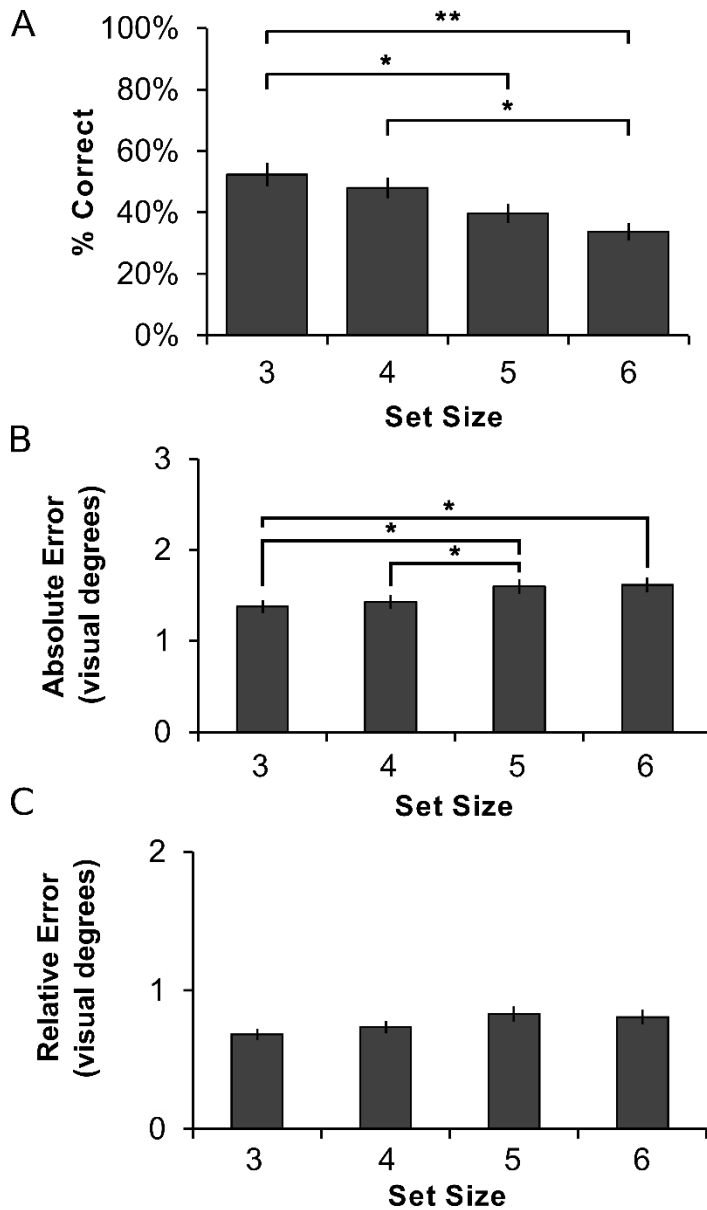


Figure 5. Influence of set size on visual working memory. (A) Average memory performance \pm SEM as the percent of total trials that were correct. (B) Average absolute error \pm SEM in visual degrees. (C) Average relative error \pm SEM in visual degrees.

Order

Since the set size of a sequence could vary from three to six targets, the order that a target was presented in sequence could be first, second, third, fourth, fifth or sixth. After separating sequences by set size, a one-way repeated measures ANOVA was conducted to compare the effect of temporal order on memory performance, absolute error and relative error at each serial position (Fig. 6). There was a significant effect of order on memory performance (Fig. 6A) for sequences with a set size of three, four, five and six targets ($F_{(2,82)} = 23.09, p < .0001, \eta_p^2 = 0.36$; $F_{(3,123)} = 21.05, p < .0001, \eta_p^2 = 0.34$; $F_{(4,164)} = 43.47, p < .0001, \eta_p^2 = 0.52$; $F_{(5,205)} = 49.64, p < .0001, \eta_p^2 = 0.55$, respectively). The overall trend regardless of set size shows that the percent of trials correctly recalled reduces as the target is presented later in the sequence.

Since spatial and random structure sequences had a non-contiguous target presentation, some of the saccades required to be made by a participant could be larger in magnitude than those in sequential structure sequences. To make sure that larger eye movement errors when analyzing absolute and relative errors were not just a result of larger magnitude saccades, we conducted an ANOVA to test whether there was any significant effect of saccade magnitude on absolute error. It was found that magnitude did not have a significant effect on errors ($F_{(1,13)} = 1.42, p = .254$), and there was no significant interaction between magnitude and structure on error ($F_{(1,13)} = 0.32, p = .582$). Thus, we were able to rule out saccade magnitude as a possible confound in any subsequent error analyses. In terms of absolute error (Fig. 6B), we can start to observe a trend of absolute error increasing with targets presented later in the sequence, however, there is only a significant difference for sequences with a set size of six.

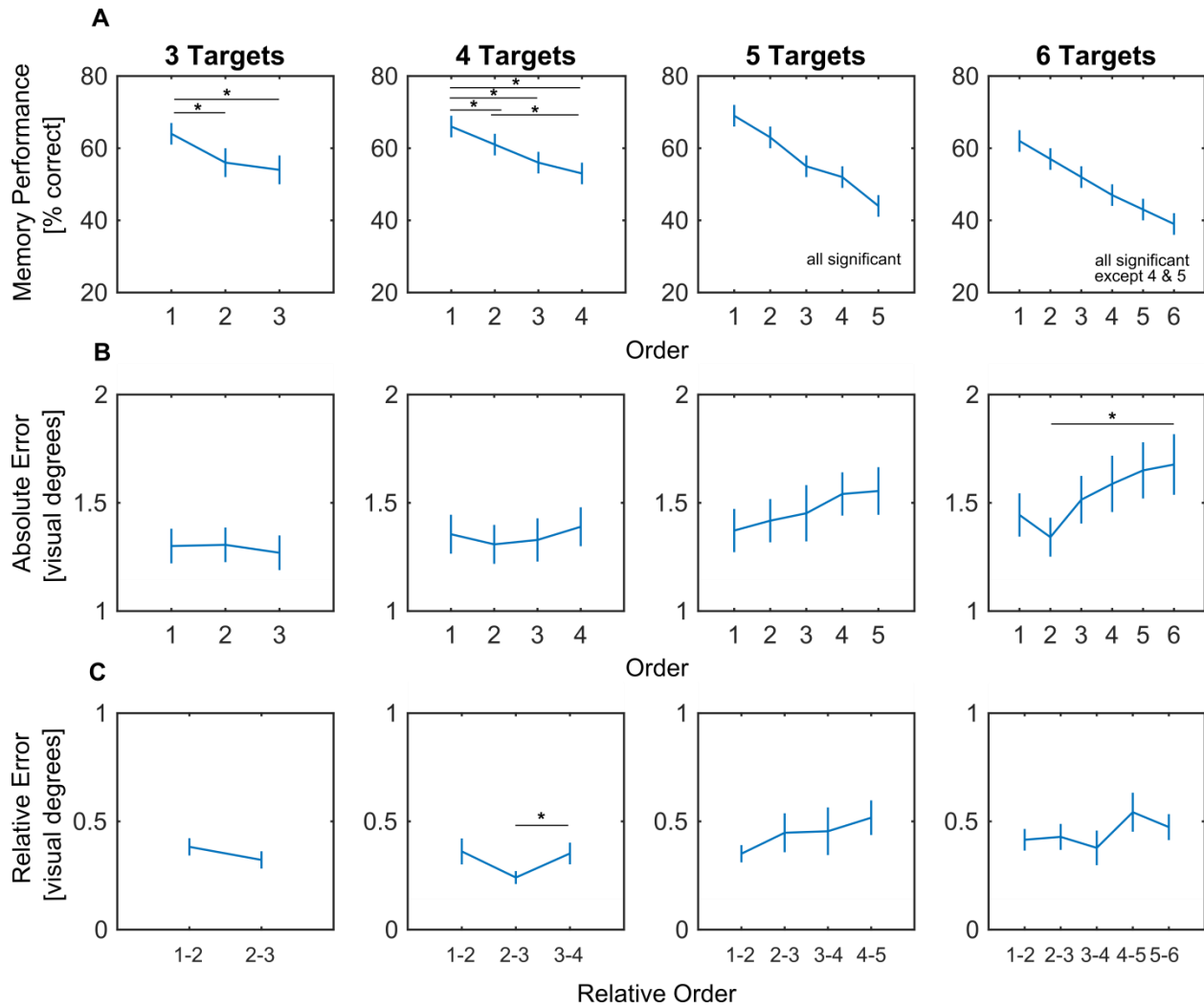


Figure 6. Influence of target order within the sequence on visual working memory. **(A)** Average memory performance \pm SEM as the percent of total trials that were correct. **(B)** Average absolute error \pm SEM in visual degrees. **(C)** Average relative error \pm SEM in visual degrees.

The effect of temporal order on relative error is shown in Fig. 6C. The trends are not as clear for relative error, with a significant difference seen in sequences of four targets when making a saccade between targets two to three and three and four. In sequences with five and six targets, there is an observable trend similar to that of absolute error, where relative error increases as sequences were presented later in the sequence.

Interaction Effects

Structure and Set Size

Figure 7A shows the interaction between structure and set size for memory performance. The ANOVA revealed a significant interaction between structure and set size ($F_{(6, 78)} = 2.28, p < .05, \eta_p^2 = 0.15$) wherein random structure sequences, there was a significant benefit to memory performance if the set size was only three compared to six ($p < .01$). In terms of absolute error, the two-way interaction between structure and set size was not significant (Fig. 7B). However, simple effects analysis showed that there was a significant effect of set size if the structure of the sequence was spatial or random. For spatial only sequences, the absolute error was significantly lower for a set size of three compared with five ($p < .001$) or six ($p < .01$), a set size of four also had a significantly lower error than a set size of five ($p < .05$). For relative error, ANOVA results showed no significant main interaction effects or simple effects of set size and structure (Fig. 7C).

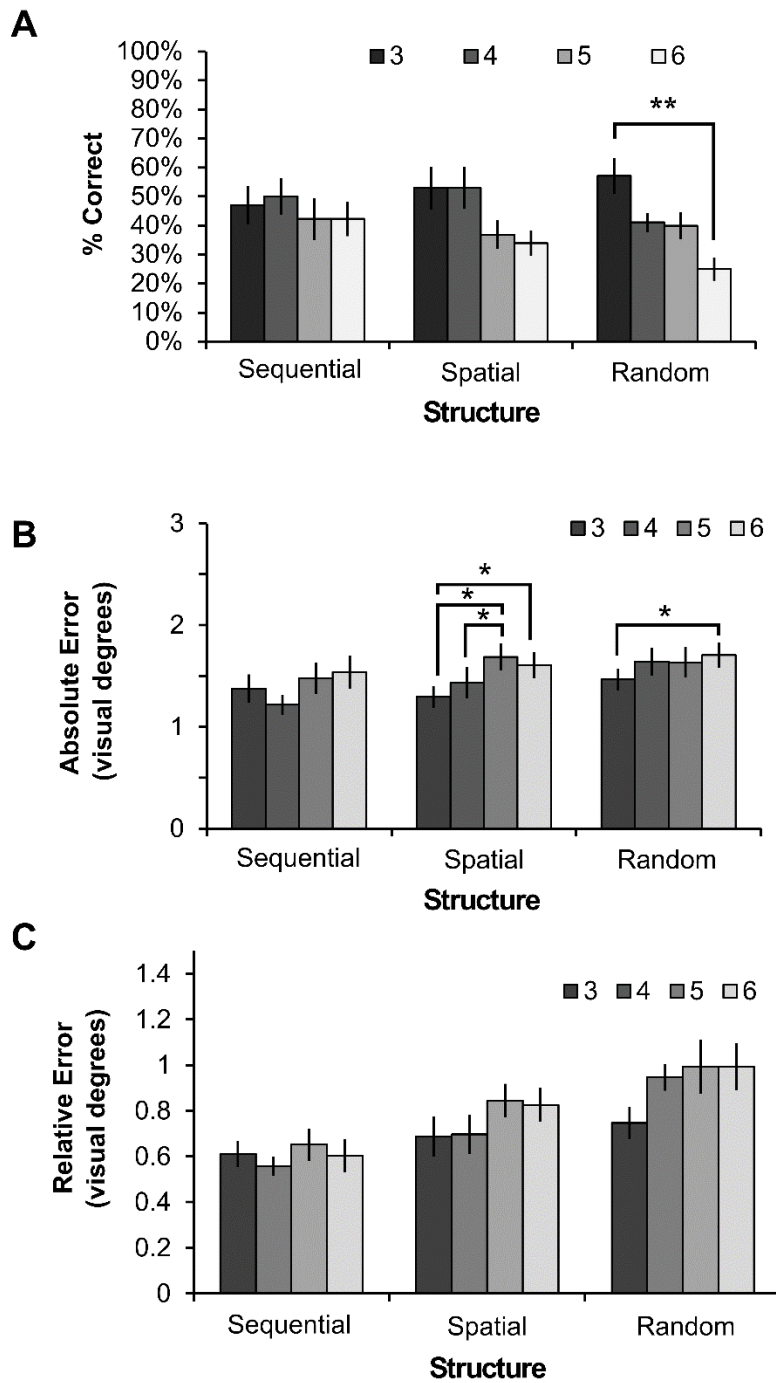


Figure 7. Interaction effects of structure and set size on visual working memory. **(A)** Average memory performance \pm SEM as the percent of total trials that were correct. **(B)** Average absolute error \pm SEM in visual degrees. **(C)** Average relative error \pm SEM in visual degrees.

Structure and Order

To examine the interaction between structure and order, the data were once again separated by set size and a two-way repeated-measures ANOVA was conducted to compare the effect of structure and order on memory performance, absolute error and relative error (Fig. 8). In sequences with a set size of three, there was a significant interaction effect of both structure and order on memory performance ($F_{(4, 52)} = 2.56, p < .05, \eta_p^2 = 0.16$), but no significant simple effects (Fig. 8A). In sequences with a set size of four, five and six targets, there were no significant interaction effects. Overall, the trend shows memory performance decreasing with temporal order, regardless of the structure and set size.

Figure 8B displays the interaction effect between order and structure on absolute error. The ANOVA revealed a significant interaction between structure and order ($F_{(4, 52)} = 3.65, p < .05, \eta_p^2 = 0.22$) in three target sequences where the absolute error for spatial structure sequences was significantly lower than random for the first target ($p < .05$). For sequences with a set size of four targets, there was a significant main effect of structure ($F_{(2, 26)} = 6.14, p < .01, \eta_p^2 = 0.32$) where average absolute error was significantly lower in sequential structures compared to random structures ($p < .01$). Simple effects analysis showed that absolute error was significantly lower when the structure was sequential as opposed to random for the second target in a sequence ($p < .05$) and third target in a sequence ($p < .05$). For sequences with a set size of five targets, there was a significant interaction between structure and order ($F_{(8, 96)} = 3.44, p < .01, \eta_p^2 = 0.22$). In sequential structures, absolute error for the third target in a sequence was significantly lower than the fifth ($p < .05$). In sequences with a set size of six, there was no significant interaction effect. Overall, the observable trend remains that absolute error increases with increasing temporal order, regardless of structure.

The interaction effect of structure and order on relative error is displayed in Figure 8C. For sequences with a set size of three targets, there was no significant interaction between structure and order which could influence relative error. For sequences with a set size of four targets there was a significant main effect of structure ($F_{(2, 26)} = 3.64, p < .05, \eta_p^2 = 0.22$) where the average relative error was significantly lower in sequential structures compared to random ($p < .05$). For sequences with a set size of five targets, there was no significant interaction effect. For sequences with six targets, there was a significant main effect of structure ($F_{(1.359, 16.308)} = 4.23, p < .05, \eta_p^2 = 0.26$). Overall, in larger set sizes of four, five and six targets, relative error increases as temporal order increases. However, it can also be observed that the relative error was always highest in random structure, followed by spatial structure, then sequential structure with the lowest relative error.

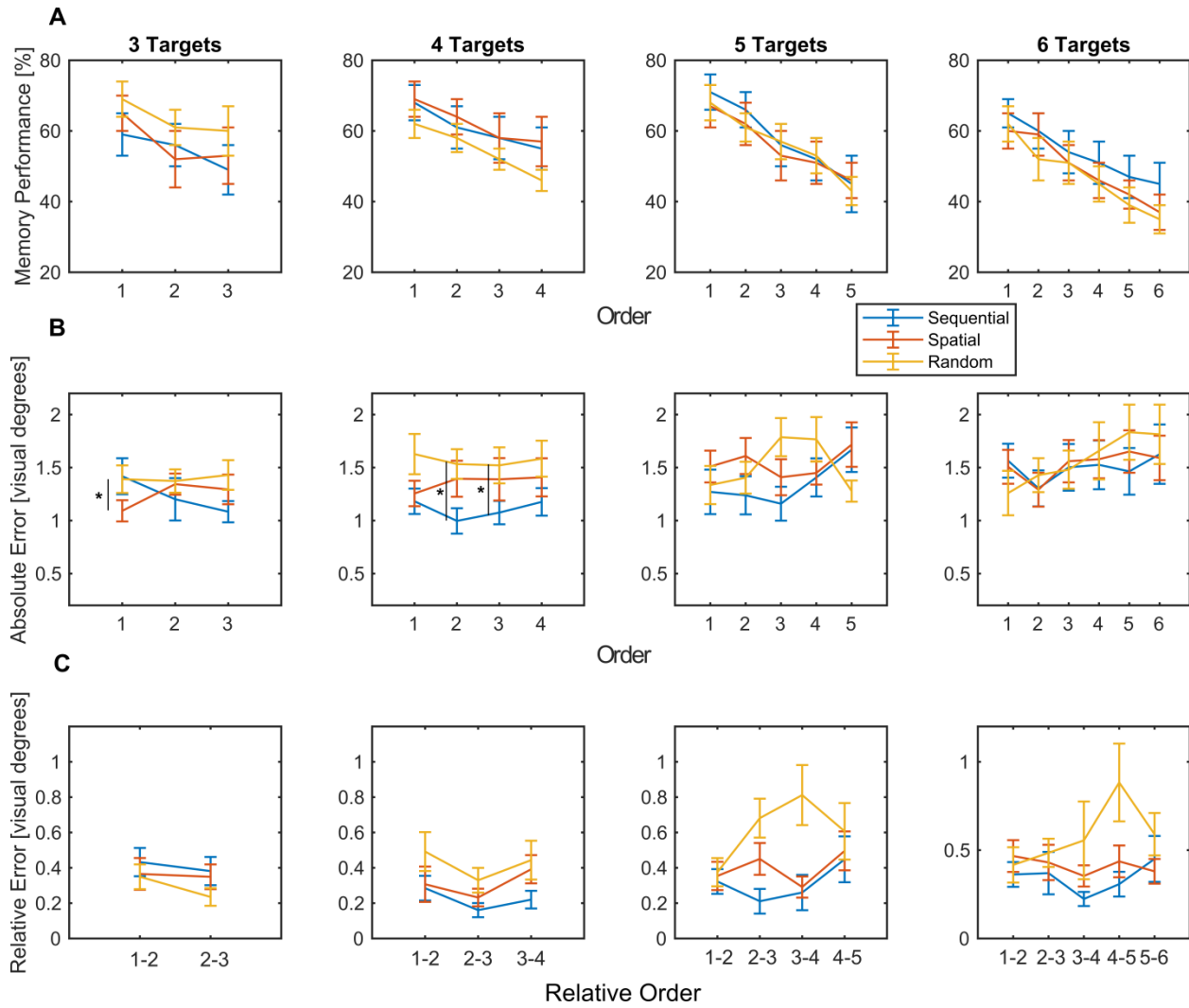


Figure 8. Interaction effects of structure and order on visual working memory. **(A)** Average memory performance \pm SEM as the percent of total trials that were correct. **(B)** Average absolute error \pm SEM in visual degrees. **(C)** Average relative error \pm SEM in visual degrees.

DISCUSSION

The aim of the present study was to investigate the influence of spatial and temporal information on performance in a memory-guided sequential saccade task. We measured VWM in three different ways: memory performance (percent of trials where all spatial locations were recalled correctly, in the order they were originally presented), absolute error (Euclidean distance between the actual target location and the remembered location) and relative error (the difference in absolute error between two eye movements). The latter was used to show the remaining error after accounting for any accumulation effects. Our results demonstrate that overall, visual working memory capacity varied based on the structure of a sequence and this, in turn, was dependent on additional factors such as set size and order. For example, in the absence of spatiotemporal cues (i.e., in the random condition) smaller set size (Figure 7A) and early temporal order (Figure 8A) became beneficial to increase VWM capacity.

Visual Working Memory Capacity

We measured VWM capacity limits by having a varying set size of three, four, five or six targets per sequence. Based on previous literature, it was expected that memory performance would be highest for set sizes of three and four, as they fall within the typical capacity range for humans (Awh et al., 2014; Ester et al., 2014; Fukuda, Awh, & Vogel, 2010; Mathy & Feldman, 2012). Our results showed that there was a significant effect of set size on all three measures of visual working memory: memory performance, absolute error, and relative error. As expected, memory performance was highest for a set size of three targets, then decreased as the set size of a sequence increased to four, five and six targets. However, performance did not completely drop to zero above a set size of three or four, as the discrete model of VWM would suggest. Flexible resource models appear to account for this because increasing set size, there is an associated

increase in cognitive load (Alvarez & Cavanagh, 2004; Haladjian & Mathy, 2015; van Moorselaar, Theeuwes, & Olivers, 2014), impeding but not obliterating target memory, saccade accuracy, and precision.

Influence of Structure

Memory performance was used as a more cognitive measure in this experiment since the motor precision of the remembered locations was not the focus. The recalled location was considered correct as long as it was not more than half the distance to the next target location (2.5° in this setup). Based on the previous literature (Bor et al., 2003), we expected that target sequences with a more regular structure would benefit memory performance, i.e., sequential > spatial > random. However, we observed no significant difference in memory performance based on the structure of the sequence. This might have been because overall, the performance was relatively poor, i.e., perhaps the task was too cognitively taxing. Alternatively, it could be that this performance measure was not sensitive enough to account for the magnitude of target selection errors and/or motor errors. This was accounted for in the following measure.

Absolute error values were analyzed for each target to see how precise and accurate the saccade endpoints to remembered target locations were, in comparison to the actual target locations. Even when the entire sequence was recalled correctly, we wanted to see if there is a performance correlate that could show underlying task difficulty that would not otherwise be seen in a purely digital right/wrong view. Our results showed a significant main effect of structure on the absolute error. The absolute error was lowest when the structure was sequential, followed by spatial only, then highest when the structure was random. This shows that eye movements were more accurate and precise when the targets were presented sequentially in a contiguous spatial

path. In random sequences, as the spatial and temporal structures were not present, there was an increase in the absolute error.

Relative error values were analyzed to determine whether these influences could still be detected when one removes the effect of accumulated error across successive eye movements. Our results again showed a significant effect of structure on the relative error, i.e., the relative error was lowest in sequential structures, followed by spatial then random structures. Thus, having contiguous spatial and temporal information helped to reduce the accumulation of error both across and within individual saccades. These results taken together, indicate a dichotomy of sorts when it comes to cognitive and motor errors, with motor errors being more affected by spatiotemporal information.

Previous studies have shown that spatial locations in working memory can be coded configurationally, using allocentric frames of reference (Avons, 2007; Avons & Oswald, 2008; Treisman & Zhang, 2006; Zhou, Zhang, Ding, Shui, & Shen, 2016). This would provide a benefit in both our sequential and spatial tasks. In addition, in the sequential task the order is likely easier to remember, and each saccade provides a cue to the location of the next target. Thus, when stimuli had a sequential structure in this experiment, both configurational representation and order likely helped make eye movements more accurate and precise, while reducing the chance of very large errors.

Influence of Presentation Order

A requirement of the task in this experiment is to recall the location of targets in the order they were presented, therefore, we were able to analyze the effect of presentation order on memory performance, absolute error, and relative error. It is common in serial recall tasks to see primacy and recency – primacy occurring when VWM is stronger for items closest in time to execution or

recall (Baddeley & Hitch, 1974; Boduroglu & Shah, 2017; S. Chen, Swartz, & Terrace, 1997; Mirpour, Bolandnazar, & Bisley, 2019). Alternatively, a recency effect can occur when memory representations deteriorate with time, sometimes referred to as the serial position effect (Carpenter, Baud-Bovy, Georgopoulos, & Pellizzer, 2018; De Lillo et al., 2016).

Our results showed a significant effect of the order on memory performance in sequences of all four possible set sizes. The performance was highest for the first target presented in the sequence, then gradually decreased for targets that were presented later in the sequence. In terms of absolute error, order only had a significant effect if sequences had a set size of five or more. The absolute error increased as the target was presented later in the sequence, which could also be due to a degradation of the memory representation over time. However, there was no significant effect of the order on the relative error which suggests the main influence was on errors accumulated across saccades. This suggests that the main degradation in memory did not occur during encoding, but rather during the recall/motor execution phase of the task.

Interaction between Structure and Set Size, Structure and Order

The influences of stimulus structure, set size, and order of presentation on memory recall and motor sequence planning have been studied previously, so perhaps the most novel contribution of the current study was the opportunity to study the quantitative interactions between these factors. There was a significant interaction between structure and set size for memory performance where the set size of a sequence determined performance in random structure sequences. In random structure sequences, having a smaller set size resulted in better memory performance. Interestingly, the interaction is seen only in random structure sequences, which lack both spatial and temporal structure, making it more difficult to remember. When the sequence lacks a contiguous spatial path and the order of target presentation does not follow the minimum step-route, it could be more

difficult to create a mental image of the sequence (Bergmann, Daselaar, Fernández, & Kessels, 2016; De Lillo et al., 2016), however, when the random sequence only has three targets, it is within typical VWM capacity that the loss of spatiotemporal information doesn't hinder one's ability to remember that sequence. For absolute error, there was no significant interaction between structure and set size, but there are simple effects where smaller set sizes have a lower average absolute error when the structure is spatial or random. In sequential structures, there was no difference in absolute error based on the set size. This could be due to the sequential structure being easy enough to remember that the set size of the sequence didn't matter. For relative error, there was no significant interaction.

The interaction between structure and order was less consistent. In terms of memory performance, there was a significant interaction of structure and order on memory performance in three target sequences. When the target was presented later in the sequence, the performance dropped. For absolute error, there was a significant interaction between structure and order in set sizes of three and five targets. The absolute error increased with targets presented later in the sequence the most for sequences with random structure. For relative error, there were no significant interaction effects, so again, this may have been an accumulative effect. Collins (2010) conducted a study in which it was also found that errors increased as the number of targets increased. The author concludes that this trend is not strictly due to the increased load of larger set sizes on memory, but that each memory-guided saccade depends on a self-motion execution of the movement which can cause small discrepancies during the actual movement that compound with each successive movement. This is a possible explanation for why the accumulation of error can be seen with successive targets, regardless of the set size.

Another explanation could also relate to the complexity of the sequences (Eng, Chen, & Jiang, 2005). By varying the spatial and temporal structure, the complexity of the sequence also varies. Sequences that had spatiotemporal structures were less complex in comparison to spatial and random structures. Random structures had the most complexity, therefore, errors were low for the early targets but as more targets were presented, the complexity increased which resulted in larger eye movement errors. In a study conducted by Boduroglu & Shah (2017), participants were required to use a mouse to point to remembered target locations in sequences of varying set sizes. Their results show that pointing errors were the lowest for targets that were presented first in the sequence, followed by increases in error, until there was a drop again for the targets presented last. This showed a primacy and recency effect that has also been observed in other studies (Berry, Waterman, Baddeley, Hitch, & Allen, 2018; Farrand, Parmentier, & Jones, 2001; Martin et al., 2017). Similarly, in a study conducted by Kemps (1999), three different structures were used for presenting sequences in a Corsi block-tapping task. Sequences with the least complexity were presented in a 3x3 matrix, a semi-structured condition had the sequences of blocks appear within a 5x5 matrix in random positions, and the most complex sequence type did not appear within any matrix structure. The author found that recall performance was highest in sequences that had the least complexity. Therefore, the complexity of the sequence could be accounting for the recruitment of additional cues when necessary to increase VWM capacity.

Implications for Models of VWM and Chunking

VWM capacity has been studied for a long time but there is still an ongoing debate about the mechanism of VWM and what exactly its capacity can be. As our task required participants to recall the entire sequence of targets to be correct, we were able to see that people could recall sequences of five and six targets which are outside of the typical three to four-item limits proposed

by slot-based models of VWM (Zhang & Luck, 2008). These higher limits were not just an anomaly reached by one person, they were observed across all participants. Our results show that absolute and relative errors increased with larger set sizes, which could represent the allocation of fewer resources as the set size increased, as described in resource models of VWM (Paul M. Bays & Husain, 2008). We also see in our results that VWM limits depend on the structure of the sequence. Significant interaction results show us that VWM performance and errors were influenced by the interaction between structure and set size as well as structure and order. When sequences lacked spatiotemporal structure, they became more complex, in which case it could be beneficial to recruit additional cues if available, to help increase capacity.

These interaction results can provide more information on how participants could be using chunking to boost their memory capacity. Chunking of memory involves the grouping of information together in a meaningful way to reduce the amount of encoding required or increase memory capacity. Although it is well known that the brain “chunks” information, the way it does so and when it occurs is not very clear (Mathy & Feldman, 2012). Previous studies have shown that visual information can also be chunked (Brady & Tenenbaum, 2013). If visual information can also be chunked, it is important to account for this when attempting to quantify VWM capacity limits.

The principles of grouping or Gestalt laws of grouping are used to explain how humans have a tendency to perceive patterns and group together information based on certain features such as proximity, continuity, similarity and common colour or movement (Duncan, 1984; Treisman, 1982). Principles of grouping could be used as a mechanism for chunking information. VWM capacity has been shown to improve when stimuli can be organized according to principles of grouping (De Lillo et al., 2016; Magen & Berger-Mandelbaum, 2018; Woodman, Vecera, & Luck,

2003; Xu & Chun, 2006). In our task, sequential structure follows a contiguous spatial path that can be described as having continuity and the targets themselves are also in close proximity to each other. It can be expected that the information in sequential structures can be easily chunked compared to those in spatial or random sequences.

Possible Neural Mechanisms

Although we did not directly measure neural activity in this experiment, one can speculate with reasonable confidence about some of the areas involved based on past literature. The generation of intentional saccades are usually attributed to three frontal lobe areas of the brain: the frontal eye field (FEF), supplementary eye field (SEF) and dorsolateral prefrontal cortex (dlPFC) (Baumann, Frank, Rutschmann, & Greenlee, 2007; René M Müri, Rivaud, Timsit, Cornu, & Pierrot-Deseilligny, 1994; Charles Pierrot-Deseilligny et al., 2004; Reuter et al., 2016). Further, these areas are implicated in a VWM network that also includes the lateral intraparietal cortex (LIP) and several subcortical structures (Medendorp, Goltz, Vilis, & Crawford, 2003). For example, FEF is involved in transforming retrospective memory signals into prospective saccade plans (Sajad, Sadeh, Yan, Wang, & Crawford, 2016), SEF is involved in controlling the sequence of saccades (René M Müri et al., 1994) and dlPFC is involved in maintaining the spatial location of targets in working memory (Baumann et al., 2007; Tanaka, Dessing, Malik, Prime, & Crawford, 2014). Further, tasks that involve some kind of allocentric structure (as in our sequential and spatial tasks) likely recruit neural resources associated with the ventral stream of vision (Y. Chen & Crawford, 2017; Goodale & Humphrey, 1998; Goodale & Milner, 1992; Schenk & McIntosh, 2010) and possibly medial parietal cortex (precuneus) (Y. Chen & Crawford, 2017). One can speculate that the interactions between these areas become extremely complex when multiple

factors – set size, spatiotemporal structure, order - are involved in programming saccade sequences.

Several studies have aimed at neural correlates more specifically related to the current study. For example, Bor et al. (2003) conducted an event-related functional magnetic resonance imaging (fMRI) study to compare cortical activation during saccade sequences that had structured path types versus unstructured path types. It was found that in structured sequences, there was significantly higher activation in the lateral prefrontal cortex, inferior parietal lobe and fusiform gyrus of both hemispheres and that this was associated with the chunking of information involved in remembering structured sequences. Another fMRI study of memory-guided saccades showed that short memory delays resulted in cortical activation (specifically bilateral posterior parietal cortex and a region extending from the cuneus to the occipitoparietal region) that was absent during longer delays (Baumann et al., 2007). This could explain why there was a decrease in memory performance and an increase in errors with increasing set sizes and presentation order. Increased set size results in an extended trial duration as more targets need to be presented in a sequential manner. Finally, there is evidence in the literature to show that movement sequences are organized in a hierarchical fashion, into motor chunks (Lashley, 1951), similar to the parallel programming of multiple saccades described by Becker & Jürgens (1979). This would allow for potentially faster and more accurate execution (Rosenbaum, Kenny, & Derr, 1983). If movement sequences are also organized into motor chunks, this would explain the lower motor errors in sequential structures found in our results.

Conclusion

The results of this study demonstrate that memory-guided saccade sequences are benefitted by the presence of spatiotemporal structure, but this also depends on the interaction of additional features such as the set size of a sequence and the presentation order of targets. Furthermore, the spatiotemporal structure seems to have more impact when the sequence has more complexity, such as a larger set size. We also observed that the influence of structure depended on the way that performance was measured – memory performance, absolute error or relative error, suggesting that the motor outcomes may be more sensitive to the spatiotemporal structure. Overall, this suggests that the use of VWM to guide saccade sequences is sensitive to interactions between multiple features, spatial and temporal, which can impact the way the brain uses strategies such as chunking to remember visual information for the guidance of action.

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CHAPTER III: GENERAL DISCUSSION

Summary of Results

The aim of the current study was to determine how memory-guided saccade sequences are affected by spatiotemporal structure, set size, order and their interactions. Three dependent variables were used to measure the recall performance of individuals in this task. Memory performance was the measure of how many trials were correctly and completely recalled. The absolute error was the Euclidean distance between the target location and the saccade endpoint. Relative error was the measure of how much error accumulated between saccades. All three measures provided results that helped to better understand the mechanism of memory-guided saccades in a complex cognitive task.

Structure

Previous studies have shown that our ability to increase short-term memory capacity, whether it be through chunking or other mechanisms, greatly depends on the visual and temporal information available (Cowan 2000). Therefore, the spatial and temporal presentation of targets was manipulated in three ways to form three conditions for structure: sequential, spatial and random. For sequential structure, the targets were presented in a contiguous spatial path, and the order of presentation followed the minimum-step route. For spatial structure, the targets formed a contiguous spatial path, but the order of presentation was randomized. Finally, for random structure, the targets were presented in random structure and random order. It was expected that sequential structure would be the condition that allowed for the easiest recall of targets because previous studies have shown that spatial and temporal structure is beneficial for VWM (Bhutani, Sengupta, Basu, Prabhu, & Murthy, 2017; De Lillo et al., 2016; Fagot & De Lillo, 2011; Gavornik & Bear, 2014). The results for memory performance however, showed no significant difference

between the three types of structures. The average performance for all three structures was low at approximately 40%, which indicates that the task itself was difficult. The difficulty of the task could have limited the ability for people to use strategy. The results for absolute error and relative error, however, do follow the predicted trend of the lowest errors in the sequential structure, followed by spatial then random structure with the highest errors. Saccade accuracy has been shown to increase with target predictability (Coëffé & O'regan, 1987; Marino & Munoz, 2009), perhaps higher target predictability for the sequential and spatial structure is attributing to lower errors as they maintain a regular spatial structure as opposed to random.

One proposed reason for the beneficial effects of structured sequences was that structured sequences have shorter path lengths between targets (Parmentier et al., 2006). When each consecutive target always appeared in the next row, column or diagonal axis, there was much less distance between the items compared to unstructured sequences where consecutive targets could appear anywhere. This would also hold true for the sequential structure condition in our study, as targets are presented in an order which follows the minimum-step route. Parmentier et al. (2006) proposed that having this decreased distance between targets facilitates easier recall of the sequence. However, De Lillo et al. (2016) conducted a study to test this idea of path length as the key factor for better performance in structured path types. They hypothesized that if path length was the distinguishing factor, sequences with unstructured path type and short path lengths should have better recall than sequences with structured path type and long path lengths. Their results showed that there was still significantly higher recall for structured path types regardless of their path length. The investigators concluded that rather than path length, it may be the ability of people to build better mental images of structured sequences that contributes to their easier recall.

Set Size

The sequences in this experiment had varying set sizes of three to six targets to determine the extent of possible capacity limits for participants in this task. The results show a significant effect of set size for memory performance and absolute error. For memory performance, the results reveal memory performance decreasing with larger set sizes. Therefore, the more targets that had to be recalled, the more difficult it was to correctly recall the entire sequence. Similarly, for absolute error, the larger the set size the larger the error. This is in line with the large body of literature which has shown that human cognition has strong capacity limits, constrained by set size. As the results of the current study show errors increasing with larger set sizes, there is a resulting decrease in accuracy and precision, which fits well with resource models of VWM capacity (P. M. Bays, Catalao, & Husain, 2009).

Resource models of VWM limits propose that the precision of VWM decreases with more information to maintain (Paul M. Bays, 2018b; Huang, 2010; Ramaty & Luria, 2018). The results of this study show that participants were able to remember sequences that had more than the typical three to four-item capacity proposed by the slot-based model of VWM (Adam et al., 2017; Barton et al., 2009; Ester et al., 2014; Fukuda et al., 2010; Zhang & Luck, 2008). However, there is a limitation in the understanding of these results because it is not possible to know if participants have simply correctly guessed the later targets in the sequence. Vogel and Machizawa (2004), attempted to account for guessing by having a measure of memory capacity where they would subtract the false alarm rate from the correct hit rate and multiplied it by the number of items. Perhaps in a future experiment, implementing a method to correct for guessing may help clarify the capacity limits.

Order

A temporal feature that was examined in this experiment was the presentation order. Since the targets were presented sequentially on screen, there was a possibility for memory performance to vary over time. Since there were four different set sizes in this study, the presentation order was analyzed separately for each set size group. Overall, the results showed a significant influence of presentation order on memory performance in sequences of all set sizes. Whether the sequence had three, four, five or six targets, memory performance was always highest for the first targets in a sequence and dropped with each successive target, which is primacy. This result agrees with previous findings that have found a serial position effect in serial recall tasks similar to ours (Carpenter et al., 2018; Farrand et al., 2001; Gibson et al., 2014; Gmeindl, Walsh, & Courtney, 2011).

The primacy effects observed in this study could be due to a variety of factors. According to Wang et al. (2019), there could be a reinforcement of the early targets within a sequence, consistent with nested sequence encoding. The results of their study show that participants discover the most compact description of a sequence of saccade targets, then use a nested rules method to compress the sequence in memory and predict the next items. This nested method would be helping to reinforce the earlier targets within a sequence up to a point, however, presumably there will be a point where resources may become limited and negatively impact the memory of later targets.

Another reason why primacy was prevalent in our data was that there could have been an accumulation of error when there were more saccades to be performed. In a recent study conducted by Peters et al. (2018) to examine how well multiple items can be reported from working memory.

Their behavioural study involved the presentation of a memory array with two, four, six, or eight Gabor patches that were randomly oriented. After a delay period, participants were given a random probe location and using the mouse, they were required to adjust the orientation of the probe to the orientation of the target that was presented earlier at the same location. This was repeated until they reported the orientations of all the Gabor patches they were presented with at the beginning of the trial. The errors were computed as the angular difference between the participant's response and the target's presented orientation. They also calculated precision values as the inverse standard deviation of the error distribution. Their results showed that precision decreased with increasing set size. Importantly, they also found that precision was significantly reduced with each successive report. Our findings are also consistent with the results reported by Peters et al., (2018).

Interactions

In addition to the individual influence of these spatial and temporal factors, our results also showed significant interactions between structure and set size, and structure and order. There was a significant main interaction between structure and set size that influenced memory performance, revealing a benefit of smaller set sizes when the structure of a sequence was random. The interaction was not observed for measures of absolute or relative error. It is well known that there are capacity limits for VWM, whether it is a discrete number of items or a decreased amount of resources, it is evident that larger set sizes are more difficult to remember (Adam et al., 2017; P. M. Bays et al., 2009). It is also known that items with familiar and regular structures are easier to remember (Bor et al., 2003). When the results of this experiment show the lowest memory performance for the six target sequences with random structure, it could be because these sequences lack spatial and temporal structure as well as having a set size that reaches participants'

VWM capacity limits. When the sequence only has three or four targets, this could be within the capacity of VWM such that participants are still able to extract spatial and temporal information well enough to perform the task correctly. When the structure was sequential or spatial however, there was enough spatiotemporal structure present in the stimuli that there was no cost to having larger set sizes.

There was also a significant interaction between structure and order in three target sequences that influenced memory performance. For absolute error, there was a significant interaction effect between structure and order in three target sequences where the absolute error was lower for spatial structures compared to random structure, starting at the first target. The interaction was also significant in five target sequences. The interaction was not significant for relative error measures. It was expected for this interaction that with the removal of spatial and temporal structure, the effect of presentation order should worsen performance and increase error. However, our results only show a significant interaction effect between these two features in very few situations and in the opposite direction to that which was expected. For example, there was a significant interaction effect of structure and order in three target sequences which influenced memory performance. Contrary to what was expected random structure sequences have the highest memory performance and there is no steep decline in performance with increasing presentation order. Overall, the results show the expected effect of order that targets presented later in the sequence would have lower memory performance and higher errors, regardless of what the spatiotemporal structure was. Whether or not there was a contiguous spatial path or minimum-step route presentation order – the later the target was presented, the poorer the task performance.

In a study conducted by Parmentier et al. (2006) the aim was to understand how spatial and temporal grouping may influence the organization of information in visuo-spatial serial memory.

Their task involved the presentation of a series of nine black dots in various spatiotemporal configurations. The control condition involved the presentation of targets evenly spread out in space with no spatial clustering. In the converging condition, dots in the same spatial cluster followed each other temporally and in the diverging condition, dots following each other temporally were from a different spatial cluster. After the dots were presented, participants had to use a mouse to click on the targets in the order they appeared. The results showed when compared with the control, the performance was better in the converging condition and weaker in the diverging condition. In terms of errors, they were classified as within-group if the incorrect item was in the same spatial cluster or they were classified as between-group error if the incorrect item was from a different spatial cluster. The results showed within-group errors were more common for the converging condition and between-group errors were more common for diverging conditions. Overall, it shows that there is a hierarchical organization that prefers spatial grouping before temporal grouping. The results of our study did not show that performance was significantly different between the three structures however, absolute error and relative errors were smallest in sequential structure, followed by an increase in error for spatial structure and the largest errors in random structure. This follows the same hierarchy as Parmentier and colleagues since the structures with contiguous spatial paths had lower errors compared to those that were random.

In a study conducted by Woodman & Vecera (2011) the aim was to identify how humans access information held in working memory. The task was for participants to sequentially report multiple features from three objects stored in VWM. On each trial participants were shown three rectangles that were red, blue or green in colour, they could be thick or thin rectangles, and they could be tilted 45° to the right or left. After a mask, participants were asked to recall four features from the memory array as a series of four questions that required a keyboard response. From their

results, they were able to see that selectively accessing one item from VWM led to a decrease in accuracy when reporting the subsequent items. This supports the idea that accessing an item from VWM occurs at a cost to the other items that may be maintained. This idea would also provide an explanation as to why we see memory performance decreasing as targets were presented later in a sequence – because the selection of the first target in a sequence results in a detrimental effect on the subsequent targets that need to be recalled.

With the results of the interaction analyses from our current study, it is difficult to make a precise conclusion about how multiple factors influence VWM. There are differences in how each factor influences our three measures of VWM: memory performance, absolute error, and relative error. The data seem to show that there are potential differences in cognitive performance and motor errors as we never saw the same trend across all three measures of VWM. This indicates that further research must be conducted on how the brain processes complex stimuli such as those in our experiment, to understand strategies that may be used to manipulate VWM load.

The term chunking has been used to generally describe our ability to group information together in a useful way to reduce memory load and increase capacity (Khader, Ranganath, Seemüller, & Rösler, 2007; Portrat et al., 2016). In visual working memory, it is not quite clear what the mechanisms of chunking may be. For visual stimuli, it is evident from our results and several other past studies that spatiotemporal structure is important for how information is represented in VWM. Spatiotemporal structure may be beneficial because it could be conducive to perceptual grouping. The principles of grouping or Gestalt laws of grouping are used to explain how humans have a tendency to perceive patterns and group together information based on certain features such as proximity, continuity, similarity and common colour or movement (Duncan, 1984; Treisman, 1982). Principles of grouping could be used as a mechanism for chunking information.

VWM capacity has been shown to improve when stimuli can be organized according to principles of grouping (De Lillo et al., 2016; Magen & Berger-Mandelbaum, 2018; Woodman et al., 2003; Xu & Chun, 2006). In our task, sequential structure follows a contiguous spatial path that can be described as having continuity and the targets themselves are also in close proximity to each other. It can be expected that the information in sequential structures can be easily chunked compared to those in spatial or random sequences. Therefore, future explorations may benefit from examining the capacity of VWM in terms of chunks as a unit of memory rather than individual targets.

There is some evidence in the literature that suggests there is a shared representation for working memory and mental imagery in early visual cortex (Albers, Kok, Toni, Dijkerman, & De Lange, 2013; Keogh & Pearson, 2011). In a study conducted by Keogh & Pearson (2011), results indicated that performance in VWM could be predicted by the strength of mental imagery. They used a task in which participants were given a sequential display of two different Gabor patches, followed by a cue of which one to remember, after a retention interval they had to match the orientation of a randomly oriented Gabor patch to the one that they had to remember. In addition to a task where they tested participants' skills in mental imagery, they were able to conclude that participants who were better at mental imagery also performed better in the VWM task. This is further corroborated by an fMRI study conducted by (Albers et al., 2013) where they were able to decode stimulus identity from neural activity patterns in early visual cortex. They also mention the neural activity similar to bottom-up stimulation, which indicates mental images are similar to perception. Therefore, if the spatiotemporal structure provides information for ease of perceptual grouping, this could help produce better mental images which in turn decreases VWM load.

Limitations

One of the limitations in this study arises from the requirement that participants had to recall the target locations in the exact order that they were presented. By having this constraint, we limited our ability to detect additional strategies that people may have been using. For example, in spatial only sequences, since temporal order is randomized, participants may have had a strong spatial memory for the final sequence, but had difficulty remembering the order. In that case, it is not possible to see such trends in our results because of the requirement to only recall targets in the order they were presented.

Another factor to consider when interpreting the results of this study is that there were still absolute and relative errors despite the presence of placeholder circles that were continuously present on the screen. The placeholder circles provided a constant allocentric cue as to where the targets will appear and where saccades must be directed, which should have allowed for very accurate saccade endpoints. However, there may be other factors that contributed to the presence of errors despite obvious allocentric cues. According to a study by Thaler and colleagues (2013), the best kind of fixation target is one that is a combination of a bullseye and crosshair. This combination resulted in low dispersion and microsaccade rate. Since our placeholders were hollow rings without crosshairs, it could have attributed to participants having dispersed saccade endpoints that resulted in the varying levels of absolute and relative errors. McSorley and colleagues (2019) showed that the execution of saccades to isolated targets was more difficult when they were in the presence of other targets. Saccade landing position control was more variable with errors getting worse when there was more information available. In our study, when participants are executing their saccades to the remembered target locations, there is an abundance of information available in the form of the placeholder rings, spatiotemporal structure, and information being held in VWM

regarding the targets that have already been located. The target location information from multiple sources along with the limited resources as set sizes increased could have attributed to interference that caused higher errors overall and especially in higher set size sequences with random structure.

Future Directions

The results of this study show that spatiotemporal structure is beneficial for VWM. It would be interesting for future studies to determine which areas of the brain are affected by the spatiotemporal structure of visual stimuli. This paradigm could be modified to test for additional features and behaviors or adapted into a neuroimaging study.

This experiment can be expanded in the future to also test for effector specificity. An effector is any type of body part that the brain selects to perform an action (Medendorp, Goltz, Crawford, & Vilis, 2005). If participants were asked to complete the same saccade task but with the addition of another experimental session or block where they were required to use a different effector such as reaching to the target, the accuracy of recall could be compared for different effectors. Especially for goal-directed actions, coordination of eye and hand movements are of utmost importance to complete any task. To make a movement such as pressing an elevator button or reaching for a coffee, the brain has to maintain spatial information in working memory and for a motor plan in order to execute the movement (Cappadocia, Chen, Blohm, & Crawford, 2016; Medendorp, Buchholz, Van Der Werf, & Leoné, 2011). For example, in a previous study (Hagler, Riecke, & Sereno, 2007), fMRI was used in a delayed visuomotor response task to examine whether effector-specific cortical areas could be found. While fixating at the centre of the display target would be briefly presented in the periphery. After a delay period, participants were cued to indicate whether they should saccade or point to the remembered target location. The researchers found that activation patterns were similar for both effectors, with a lot of overlap in the posterior parietal cortex (PPC) and superior frontal cortex (SFC). Specific to pointing, they found some

areas in the left motor and somatosensory cortices contralateral to the pointing hand. However, they conclude that future studies are still required to clarify the roles of PPC and SFC, as they have a lot of overlap.

This experimental design could also be used for brain imaging studies in the future. There are a large number of studies that use fMRI and transcranial magnetic stimulation (TMS) to investigate the involvement of brain areas specifically involved in memory-guided saccade tasks and visual working memory (Bor et al., 2003; Heuer, Schubö, & Crawford, 2016; Rademaker et al., 2017)). Similar studies can also be designed to investigate conditions that show irregular or impaired saccades. For example, it has been shown that schizophrenia patients, ultra-high-risk patients, and siblings of schizophrenia patients have significantly higher errors in memory-guided saccades compared to control populations (Caldani et al., 2016).

Since it is rarely the case that humans only view simple dot stimuli in our environment, it would also be interesting to use real-world stimuli such as scenes or video clips. Visual working memory is important for real-world situations that involve spatial navigation and object identification such as driving a vehicle or playing sports (De Lillo et al., 2016; Schmidt et al., 2007). A future experiment could present a video of an intersection in the viewpoint of a driver, then ask participants to remember sequences of events in their surroundings.

Conclusions

This research has important implications in neuroscience because saccadic eye movements are controlled by the oculomotor system in such a way that they are representative of underlying neural mechanisms (Abrams et al., 1989; Robinson, 1981). This type of behavioural research is important for further studying the functions and mechanisms of visual working memory as well as

how it is influenced by different stimuli in our environment. The field of VWM research also needs further exploration to better understand the mechanism of VWM storage and how information is retrieved from VWM. Neuroimaging studies can then be influential in elucidating the differential activation patterns of brain regions that are involved in various stages of human actions such as memory-guided sequential saccades and their relationship with visual working memory. In addition, behavioural studies using similar paradigms to the current study which characterize properties of saccadic eye movements can help to further design diagnostic tools in patients with neurological disorders such as schizophrenia, stroke, and Parkinson's disease.

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