

ANGLIA RUSKIN UNIVERSITY

VISUAL WORKING MEMORY AND
SACCADIC EYE MOVEMENTS

KEISHA JOY NOTICE

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To my family and friends who have stuck with me throughout this journey; I couldn't have done it without you.

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ABSTRACT

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DOCTOR OF PHILOSOPHY

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Saccadic eye movements, produced by the oculomotor system, are used to bring salient information in line with the high resolution fovea. It has been suggested that visual working memory, the cognitive system that temporarily stores and manipulates visual information (Baddeley & Hitch, 1974), is utilised by the oculomotor system in order to maintain saccade programmes across temporal delays (Belopolsky & Theeuwes, 2011). Saccadic eye movements have been found to deviate away from information stored in visual working memory (Theeuwes and colleagues, 2005, 2006). Saccadic deviation away from presented visual stimuli has been associated with top-down suppression (McSorley, Haggard, & Walker, 2006). This thesis examines the extent to which saccade trajectories are influenced by information held in visual working memory. Through a series of experiments behavioural memory data and saccade trajectory data were explored and evidence for visual working memory-oculomotor interaction was found. Other findings included specific interactions with the oculomotor system for the dorsal and ventral pathways as well as evidence for both bottom-up and top-down processing. Evidence of further oculomotor interaction with manual cognitive mechanisms was also illustrated, suggesting that visual working memory does not uniquely interact with the oculomotor system to preserve saccade programmes. The clinical and theoretical implications of this thesis are explored. It is proposed that the oculomotor system may interact with a variety of sensory systems to inform accurate and efficient visual processing.

Key words: Eye movements, saccades, visual working memory.

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Abbreviations

VWM	visual working memory
SC	superior colliculus
VSWM	visuo-spatial working memory
NS-VWM	non-spatial working memory
VF	visual field
LIP	lateral intraparietal area
LGN	lateral geniculate nucleus
M- Pathway	magnocellular pathway
P- Pathway	parvocellular pathway
VLPFC	ventrolateral prefrontal cortex
DLPFC	dorsolateral prefrontal cortex
FEF	frontal eye fields
SEF	supplementary eye fields
CB	cerebellum
TH	thalamus
IPS	intraparietal sulcus
CN	caudate nucleus
GPe	globus pallidus externa
STN	subthalamic nucleus
SNr	substantia nigra pars reticulata
SCi	superior colliculus intermediate layer
SCs	superior colliculus superficial layer
RF	reticular formation

PEF	parietal eye fields
PPRF	paramedian pontine reticular formation
IOR	inhibition of return
PCS	precentral sulcus
GPI	globus pallidus interna
SNr	substantia nigra pars compacta
VIP	ventrolateral prefrontal cortex

Copyright Declaration

I, Keisha Notice, hereby certify that this thesis has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

Chapter 1

Introduction

This thesis is concerned with the nature, and the extent, of visual working memory (VWM) interaction with the oculomotor system. VWM is a theoretical cognitive concept used to describe the temporary storage, maintenance, and manipulation of visual information (Baddeley & Hitch, 1974; Baddeley, 2000; Baddeley, 2002). Previous research has suggested that saccades (the rapid eye movements between fixation points) may deviate away from information stored in VWM (Theeuwes and colleagues, 2005, 2006). Saccade deviation has been associated with inhibition in a topographical map in the superior colliculus (SC; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994; Tipper, Howard, & Houghton, 2000). Furthermore, it has been proposed that the VWM system is utilised in order to maintain saccade preparation in the oculomotor system and that VWM underpins oculomotor action (Belopolsky & Theeuwes, 2011). It has also been suggested that models of saccade deviation should incorporate the VWM system (Theeuwes, Belopolsky, & Olivers, 2009). This thesis attempts to further clarify VWM interaction with the oculomotor system.

Chapter 2 of this thesis contains the literature review and informs background knowledge of areas including the oculomotor system and the VWM system. It also provides information on studies conducted in the area of interest and highlights the specific gaps in knowledge that this thesis attempts to address. Chapter 3 outlines the eye tracking methods employed to collect saccade trajectory data throughout the investigations. In order to accurately analyse saccade data throughout this thesis different exclusion criteria were assessed in chapter 3. Moreover, in this chapter, the measures used to quantify saccade characteristics are outlined.

VWM interaction with the oculomotor system has been disputed by König (2010) who has suggested that the active rehearsal of visual information is not necessary to induce saccade deviations away from distractor stimuli. König (2010) suggests that prolonged inhibition of neurons in the superior colliculus can also result in saccade deviation away from distractors. Thus, two explanations have been provided for saccade deviation away from distractor stimuli: 1, VWM facilitation of oculomotor inhibition (Belopolsky & Theeuwes, 2011) and 2, prolonged inhibition of collicular neurons (König, 2010).

The first two experimental chapters of this thesis explored the extent of VWM interaction with the oculomotor system. In the first experimental chapter (chapter 4), a dual-paradigm experiment is presented. This experiment explored how oculomotor inhibition is influenced by the concurrent running of a saccade and a VWM task. In doing so, the trajectories of saccades executed without the possibility of full VWM utilisation could be observed. It was hypothesised that if VWM is unnecessary during the facilitation of oculomotor inhibition, saccade trajectories across conditions in which VWM was 'available' and 'unavailable' would not differ. The results from this chapter highlighted a reduced degree of saccade deviation after the concurrent running of VWM and saccade tasks in comparison to a saccade-only task. In turn, this finding highlighted that although active rehearsal of information was not *required* for saccade deviation (in support of König, 2010); the VWM system was utilised to hold temporary memory representations to facilitate oculomotor inhibition (in support of Theeuwes and colleagues, 2005, 2006, 2009).

The second experimental chapter of this thesis (chapter 5) investigated the extent to which non-active processing in the VWM system influences the trajectories of saccades. For the purposes of this thesis, non-active processing in VWM is defined as the temporary storage of task-irrelevant information. By contrast, active processing is defined as the storage and rehearsal of task-relevant information. This chapter also attempted to understand if non-active, and active, processing in the VWM differentially influences the trajectories of saccades. In this chapter participants were required to complete two conditions: 1. a non-active rehearsal VWM condition, and 2. an rehearsal active VWM condition. The active rehearsal VWM condition required participants to state whether a test stimulus was the same as the previously presented distractor stimulus. During the non-active rehearsal VWM condition, participants were presented with a task-irrelevant distractor stimulus. The findings from this chapter highlighted the dissociable nature of non-active and active VWM-oculomotor interaction. Results illustrated that the facilitation of oculomotor inhibition during non-active employment of VWM can be observed. However, the degree of saccade trajectory deviation found during the active rehearsal VWM condition, compared to the non-active rehearsal VWM condition, was reduced after the presentation of task-relevant distractor stimuli in close proximity to saccade target stimuli. Moreover, shorter saccade latencies after the presentation of close proximity distractors were also observed.

Theeuwes and colleagues (2005, 2006), in contrast to the findings of chapter 5, found that when participants were required to remember the spatial locations of distractor stimuli, increased saccade deviation away from remembered locations could be observed. This result was in comparison to deviation observed after the presentation

of task-irrelevant stimuli. The findings from chapter 5 suggested that oculomotor interaction with the VWM system may be differentially affected depending on the type of information stored. Furthermore the findings suggested that saccade latency, as opposed to deviation, was facilitated by holding object information in VWM. Implications from this experiment were discussed in relation to top-down and bottom-up processing, and also with respect to the visual processing pathways.

VWM has been conceptually separated into two subsystems responsible for the processing of visuo-spatial working memory (VSWM) and non-spatial VWM (NS-VWM; Baddeley, 2002). These subsystems have been theorised to occur across two distinguished (though interacting) cortical processing pathways (the dorsal and the ventral processing pathways; D'Esposito et al., 1998; Ungerleider & Haxby, 1994; Ungerleider, Courtney, & Haxby, 1998). VSWM has been associated with processing along the dorsal pathway whilst NS-VWM has been associated with processing along the ventral pathway. Current research highlights oculomotor interaction with the VSWM subsystem (Theeuwes and colleagues, 2005, 2006). Common cortical networks sub-serving both the oculomotor system and VSWM are implicated to have linked behavioural outcomes associated with these systems (Theeuwes & Belopolsky, 2009). However as previously noted, NS-VWM (or the holding of object characteristics in VWM) is suggested, in chapter 5, to reduce the latencies of saccades. In turn, it was proposed that both VWM subsystems can be seen to interact with the oculomotor system and research should endeavour to identify NS-VWM interactions also.

Chapter 6 of this thesis explored oculomotor interaction with the VWM subsystems with a mind to better understand how the dorsal and ventral processing pathways

contribute to oculomotor action and to the described VWM-oculomotor interaction. The previous chapter had identified the possibility that different processing modalities resulted in saccade deviation via top-down or bottom-up processing. VWM facilitated prolonged inhibition had been evident in non-active rehearsal VWM conditions, a task characterised by processing along the dorsal pathway (Ro, 2008). It was hypothesised that dorsal pathway interactions with the oculomotor system were characterised by both bottom-up (as evident from the results of non-active rehearsal VWM interactions in chapter 5) and top-down (as evident from Theeuwes and colleagues [2005, 2006]) processing. In contrast it was hypothesised that, ventral pathway, NS-VWM interactions with the oculomotor system are characterised primarily by top-down influences (as evident from results presented in chapter 5).

Three conditions were presented to participants in the experiment in chapter 6; a non-active rehearsal VWM condition, a VSWM condition, and a NS-VWM condition. The non-active rehearsal VWM condition was the same as that presented in chapter 5. Similarly, the NS-VWM was the same as the active rehearsal VWM condition also presented in chapter 5; participants were required to state whether a presented task-relevant distractor stimulus was the same as a test stimulus displayed at the end of a trial. The VSWM condition, in contrast, required participants to state whether a test stimulus was presented in the same spatial location as the previously displayed task-relevant distractor stimulus.

Results from chapter 6 provided evidence of a dissociable oculomotor influence via dorsal and ventral processing pathways. Whereas similar saccade trajectory deviations were noted during the VSWM and non-active rehearsal VWM conditions, the NS-VWM

conditions did not present the same pattern of results. Moreover, VSWM and non-active rehearsal VWM conditions expressed saccade deviation away from presented distractors supporting a theory of both bottom-up and top-down processing during dorsal pathway interactions with the oculomotor system. In contrast, the NS-VWM condition produced reduced deviation for saccades after the presentation of close proximity distractors, and a propensity for improved saccade accuracy after the presentation of close proximity distractors for saccades directed to the upper visual field (VF). The upper VF has been associated with processing along the ventral pathway whilst the lower VF has been associated with processing along the dorsal pathway (Previc, 1990). These NS-VWM results indicate that top-down processing may facilitate saccade accuracy.

The results of these previous studies suggested that the VWM system does indeed interact with the oculomotor system in a variety of ways with a variety of measurable effects. VWM subsystems underpinned by the dorsal pathway appear to influence the trajectories of saccades via top-down and bottom-up processing. VWM subsystems underpinned by the ventral pathway appear to influence saccade accuracy and saccade latency but not, to a great extent, the deviations of saccades. In turn, NS-VWM was theorised to interact with the oculomotor system in a mainly top-down fashion. Moreover, NS-VWM oculomotor interaction did not appear to be as automatic as dorsal pathway interactions. This theory was specifically highlighted during the saccade accuracy results reported in chapter 6 indicating that increased accuracy was contingent on the VF of a saccade target.

In order to account for the theoretical and clinical implications of VWM facilitated oculomotor inhibition, chapter 7 was designed to explore the consequence of bottom-up and top-down VWM-oculomotor interaction. In chapter 7, two experiments were conducted. In the first experiment saccade characteristics were observed after the presentation of distractor stimuli either in a previously presented, or in a newly presented, spatial location. Non-active rehearsal VWM and NS-VWM were analysed in this experiment as representatives of conditions characterised primarily by bottom-up and top-down processing respectively. Oculomotor inhibition has been functionally and theoretically distinguished from attentional inhibition of return (IOR; Godijn & Theeuwes, 2004); a cognitive concept defining the propensity to inhibit previously attended to stimuli in favour of 'new' stimuli. Thus, in the first experiment of chapter 7, it was hypothesised that saccade characteristics during the non-active rehearsal VWM condition would be mainly attributable to saccadic IOR in comparison to saccades characteristics during the NS-VWM condition which would be mainly attributable to attentional IOR.

The results from the first experiment supported a dissociable oculomotor interaction relevant to bottom-up and top-down processing along the dorsal and ventral pathways. It was theorised that regions involved in visual attention, and found to interact with the ventral pathway, may result in NS-VWM interactions with the oculomotor system. For instance, the lateral intraparietal area (LIP) has been implicated in visuo-spatial attention (Powell & Goldberg, 2000), saccade deviation (Godijn & Theeuwes, 2004) and in shape selectivity (Serenio & Maunsell, 1998). This theory is supported by previous evidence of ventral pathway interaction with frontoparietal areas specialised in processing spatial attention to promote efficient

visual processing (Corbetta et al, 1998). This experiment suggested that if VWM was to be incorporated into models of saccade deviation, two processing pathways should be accounted for; a pathway along the LIP representing top-down input from both VSWM and NS-VWM memory subsystems, and an unconscious pathway between the dorsal pathway and the SC. Such a pathway specialised for the processing of unconscious information has been proposed by Ro (2008).

The second experiment of chapter 7 was designed to test the clinical implications of VWM-oculomotor interaction. VWM facilitation of saccade characteristics suggests that visual processing may be influenced by individual differences related to VWM capacity. For instance, the extent of neural activity has been found to be mediated somewhat by VWM capacity (Vogel & Machizawa, 2004). Thus, during visual processing and oculomotor action, the ability to utilise VWM efficiently may influence saccade trajectories. Non-active rehearsal VWM, and NS-VWM, conditions were again analysed. Participants were ranked on VWM performance in the NS-VWM task and separated into two groups: a low VWM performance group and a high VWM performance group.

The second experiment presented in chapter 7 highlighted differential visual processing for high and low performing VWM participants. Low performing VWM participants generated saccades contingent on VF and distractor proximity during the NS-VWM condition. In comparison, during the NS-VWM condition, high performing VWM participants produced increased deviation for close proximity distractors, in comparison to far proximity distractors, regardless of saccade target VF. It is proposed that NS-VWM facilitates saccade deviation in high performing VWM participants in

order to promote efficient saccades; a result not found in low performing VWM participants.

The results also indicated that low performing VWM participants generated saccades that deviated to the right. In comparison, high performing VWM participants produced saccades deviating to the left during the non-active rehearsal VWM condition and to the right during NS-VWM condition. This result appears to display high VWM performers preferentially utilising lateralised cortical areas specialised to process spatial and non-spatial information. The left hemisphere has been associated with non-spatial VWM whereas the right hemisphere has been associated with spatial VWM (D'Esposito et al., 1998). High VWM performers appear to generate saccades to the contralateral side of the hemisphere theorised to be specialised in processing the performed task. Thus, saccades during a task characterised by dorsal pathway processing generated saccades predominately to the left VF whilst saccades during a task characterised by ventral pathway processing generated saccades predominately to the right VF.

It is proposed that high VWM performers utilise cortical networks more appropriately in order to process information more efficiently. This proposal is further supported by results indicating that the high VWM performance group produced shorter latencies for upper VF saccades during the NS-VWM condition in comparison to the non-active rehearsal VWM condition. As previously stated, the upper VF has been associated with the ventral pathway (Previc, 1990), as has NS-VWM. Low performance VWM participants, in contrast, did not display differential saccade latencies during either condition for saccades directed to the upper VF.

The results of the second experiment of chapter 7 raise clinical implications regarding VWM interactions with the oculomotor system. Oculomotor behaviour was shown to be differentially affected in participants who performed well in VWM tasks and participants who performed less well. Though these results were anticipated, the extent of the differential saccade trajectories, especially in relation to saccade directions, was not anticipated. Clinical implications were discussed in relation to how populations known to have executive dysfunctions, and thus reduced VWM capacity and ability, may interact with their visual environments.

The final experimental chapter (chapter 8) of this thesis aimed to clarify whether VWM should, and could, be integrated into models of saccade deviation. VWM interaction with the oculomotor system is supported throughout this thesis. However, it is argued that if VWM does not uniquely facilitate oculomotor inhibition across temporal delays, models of saccade deviation should incorporate a network of cortical interaction as opposed to a solitary VWM incorporation. Thus, chapter 8 aimed to ascertain if comparable saccade deviation, as apparent during VSWM and non-active VWM tasks, could be replicated in tasks not requiring VWM but requiring manual responses.

Three conditions were presented to participants: 1. a non-active rehearsal VWM condition, 2. a saccade condition with a manual tapping exercise, and 3. a saccade condition with a spatial manual tapping exercise. The manual tapping exercise was such that participants were required to repetitively tap, with a stylus, on a touch tablet at either a point representing the central fixation stimulus or, during the spatial manual tapping condition, at a point representing a presented distractor. It was

predicted that no difference in saccade deviation should be observable across any of the conditions if saccade deviations were uniquely facilitated by VWM after the brief presentation of distractor stimuli. Results from this chapter indicate that manual facilitation of oculomotor inhibition can be observed across temporal delays. Models of saccade deviation should therefore focus on how the oculomotor system employs various cognitive systems, across a network of cortical activations, to inform oculomotor action, as opposed to solely incorporating specific cognitive systems such as the VWM system.

Finally, chapter 9 summarises the major findings of the thesis and proposes how these findings may be integrated with current knowledge and understanding of saccade characteristics. VWM facilitated oculomotor inhibition has been found to influence the deviation and characteristics of saccades. However, VWM does not act uniquely in inducing saccade deviations after the brief presentation of stimuli and it is proposed that the oculomotor system draws on information garnered across a range of cognitive systems to facilitate action.

Chapter 2

Literature Review

This literature review will firstly focus on the mechanisms involved in the programming, generation and completion of saccadic eye movements. Secondly, it will describe the characteristics of saccades and how saccades are influenced by environmental stimuli. Lastly, this review will be concerned with how VWM may influence the trajectories of saccades.

THE PHYSIOLOGY OF SACCADDES

The Eye

Saccadic eye movements bring visual information to the high resolution fovea which forms a part of the retina. The retina is a layer of nervous tissue that converts light into chemical energy via photoreceptors called 'rods' and 'cones'. Cone photoreceptor cells respond to bright light and are used during colour vision and fine detail perception. In contrast rod cells are sensitive to light of various intensities and are responsible for perceiving the feature characteristics of visual images; for instance, the size, shape and brightness of an image. The central region of the fovea (the fovea centralis) consists exclusively of densely packed cone photoreceptors. It measures 400µm in diameter and subtends 1.3° (Duchowski, 2007). By utilising a fixation-saccade-refixation pattern a steady stream of visual information is able to be processed by the visual system.

Eye movements are controlled via six extraocular muscles; the medial and the lateral recti, the superior and inferior recti, and the superior and inferior obliques. These muscles are configured as antagonist pairs (Bell, 1823). The recti muscles control movements directed sideways (the medial and the lateral recti) and along the vertical plane (the superior and the inferior recti). Comparatively the oblique muscles control the 'twist' motion of the eyeball; the superior oblique directs movements downwards

and outwards whilst the inferior oblique directs movements upwards and inwards (Bell, 1823). These muscles, as well as the trochlea, can be seen in *fig. 2.1*.

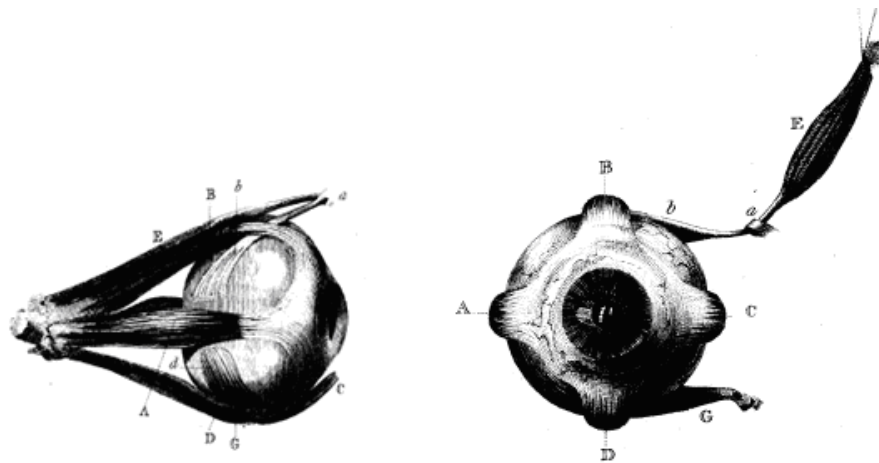


Fig. 2.1. The muscles of the eye (image from Bell, 1823). A & C are the medial and lateral recti, B & D are the superior and inferior recti, and E & G are the superior and inferior obliques. The trochlea (a) and the tendon of the trochlea (b) are also shown.

Innervation of the Eye for Saccadic Eye Movements

The muscles of the eye are innervated by the motor neurons in the oculomotor, trochlea, and the abducens cranial nerve nuclei located in the brain stem (Munoz, 2002). The ipsilateral medial rectus, the contralateral superior rectus and the inferior oblique is innervated by the oculomotor nucleus. In turn, the trochlea nucleus innervates the contralateral superior oblique and the abducens nucleus innervates the lateral rectus muscle (Yarbus, 1967).

Vision Processing Pathways

Neural afferents from the retina project to the visual cortex via a primary pathway along the optic nerve through to the lateral geniculate nucleus (LGN; Findlay & Gilchrist, 2003). The LGN receives topographically represented input from the retina

from the magnocellular pathway (M- pathway) and the parvocellular pathway (P- pathway). The M- and P- pathways have been functionally and anatomically distinguished as being specialised for the processing of visual action (M- pathway) and visual form (P- pathway; Findlay & Gilchrist, 2003).

It has been proposed that the M- and P- pathways align along the dorsal and ventral pathways. The ventral pathway projects from the primary visual cortex along the occipito-temporal cortex and extending into the ventrolateral prefrontal cortex (VLPFC). Contrarily, the dorsal pathway projects from the primary visual cortex along the occipito-parietal cortex and extending into the dorsolateral prefrontal cortex (DLPFC; Badre, 2008; see *fig. 2.2*). The dorsal and the ventral pathways are also thought to be functionally distinguished. The dorsal pathway has been associated with visuo-spatial and visual action information processing whilst the ventral pathway has been associated with non-spatial visual information processing. This has led these pathways to be labelled the 'what' (ventral pathway) and 'where' or 'how' (dorsal pathway; Goodale & Milner, 1992; Ungerleider & Haxby, 1994).

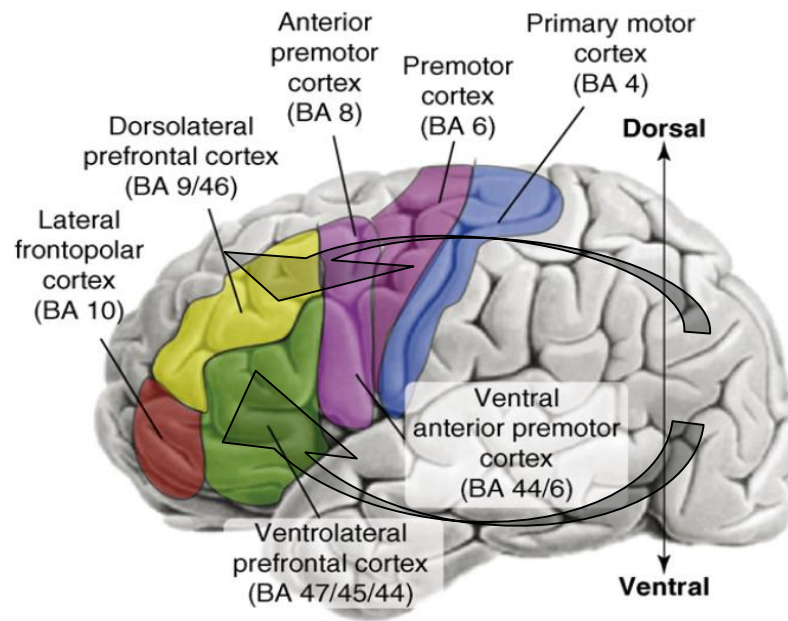


Fig. 2.2. The dorsal and the ventral pathways (image adapted from Badre, 2004). BA = Brodmann's areas.

THE NEURAL COMPONENTS OF SACCADIC EYE MOVEMENTS

A Network of Activation for Saccade Generation

Cortical and subcortical regions implicated in the generation of saccades include areas in the frontal cortex (the frontal eye fields [FEF], the supplementary eye fields [SEF], the DLPFC, the cerebellum [CB], the SC, the thalamus [TH] and the basal ganglia; Girad & Berhoz, 2005; Munoz, 2002; Munoz & Everling, 2004). Fig. 2.3. shows a conceptual representation of these brain areas and connections. Fig. 2.4. shows the cortical locations of these areas.

Differential cortical activations in these regions have been identified according to the type of saccade initiated. In an fMRI (functional magnetic resonance imaging) study, voluntary saccades were found to produce greater activation in the FEF and the intraparietal sulcus (IPS) located in the LIP relative to reflexive saccades (Mort et al. 2003). Reflexive saccades are defined as a saccade initiated due to the appearance of a

peripheral onset; for instance the onset of a visual target stimulus a saccade is required to be directed to. In contrast a voluntary saccade is defined as a saccade initiated due to a 'cognitive judgement'; for instance after instructional criteria have been met.

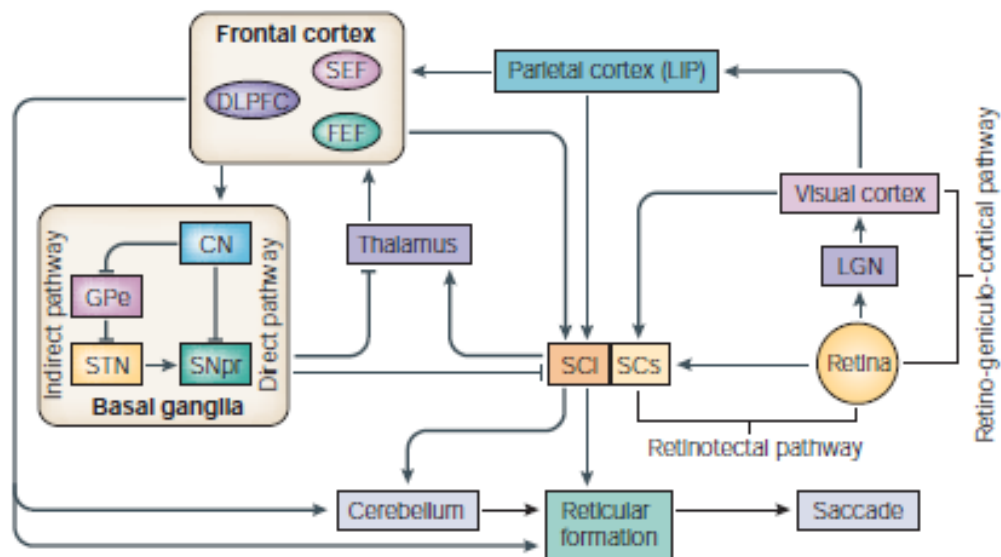


Fig. 2.3. Conceptual representation of brain regions associated with saccadic eye movements (image from Munoz and Everling, 2004). Areas include the SC (SCi [superior colliculus intermediate layers], SCs [superior colliculus superficial layers]), the LGN, the LIP, the FEF, the SEF, the DLPFC, the caudate nucleus (CN), the globus pallidus externa (GPe), the subthalamic nucleus (STN), the substantia nigra pars reticulata (SNr).

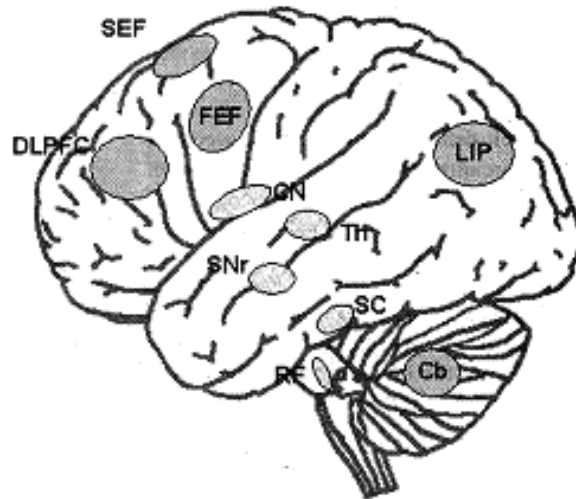


Fig 2.4. Cortical locations of brain regions associated with saccadic eye movements. Image adapted from Munoz (2002). Brain regions shown include the SC, the CB, the reticular formation (RF), the TH, the LIP, the FEF, the SNr, the CN, the DLPFC, and the SEF.

Matsuda et al. (2004) observed notable activation in the FEF, SEF, and the parietal eye fields (PEF) located in the IPS and superior parietal lobule as well as activation in the bilateral occipital cortices (visual cortex) during visually guided saccade tasks. Antisaccade tasks found further activation in the thalamus and the DLPFC as well as those previously stated. An antisaccade task requires participants to make a saccade in the opposite direction, or the opposite hemifield, of a presented peripheral ‘target’ stimulus. Antisaccade tasks require the inhibition of a reflexive saccade response in order to make a voluntary saccade to a correct location.

It is proposed that saccade generation is reliant on the dorsal processing stream of the human visual system. In a study by Irwin and Brockmole (2004), it was found that the response time during an object recognition task was not related to saccadic amplitude. Comparatively, saccade amplitude was associated with response time when participants were required to discern the spatial characteristics of objects. Dual task

interference, the diminishing of task ability due to over-reliance on one cognitive system, resulted in a decreased task performance. It was argued that these results support a dorsal stream role for the generation of saccades.

The Brainstem Burst Generator and Saccades

Extraocular muscles are innervated via a pulse-step discharge in the motor neurons in the cranial nerve nuclei. The 'pulse' component of this pattern precedes a saccade and continues throughout a saccade and the 'step' component holds the eye stable at the new eccentric orbital position against the elasticity of the extraocular muscles (Scudder, Kaneko, & Fuchs, 2002; Munoz, 2002; Sparks & May, 1990). The horizontal and vertical aspects of saccades are produced via two populations of short-lead burst neurons. Burst neurons in the paramedian pontine reticular formation (PPRF) and the contralateral medullary reticular formation discharge most vigorously for horizontal saccades; burst neurons in the mesencephalon discharge most vigorously for vertical saccades (Scudder, Kaneko, & Fuchs, 2002; Sparks, 2002).

The Superior Colliculus and Saccades

The burst neurons in the mesencephalon and the RF receive inputs from the SC (Scudder, Kaneko, & Fuchs, 2002; Sparks, 2002). Direct retinal input is received by the superficial layers of the SC (Munoz, 2002). This direct, retinotectal, pathway has been implicated as important for both involuntary attentional capture and stimulus-driven eye movements (Sumner, Adamjee, & Mollon, 2002). The retinotectal pathway has also been implicated as the pathway responsible for a 'saccadic' IOR. Evidence suggests that there is a distinction between 'saccadic' IOR (defined as IOR elicited via collicular mediation through the direct, retinotectal pathway) and traditional IOR

(defined as IOR via a cortical pathway). Sumner, Nachev, Vora, Hussain, and Kennard (2004) found evidence of IOR after presenting stimuli invisible to the retinotectal pathway (S cone stimuli). It is thought that S cone stimuli (short-wave sensitive cones) do not project to the SC. Thus IOR found after the presentation of these stimuli cannot be said to be due to the retinotectal pathway. Sumner et al. (2004) also report that no IOR was found when saccadic eye movements were required. This evidence suggests a distinction between traditional IOR as a function of a cortical pathway and mediating attention and saccadic IOR mediated by a collicular mechanism (Sumner et al., 2004).

The deeper layers of the SC contain a topographically, or retinotopically, organised map of neurons; the discharge of which is modulated by saccadic eye movements (Lee, Rohrer, & Sparks, 1988; Munoz, Pélisson, & Guitton, 1991; Munoz, 2002; Sparks & May, 1990). There are two main types of neurons in the intermediate and deep layers of the SC; burst and build-up neurons. Burst neurons discharge before saccade initiation. Comparatively build-up neurons express target related activity before saccade onset and discharge just before saccade initiation (Munoz, & Everling, 2004; Ramat, Leigh, Zee, & Optican, 2007).

The neuronal topographic map in the SC is organised such that rostrally positioned neurons generate saccades with small amplitudes whilst caudally positioned neurons generate larger amplitude saccades. Saccades directed upwards are represented medially in the SC and downward saccades represented laterally (Sparks, 2002). Populations of collicular neurons are thought to be responsible for the temporal onset, as well as the spatial properties, of saccades; activation in these populations before

the onset of a saccade being indicative of the direction, amplitude and velocity of saccades (Lee, Rohrer, & Sparks, 1988).

Early studies of lesions to the SC showing no impairment in the generation of saccades led researchers to suggest that the SC was not essential for the production of saccadic eye movements (Sparks & Hartwich-Young, 1989). This early research is disputed as evidence shows that, in the absence of the SC due to chemical inactivation (as opposed to ablation), the FEF-brainstem pathway is not enough to generate accurate saccades (Hanes & Wurtz, 2001). These researchers suggest that continued saccade generation and accuracy after SC ablation demonstrates neural plasticity in the saccade system as opposed to the relative unimportance of the SC during saccade production.

The Frontal Eye Fields and Saccades

Neuronal activity in the FEF has an important role in the generation of saccades (Bruce & Goldberg, 1985). As with the SC, this region also contains a topographical neuronal map; short saccade amplitudes are represented ventrolaterally whilst saccades with longer amplitudes are represented dorsomedially (Schall, 1995).

Rosano et al. (2002) localise the FEF to the anterior wall of the precentral sulcus (PCS); furthermore it is suggested that separable regions of the PCS play differential roles in the generation of eye movements. Using fMRI these researchers suggest that the anterior wall of the PCS is preferentially activated during saccades tasks whereas for smooth-pursuit tasks (tasks requiring participants to follow the path of a moving visual object) the fundus areas of the PCS were more preferentially activated.

The FEF projects extensively to the intermediate layers of the SC and to the brainstem burst generator (Hanes & Wurtz, 2001). The FEF also projects indirectly to the deeper layers of the SC via the basal ganglia (Sparks & Hartwich-Young, 1989). However, the direct role of the FEF in the generation of saccades is disputed. Hanes and Wurtz (2001) chemically inactivated the SC in order to ascertain the contribution of the FEF and the direct pathway from the FEF to the brainstem burst generator. They found that accurate saccades in the Macaque monkey were not made in the absence of the pathway from the FEF through the SC to the brainstem generator.

The Dorsolateral Prefrontal Cortex and Saccades

The DLPFC sends neuronal signals, selective for the spatial characteristics of stimuli and saccade direction, directly to the SC (Johnston & Everling, 2006). A direct, or indirect, excitatory drive from the DLPFC to the SC is such that saccade related neurons in the SC are suppressed or disinhibited (Johnston, Koval, Lomber & Everling, 2013). For example, in order to generate a goal-directed saccade to a target stimulus in the visual environment, the DLPFC would provide an excitatory drive to the ipsilateral SC (the ipsilateral area of the SC corresponding with the saccade target stimulus location). This excitatory drive would lead to reduced activity in the contralateral SC; hence ipsiversive saccade preparation would be facilitated.

DLPFC facilitation of goal directed saccades has been observed in studies utilising an antisaccade paradigm. Increased bilateral DLPFC activation has been noted during anti-saccade tasks (Matsuda et al., 2004). Moreover lesions to the DLPFC have been found to result in an increased percentage error rate during antisaccade tasks (Pierrot-Deseilligny et al., 2002). Thus, the role of the DLPFC during saccade preparation is

thought to be the facilitation of goal-directed saccades and the suppression of task-irrelevant saccades.

The Basal Ganglia and Saccades

The basal ganglia consist of the striatum (including the putamen and the CN, the GPe and the globus pallidus interna (GPi), the STN, the SNr and the substantia nigra pars compacta (SNc). The dopaminergic pathway of the basal ganglia controls the level of communication between the thalamus and various regions of the cortex (Smith et al. 1998). Inhibition processes via the SNr and CN in the basal ganglia influence saccadic eye movements. Removal of the inhibitory action of the SNr on the presaccadic neurons in the SC results in a saccade to the contralateral side. The CN is responsible for inhibiting the SNr and thus disinhibiting the SC (Hikosaka, Takikawa, & Kawagoe, 2000).

The Lateral Intraparietal Area and Saccades

LIP projections to the FEF and SC (Blatt, Anderson, & Stoner, 1990) have been reported. It has already been mentioned that the LIP is activated during the execution of voluntary saccades (Mort et al., 2003). Powell & Goldberg (2000) investigated activation in neurons in the LIP of two Rhesus monkeys during two tasks; a memory guided and a distractor task. The memory guided task required the monkeys to make a saccade to the remembered location of a target stimulus. The distractor task included a visual distractor in addition to the memory guided task. Neurons in the LIP expressed a normal or increased level of activation as a response to the distractor; this neuronal response remained consistent or reduced when the distractor was presented at the

site of the saccade target. These researchers suggest that these results indicate the LIP activation during visual attention and not an LIP role for the generation of saccades.

The Cerebellum and Saccades

The CB has been implicated in the control of saccades. Lesions to the CB result in inaccurate and slow saccades though the eye movements are still initiated (Robinson & Fuchs, 2001). The oculomotor vermis in the CB is characterised as a region in which, when microstimulation is applied, results in saccade generation. The oculomotor vermis is associated with saccade related neuronal activity and has Purkinje cell discharge modulated by eye movements (Noda, Murakami, Yamada, Tamaki, & Aso, 1988).

It has been suggested that the cerebellum and the SC form a parallel pathway for the control of saccades (Lefèvre, Quaia, & Optican, 1998, Quaia, Lefèvre, & Optican, 1999). In a model for the control of saccades, these researchers suggest that a 'main' collicular pathway encodes the desired displacement of the eyes via a path from the FEF to SC and brainstem burst generator. A cerebellar pathway from the FEF to the SC, nucleus reticularos tegmenti pontis to the CB is thought to provide directional drive. McSorley, Haggard and Walker (2004) suggest that the CB provides a directional drive towards saccade target stimuli.

THE CHARACTERISTICS OF SACCADES

Cortices and Saccade Characteristics

The cortical and subcortical regions responsible for the generation and control of saccadic eye movements also play important roles in the characteristics of those

saccade trajectories. It has already been noted that damage to the CB leads to saccade slowing and inaccuracy (Robinson & Fuchs, 2001; Takagi, Zee, & Tamargo, 1998). Schiller, Sandell, and Maunsell (1987) suggest that the SC is important for the production of short-latency saccades. Short-latency saccades, or express saccades, are defined as saccades with extremely short reaction times; for instance a saccade onset of less than 100msec (Fisher & Weber, 1993). Saccadic latencies in studies exploring saccades and saccade trajectories are defined as the time it takes for a saccade to be initiated after subjects receive the saccade 'go' cue.

Schiller, Sandell & Maunsell ablated either the FEF or the SC of Rhesus monkeys. After ablation of the FEF no discernable effect was found on the latencies of saccades. In contrast, ablation of the SC resulted in the elimination of express saccades (short-latency saccades) made to the visual field represented by the ablated SC. Moreover, overall saccade latencies increased with SC ablation.

Although Schiller, Sandell, & Maunsell (1993) found that the FEF, unlike the SC, was not necessary in the production of express saccades, Connolly, Goodale, Goltz, & Munoz (2005) suggest that there is a relationship between the FEF and saccade reaction times. In their fMRI study, these researchers found pre-target preparatory neural activity in the FEF was related to saccade latency. In this study saccades were initiated after zero second, or a two second, gap period that interceded a fixation and saccade cue. FEF activity after the two second gap correlated with saccade latency.

Waitzman, Ma, Optican, and Wurtz (1991) found that the SC contributes to saccade velocities. Waitzman et al. (1991) place the SC in a collicular feedback model

suggesting that the SC encodes information regarding the difference between the desired and the actual eye displacement (motor error). In their study, these researchers found that the level of SC activity was related to motor error. A decrease in spike activity in SC neurons was associated with a decreased level of motor error.

Abrams, Meyer, & Kornblum (1989) present evidence of a linear relationship between the speed and the accuracy of saccades; as the velocity of saccades increases, the variability of saccade endpoints also increase. This increase in the variability of saccade endpoints represents a saccade accuracy decrease. These researchers describe an impulse-variability model of movement control usually adopted for limb control. In this model movement is said to be the result of a pulse of force from antagonist and agonist muscles. Small or low velocity movements require a small amount of force whereas larger or high velocity movements require a larger force. Larger force movements are subject to increased variability.

Visual Pathways and Saccade Characteristics

It has been noted that the visual pathways can be anatomically and functionally separated into the M- and P-, or the dorsal and ventral, pathways. Saccade characteristics have been found to be influenced by the visual processing pathways. For example, studies exploring 'altitudinal' effects highlight how processing along one of these pathways can influence saccade characteristics (for example, Zhou & King, 2002).

The VF can be separated into four quadrants based on the upper and lower, and left and right, regions of the VF. The upper and lower VFs are thought to specialise in the

processing of non-spatial and spatial properties respectively. Thus the upper VF is thought to be primarily specialised for processing along the ventral pathway whilst the lower VF is thought to be primarily specialised for processing along the dorsal pathway (Previc, 1990). These specialisations of the altitudinal VFs are based on evolutionary theories. It is thought that spatial specialism in the lower VF is consequent of a need to perceive moving stimuli located in this VF (for example, the need to perceive terrain when walking). In turn, non-spatial specialism in the upper VF is thought to be consequent of a need for object identification outside the peripersonal (near vision) space (Previc, 1990). Altitudinal specialism in the VF is such that saccade latencies to target object have been found to be shorter for upper VF targets in comparison to lower VF targets (Zhou & King, 2002) whilst visually guided reaching advantage can be seen in the lower VF in comparison to the upper VF (Culham et al., 2003; Dankert & Goodale, 2001).

The lateralised (left and right) VFs have also been associated with processing along the dorsal and ventral pathways. The dorsal pathway is thought to preferentially activate right-sided brain regions whilst the ventral pathway is thought to preferentially activate left-sided brain regions (D'Esposito et al., 1998; Köhler et al. 1995). Thus, the right VF is characterised by ventral stream processing whilst the left VF is characterised by dorsal stream processing (due to contralateral projections).

THE CURVATURE AND DEVIATION OF SACCADIC TRAJECTORIES

Peripheral Stimuli Influence Saccadic Trajectories

Visual stimuli in peripheral vision can influence the trajectories of saccades. For instance, in a study by Doyle and Walker (2001) saccades were found to deviate away

from attended to irrelevant distractor stimuli. In this study participants were required to make either a voluntary saccade or a reflexive saccade in the presence of an irrelevant distractor. In both conditions, Doyle and Walker (2001) found that saccade trajectories deviated away from the irrelevant distractor location when the distractor was presented in the same hemifield as the target.

If more than one distractor is presented, saccade trajectories will also be influenced. McSorley, Haggard, & Walker (2004) found that single distractor stimuli evoked saccades deviating away from distractor locations. When two distractors were presented at mirror locations in opposite hemifields, saccade trajectories straightened. Comparatively when two distractor stimuli were presented in non-mirrored locations there was no observed relationship between distractor location and saccade deviation.

The distance of a distractor stimulus to fixation or target stimuli can also affect saccade trajectories. In their study, Van der Stigchel and Theeuwes (2005) found that saccades made to a target with distractor stimuli presented in close proximity to a fixation results in saccade trajectories deviating away from the distractor. In contrast a saccade made to a target with a distractor in close proximity to a target resulted in saccade trajectories deviating toward the distractor.

The expectation of a distractor stimulus appearing in peripheral vision is sufficient to induce saccade deviation (Van der Stigchel & Theeuwes, 2005). In the two experiments of this study, Van der Stigchel and Theeuwes (2005) presented a distractor stimulus simultaneously with a target stimulus in 80% of trials, in the other 20% of trials no distractor would appear. The results suggest that under these conditions, the

expectation of a distractor's appearance would induce saccades to deviate away from location of the expected distractor.

The distractor effect on prosaccades, antisaccades, and memory-guided saccades has been investigated by van Zoest, Van der Stigchel and Barton (2008). A prosaccade is a saccade made to the target stimulus in contrast to an antisaccade which is made away from a stimulus. It was found that memory-guided saccades and antisaccades induced a greater amount of saccade deviation than prosaccades. Furthermore, memory-guided saccades induced a greater amount of deviation than antisaccades (van Zoest, Van der Stigchel, & Barton, 2008). It was also observed that the time of target offset did not influence the amount of deviation expressed.

The feature characteristics of distractor stimuli can also influence the trajectories of saccades. If distractor and target stimuli share characteristics saccade deviation increases. Ludwig and Gilchrist (2003) found that when manipulating the luminance of distractor and target stimuli so that they were either similar or dissimilar, saccade trajectories increased as a function of similarity. As distractor and target similarity increased so too did the degree of saccade deviation. Furthermore saccade deviation increased as a function of increased saccade latency.

The effect of stimulus similarity on the deviation of saccade trajectories has also been observed (e.g., Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). These researchers investigated how saccade latency interacted with stimulus similarity and the deviation of saccades. A short latency saccade made to a target after the onset of a similar distractor resulted in deviation toward a distractor. In contrast dissimilar distractor

stimuli elicited saccade deviations away from a distractor. Longer latency saccades did not show this modulation for distractor similarity to target; similar and dissimilar distractors resulted in deviation away from the distractor.

Theories of Saccade Deviation and Curvature

We have seen that peripheral stimuli can influence the trajectories of saccades (for instance, Doyle & Walker, 2001; Ludwig and Gilchrist, 2003; van Zoest, Van der Stigchel, & Barton, 2008). Explanations for the curvature and deviation of saccades highlight neuronal inhibition in the SC and FEF.

Observations of perisaccadic activity of neurons in the FEF suggest that saccade trajectory curvature is associated with distractor related activity in these regions. McPeck (2006) investigated the role of the FEF in the expression of curved saccades. For saccades that curved toward a distractor, perisaccadic activity in the FEF increased whereas for saccades that curved away from a distractor perisaccadic activity in the FEF was decreased.

McPeck, Han, & Keller (2003) also found evidence that the SC contributes to the production of saccade curvature. They investigated the degree of presaccadic activity in neurons in the SC of monkeys. Increased activation in the SC at the neuronal site coding the distractor location resulted in saccades that deviated towards the distractor location. Using microstimulation, these researchers also found that by activating sites in the SC corresponding to the location of the distractor saccades were produced that curved away from the stimulated site.

Port and Wurtz (2003) measured burst and build-up neuron activity in two regions of the SC. Curved saccades made in the presence of two target stimuli were the result of ‘sequential’ activity in the two measured regions. In contrast, relatively straight saccades were observed when activity in the two regions of the SC was simultaneous. These researchers conclude that curved saccades are the result of differing levels of neuronal activity in the SC with some regions reaching peak activity sooner than others.

The *population coding theory* (Tipper, Howard, & Houghton, 2000) and the *premotor theory of attention* (Rizzolatti, Riggio, Dascola, & Umiltá. 1987; Rizzolatti, Riggio, & Sheliga, 1994) are used to explain saccade curvature towards and away from presented distractor stimuli. These theories are explained below.

The Premotor Theory of Attention

The premotor theory of attention indicates that spatially-coded, goal-directed movements, such as saccadic eye movements, are the consequence of interplay between spatial attention and ‘spatial pragmatic maps’ that code spatial locations. This theory suggests that attention is sub-served by the same mechanisms used to produce spatial, goal-directed movements (Rizzolatti, Riggio, & Sheliga, 1994). For instance, the topographical neuronal map in the SC is integral to the production of stimulus driven saccadic eye movements and involuntary attentional capture (Sumner, Adamjee, & Mollon, 2002). According to the premotor theory of attention, deviation in the trajectory of saccades due to visual distractor stimulus presence is the consequence of neuronal activity in the SC at the site correlating to the distractor stimulus.

To test this theory, Sheliga, Riggio, and Rizzolatti (1994) instructed participants to make a saccade towards a target item whilst covertly attending to another location. Participants' saccades consistently deviated away from the covertly attended location. The premotor theory of attention is also supported by studies showing activation at the spatial location of distractor sites in topographically organised movement maps in the SC (McPeck, Han, & Keller, 2003).

The Population Coding Theory

The population coding theory focuses on the topographical neuronal maps that code movement. Tipper, Howard, and Houghton (2000) claim that populations of neurons in topographical maps will broadly activate for a variety of movements. If the presence of two stimuli activates two populations of neurons in a map these populations may overlap. In this theory 'populations' of neurons code saccade programmes directed to specific locations. In turn, when a distractor stimulus is presented, two saccade programmes are initialised; one representing the distractor spatial location and one representing the target spatial location. When a distractor is in close spatial proximity to a target item, suppression of the distractor location results in some of the neurons relating to the target item also being suppressed; thus saccades will appear to deviate away from a distractor location. In support of the population coding theory, saccade curvature towards distractor locations has been shown to correspond with sequential activity in SC neurons (Port & Wurtz, 2003). Shifts in the activation in regions of the SC results in saccade trajectory deviation.

Oculomotor Inhibition

The premotor theory of attention and the population coding theory both indicate that distractor objects presented in peripheral vision activate competing neurons in the topographically organised map in the SC. Inhibition of neurons that spatially correspond to either the target or the distractor object results in saccade trajectories deviating towards or away from the presented distractors. Studies have explored the characteristics of this oculomotor inhibition.

McSorley and colleagues (McSorley, Cruikshank, & Inman, 2009; McSorley, Haggard, & Walker, 2005; McSorley, Haggard, & Walker, 2006) investigated the temporal and spatial characteristics of oculomotor inhibition. McSorley, Haggard, and Walker (2005) explored the influence of distractors on reflexive and voluntary saccades. Distractors were presented either in close proximity to the target or close proximity to the fixation. These researchers found that voluntary saccades were subject to stronger inhibition away from distractors than reflexive saccades. Moreover, as distractors were presented closer to the target, voluntary saccades showed a reduction in saccadic latency. In contrast, for reflexive saccades distractors presented closer to a target elicited an increase in saccade latency. These results suggest that oculomotor inhibitory actions are driven by the type of saccade initiated. These researchers also note that saccade deviation in this study was variable across participants.

McSorley, Cruickshank, and Inman (2009) also manipulated the latency of saccades. In this experiment distractors were presented either closer or further away from a target (distractors were presented at 10, 20, 30, 60, and 120 degrees of arc from the target). It was found that saccades initiated when distractors were presented in close

proximity (10°) to a target resulted in deviation away from the distractor regardless of the latency of that saccade. In contrast, saccades deviation in trials where distractors were presented further away from the target (20° , 30° , 60° , & 120°) were influenced by the latency of that saccade. Saccades with a short-latency resulted in saccadic deviation and saccadic landing positions toward a distractor whereas longer-latency saccades resulted in saccades with a straightened trajectory when distractors were presented at 20° and 30° and deviation away when distractors were presented at 60° and 120° . Saccade landing points showed no such relationship with saccade latencies. Researchers suggest that these results are attributable to firstly, neuronal inhibition at the distractor site leading to trajectory deviation, and secondly to subsiding inhibition in these neuronal sites leading to saccade landing positions not expressing the same pattern of results as the trajectory deviation.

McSorley, Haggard, and Walker (2006) manipulated saccade latencies by removing the fixation cross before or after target onset. Short-latency saccades resulted in saccade deviations toward a distractor whereas longer-latency saccades resulted in deviation away from a distractor. McSorley, Haggard, and Walker (2006) suggest deviation toward a distractor after short-latency saccades is the result of neuronal inhibition in the SC topographical map. Comparatively, deviation away from a distractor for longer-latency saccades is suggested to be resultant of a top-down inhibitory action generated from the FEF pathway to the SC.

It has been suggested that deviation toward a distractor is a consequence of competition between neurons activating at both the target and the distractor site. In contrast, deviation away from the distractor is thought to be the result of top-down

processing mechanisms inhibiting neurons in the SC at the distractor site (McSorley, Haggard, & Walker; Van der Stigchel & Theeuwes, 2006). White, Theeuwes, & Munoz (2012) dispute a solitary role for top-down influence leading to deviation away from distractors. They investigated the activation of visuomotor neurons in the SC and suggest that if deviation away from a distractor is the result of top-down processing this should correspond with activation in these neurons. These researchers examined neurons in the SC of two Rhesus monkeys during a task that elicited saccade deviations away from the location of a distractor. It was found that whilst some distractor-related activity was evident in the neurons, this activation did not correspond with saccade deviation. Moreover, distractor-related activity occurred 22msec before saccade onset - a time these researchers suggest is too short for top-down processing to take place.

There are some questions raised by this study. Specifically the two Rhesus monkeys (Monkey Q and Y) participating in this study expressed different saccade patterns. Individual differences have previously been noted in studies of saccade trajectories (for instance, McSorley, Haggard, & Walker, 2005). After a distractor was presented in the right hemifield, 92% of saccades made by Monkey Q deviated away, relative to 57% of saccades made by Monkey Y. After a distractor was presented in the left hemifield, 64% of saccades made by Monkey Q deviated away from the distractor; in comparison, 71% of distractors made by Monkey Y deviated away. This suggests that deviation away from distractors, in this study, could be due to factors relating to individual differences across the monkeys tested. Moreover, these researchers presented distractors either at the same time as targets, or 400msec before target onset. It was predicted that distractors presented at the same time as targets would elicit stronger competition in neurons at the distractor and target site. However, the authors did not

find that greater deviation was produced when distractors were presented at the same time as targets. Nevertheless, the researchers did describe a greater amount of directional errors for saccades made in this condition.

White, Theeuwes, and Munoz (2012) propose that saccade deviation away from a distractor location is not always a consequence of top-down inhibition at the site of the distractor location. These researchers further suggest that excitation to the site in the SC contralateral to a presented distractor may result in top-down saccade deviation away from distractor stimuli.

A framework (see *Fig. 2.5*) has been put forward which conceptualises oculomotor inhibition and saccadic deviation (Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004). It describes three cognitive subsystems; the pre-oculomotor map, the saccade map, and the inhibitory control system. The pre-oculomotor map is located in the LIP. This area has previously been associated with the generation of visual attention (Powell & Goldberg, 2000). In support of their framework, Godijn and Theeuwes (2004) examined the relationship between IOR and saccade deviations. They ascertained that both IOR and saccade deviations were distinguishable after the presentation of endogenous and exogenous attentional cues. Exogenous cueing is described as the environmental capture of attention via a peripherally presented cue. Endogenous cueing comparatively is an internal mechanism driving attention via a central cue. They also found a temporal dissociation between IOR and saccadic deviations. A long delay period between a presented cue and saccade execution generated an IOR effect. In contrast, a short delay between a cue and a saccade generated saccadic deviation (Godijn & Theeuwes, 2004). This research suggests that both IOR and oculomotor

inhibition (in the form of saccadic deviations) are distinguishable when attention is captured by peripheral stimuli. These results highlight a need to account for both IOR and oculomotor inhibition during studies of saccade programming. The framework presented by Godijn and Theeuwes (2004) suggests that activation in the topographical map in the SC leads to a ‘tag’ for inhibition flowing to the inhibitory control system located in the FEF/DLPFC. The inhibitory control system in turn sends attentional inhibition to the pre-oculomotor attentional map in the LIP and oculomotor inhibition back to the saccade map in the SC. The pre-oculomotor attentional map in the LIP sends input into the saccade map in the SC.

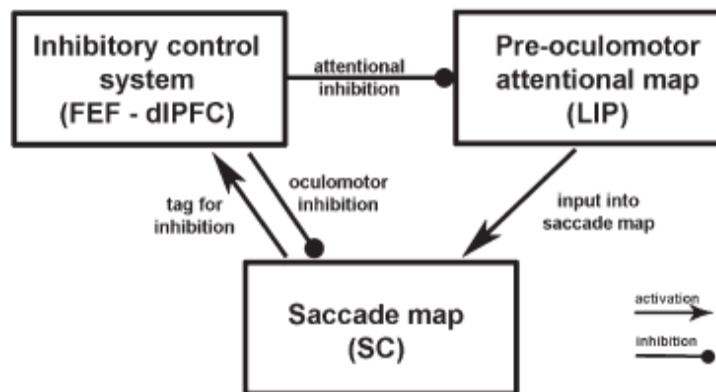


Fig 2.5. Inhibition in the oculomotor system. Image from Godijn and Theeuwes (2004). Oculomotor inhibition is controlled by three subsystems; the preoculomotor attentional map located in the LIP, the inhibitory control system corresponding with the pathway in the FEF/DLPFC, and the saccade map located in the SC.

Theeuwes and Godijn (2004) also present evidence to support the saccade deviation framework. In their experiment participants were required to make saccades to two targets. Participants executing saccades to the secondary target stimulus at a location previously displayed expressed an IOR effect. Moreover, when a distractor object was presented at an inhibited location there was a reduced amount of saccade deviation towards a distractor in comparison to when a distractor was presented at non-

inhibited location. Reduced saccade deviation at inhibited locations suggests that IOR influence reduces activation in the map in the SC (Theeuwes & Godijn, 2004). In the framework this is represented by input from the pre-oculomotor attentional map in the LIP.

VISUAL WORKING MEMORY INTERACTION WITH SACCADDES

There is evidence that information stored in VWM influences the trajectory of saccades. For example, in a study by Theeuwes, Olivers, and Chizk (2005), participants were found to execute saccades that deviated away from a remembered location. Participants were required to make an accurate saccade towards a target stimulus. In one condition participants were required to remember the location of a white pointer stimulus, but in another this stimulus was presented but did not need to be remembered. Conditions that required locations to be kept in memory induced greater saccade deviation in comparison to conditions whereby locations were merely observed.

Visual Working Memory

Working memory (Baddeley & Hitch, 1974; Baddeley, 1986) is a theoretical concept defined as a memory system allowing for the temporary storage and manipulation information. In its original form the working memory model incorporates the visuo-spatial sketchpad, the phonological loop and the central executive. The phonological loop is the sub-system responsible for the storage and rehearsal of speech-based, or auditory, information; the visuo-spatial sketchpad is the sub-system that processes and manipulates visual information, and the central executive is the attentional

controller that is responsible for the coordination of the two sub-systems. The episodic buffer was later added as a fourth component to the working memory system and is concerned with the binding of information from the two subsidiary systems (Baddeley, 2000).

Luck and Vogel (1997) found that the VWM system can hold approximately four visual items at one time irrespective of the number of features describing that item. In contrast, Xu and Chun (2006) suggest that span of visual representations in the inferior IPS are fixed at four objects whereas the span for visual representations in the superior IPS and the lateral occipital sulcus is variable as a function of object complexity. This research implicates cortical location as being indicative of VWM span.

Vogel and Machizawa (2004) found evidence, using an event-related potential (ERP) study, suggesting that the VWM capacity for an individual is related to the amplitude of cortical activity during VWM tasks. When participants with a low VWM capacity were presented with a memory array greater than their capacity limit, the associated amplitude increase of cortical activity was lower than for individuals with a higher VWM capacity. This result is indicative of a plateau of cortical activity related to VWM capacity.

Vogel, Woodman and Luck (2006) investigated the approximate timings regarding the consolidation of visual information into VWM. These researchers suggest that consolidation may take approximately 50ms. Moreover Foxe and Simpson (2002) found that the flow of activation along visual processing neurological streams is rapid. From the initial activation of visual processing areas in the occipital cortex, the DLPFC

has been seen to be active after just 80ms (Foxy & Simpson, 2002). The DLPFC has been associated with visuospatial working memory (Courtney, Petit, Haxby, & Ungerleider, 1998) and aiding the maintenance of information in working memory (Curtis & D'Esposito, 2003).

Visuo-spatial and Non-spatial Visual Working Memory

VWM can be divided into two cognitive subsystems responsible for the storage and maintenance of visual information: VSWM memory and NS-VWM. These sub-systems are thought to align along the previously discussed visual pathways (the dorsal and the ventral visual pathways). VSWM is thought to be processed via the dorsal pathway. In contrast, NS-VWM is thought to be processed via the ventral pathway.

Courtney, Ungerleider, Keil, and Haxby (1996) used positron emission tomography (PET) to examine cerebral blood flow to the through the cortex during VWM tasks. Participants completed two working memory tasks; a VSWM task and a working memory face recognition task. Participants were required to indicate whether a test stimulus had appeared in a previously presented memory set during the face recognition working memory task. In the spatial working memory task, participants were required to say whether the test stimulus appeared in a previously presented spatial location. It was found that the face recognition working memory task activated the anterior areas of the bilateral ventral occipito-temporal cortex whereas the spatial memory task activated the right dorsolateral occipito-parietal cortex. The evidence supports dissociation during cortical activation for working memory tasks.

Further evidence suggests that the PFC can be subdivided into regions responsible for the maintenance of visual object features (VLPFC), and VSWM (DLPFC; Wilson, Ó Scalaidhe, & Goldman-Rakic, 1993). Moreover it has been observed that the parietal cortex and the PFC play differing roles during VWM. The parietal lobe is thought to be associated with storage in VWM, the VLPFC associated with the maintenance of information, and the DLPFC associated with the manipulation of visuospatial working memory (Suchan, 2008). In a study by Suchan et al. (2002) cerebral activations during VWM tasks were examined using PET. During matrix comparison tasks and matrix rotation tasks it was found that the VLPFC were predominantly activated during the matrix comparison tasks. During the matrix rotation task the parietal and the DLPFC were predominately active.

D'Esposito, Aguirre, Zarahn, Ballard, and Lease (1998) explored PFC subdivisions during working memory tasks. These researchers analysed the results from 24 neuroimaging studies concluding that there was no evidence of a functional divide between dorsal and ventral regions in the PFC. They plotted the results from these studies on a standardised brain observing a wide variation of cerebral activation during visuospatial and visual object tasks. The authors suggested that the dorsal/ventral divide for VWM tasks is dissociated due to the type of processing required to fulfil that task, the DLPFC being recruited for the monitoring and manipulation of information and the VLPFC being recruited for active comparisons during working memory tasks.

Clinical studies have supported this divide in VWM separation of function dependent on processing pathways. For example, patients with Huntington's disease have been found to have selective VSWM deficits but relatively spared NS-VWM ability (Lawrence

et al., 2000). VSWM has also been found to be affected in people with Parkinson's disease; however disease progression has been related to VWM deficits in this group of patients. Parkinson's disease patients with mild symptoms did not present VSWM deficits relative to moderate Parkinson's disease symptom sufferers who showed a marked VSWM deficit and severe Parkinson's disease sufferers who showed both VSWM and NS-VWM deficits (Owen et al. 1997).

Common Cortices Sub-serve Visual Working Memory and Saccades

Shared structures utilised during the programming of saccades and implicated in VWM support an interaction between these two cognitive systems. It has been noted that the FEF, SC, LIP, CB and basal ganglia play significant roles in the programming and execution of saccades (Munoz, 2002; Munoz & Everling, 2004). Moreover, Walker, Husain, Hodgson, Harrison, and Kennard (1998) found that both saccadic eye movements and working memory were affected in a patient with prefrontal lesions.

The basal ganglia have also been implicated during the control of eye movements (Hikosaka, Takikawa, & Kawagoe, 2000) and VSWM. It has been proposed that the basal ganglia are responsible for allowing relevant information into the working memory system. Moreover, it was found that PFC and basal ganglia activity was an accurate predictor of working memory capacity (McNab & Klingberg, 2008). This evidence suggests a functional overlap between cortices involved in VWM and saccadic eye movements. This in turn suggests that information held in VWM may influence the trajectories of eye movements.

Visual Working Memory and Saccades

As previously noted, Theeuwes, Olivers, & Chizk (2005) found that saccades deviate away from information stored in VWM. In a further experiment Theeuwes, Van der Stigchel, and Olivers (2006), demonstrated that saccade deviations induced by information held in VWM were independent of the effects of IOR. In the study by Theeuwes, Van der Stigchel, and Olivers (2006), participants made a secondary saccade, after a primary saccade to a target stimulus, to either the cued 'distractor' location or to a previously uncued location. Saccade deviation away from the cued location of the remembered distractor stimulus was observed. However, the size of IOR was not affected by whether the location of the distractor stimulus was held in working memory or not. In turn this led the researchers to conclude that saccade deviation away from remembered spatial locations was separable to IOR mechanisms.

It has been found that attentional inhibition and oculomotor inhibition are separable mechanisms (Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004) as indicated by dissociation of the temporal time IOR and saccade deviation (Godijn & Theeuwes, 2004). Results by Theeuwes, Van der Stigchel, and Olivers (2006) suggest that VWM interacts with the framework put forward by Godijn and Theeuwes (2004).

Other studies have also demonstrated a relationship between working memory and saccade programming and execution. Belopolsky and Theeuwes (2011) asked participants to make a saccade either to a spatial location held in working memory or to a spatial location which was to be ignored. These researchers found that saccades deviated away from remembered spatial locations. Moreover, these researchers also

found that the latency of saccades to ignored locations were slower than the latencies of saccades to remembered locations. These findings suggest that the working memory system is utilised in order to maintain oculomotor preparation to remembered locations (Belopolsky and Theeuwes, 2011).

In a series of three experiments König (2010) investigated the influence of VWM on saccade trajectories. This researcher found that saccades deviated away from locations stored in VWM. However, it was also found that when active rehearsal of distractor locations was not induced via instructions, saccades would deviate away from previously presented distractor locations. König (2010) suggests that results presented by Theeuwes and colleagues (Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel & Olivers, 2006) can more plausibly be explained as the consequence of prolonged neuronal inhibition as opposed to active retention of distractor information. This research supports previous attention based research showing that covertly attended to locations elicited deviation away from attended locations (e.g., Sheliga, Riggio, & Rizzolatti, 1994) and further indicates that attention based oculomotor inhibition may be sustained for briefly presented stimuli.

Findings by Van der Stigchel (2010), dispute the conclusion drawn by König (2010). In this experiment the effect of cognitively 'loading' the working memory system during saccade execution was observed. By requiring participants to perform a verbal working memory task, as well as a saccade task, the influence of working memory on oculomotor inhibition could effectively be observed. If working memory is utilised in order to maintain oculomotor preparation, a secondary working memory task will decrease the efficiency by which this cognitive system is used. In this experimental

paradigm a decreased ability to perform working memory tasks should be observable. Van der Stigchel (2010) found that participants performed more saccadic errors when they were required to perform the secondary verbal working memory task. These results suggest that working memory is recruited during saccade tasks.

SUMMARY

This thesis is concerned with the relationship between VWM and saccadic eye movements. Saccades are programmed by the oculomotor system. The cortical and subcortical components theorised to interact to produce saccades have been discussed in this literature review. For the purpose of this thesis particular attention will be drawn to the oculomotor saccade map in the SC, the neurons of which are said to respond to peripheral distractor stimuli to induce saccade trajectory deviation. The population coding theory (Tipper, Howard, & Houghton, 2000) and the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994) are theories that seek to define the extent and characteristics of trajectory deviation after the presentation of distractor stimuli. It has been found that saccades deviate away from visual stimuli presented in peripheral vision during the completion of goal-directed saccadic eye movements (Doyle & Walker, 2001). Saccades have also been found to deviate away from the spatial location of briefly presented visual stimuli (Theeuwes, Olivers & Chizk, 2005). A relationship between VWM and saccade programming and execution has important theoretical and clinical implications. This thesis aims to clarify the extent, and consequence, of VWM-oculomotor interaction.

Chapter 3

Qualifying and Measuring a Saccade

The third chapter of this thesis examines the methods used to qualify and measure a saccade. Qualifying a saccade will be defined as the method used to exclude or accept a saccade for further analysis. In order to accurately draw conclusions about the influence of VWM on saccade trajectories it will be important to ensure that the methods used to qualify and measure an accurate saccade are consistent and appropriate. The first section of this chapter will explore how the measurement of saccade accuracy is affected by the employment of saccade exclusion criteria. The results from this analysis will then be used to decide which exclusion criteria will be used throughout this thesis. The second section of this chapter will define the saccade measures that will be used in this thesis.

QUALIFYING A SACCAD

Saccadic accuracy, during the experimental procedures of this thesis, will be measured with reference to violations of exclusion criteria. Saccade exclusion criteria are implemented by researchers to limit the possibility of including into analysis errant saccades, or saccades that do not represent a 'normal' population of saccades. Exclusion criteria applied during saccade trajectory analysis may be based on the start and end location of a saccade trajectory, the latency of a saccade (where latency is defined as the time it takes for a participant to initiate a saccade after they have received the saccade initiation cue), and saccade amplitude (where amplitude is defined as the shortest distance from the saccade start location to the saccade end location). For more detailed definitions and equations for these exclusion criteria see *Fig. 3.1 & Table 3.1*.

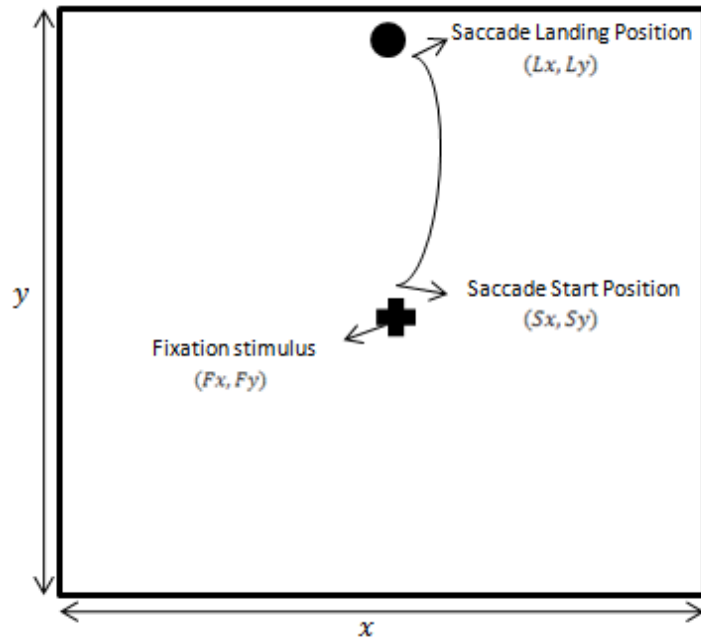


Fig. 3.1. Coordinates of interest for saccade exclusion criteria

Exclusion Criteria	Exclusion Criteria Definition	Formulae
Initial Fixation Position 1	If the saccade start position (Sx, Sy) is more than a specified distance (n) from the fixation stimulus (Fx, Fy).	$\sqrt{(Sx - Fx)^2 + (Sy - Fy)^2} > n$ (Eq. 3.1)
Initial Fixation Position 2	If the saccade start position (Sx, Sy) is further away from the fixation stimulus (Fx, Fy) than a specified distance along the horizontal plane (nx) or the vertical plane (ny).	$Sx - Fx > nx$ or $Sy - Fy > ny$ (Eq. 3.2)
Final Fixation Position	If the saccade landing position (Lx, Ly) is more than a specified distance (n) from the target stimulus (Tx, Ty).	$\sqrt{(Tx - Lx)^2 + (Ty - Ly)^2} > n$ (Eq. 3.3)
Final Fixation Angle	If the angle from the vertical, starting at the function stimulus (Fx, Fy) to the saccade landing position (Lx, Ly), is larger than a specified value (n).	$\theta > n$ $\theta = \tan^{-1} \frac{opp}{adj}$ $opp = (Lx - Fx)$ $adj = (Ly - Fy)$ (Eq. 3.4)
Saccade Amplitude	If the shortest distance for the saccade start position (Sy) and the saccade landing position (Ly) is less or more than a specified distance (n).	$(Ly - Sy) < or > n$ (Eq. 3.5)
Saccade Latency	If the time it takes to initiate a saccade (So) after the presentation of a saccade cur (Sc) is less or more than a specified value of time (n).	$(Sc - So) < or > n$ (Eq. 3.6)

Table 3.1. Exclusion criteria formula and descriptions

In this thesis a stringent and consistent method for qualifying accurate saccades will be required in order to explore the relationship between saccades and VWM. It has been

accepted that saccade characteristics used to exclude errant saccades can influence the trajectory of a saccade. For example, the latency of a saccade has been shown to have a direct relationship with saccadic deviation towards, or away from, distractor stimuli presented in peripheral vision. Shorter latency saccades have been found to deviate towards distractors whilst longer latency saccades have been found to deviate away from distractors (McSorley, Haggard, & Walker, 2006). During this thesis it will be important that saccade latencies are evaluated to ascertain saccade latency influence on saccade trajectories.

The 'main sequence' of a saccade (Bahill, Clark & Stark, 1975) remains relatively constant across 'normal' saccades. Normal saccades in this respect are defined as a saccade generated by a non-clinical, 'healthy', individual. A relationship between peak velocity and magnitude and between duration and magnitude has been documented. As the duration of a saccade increases so too does the average velocity of that saccade. Moreover, as the peak velocity of a saccade increases so too does the amplitude of that saccade (Bahill, Clark & Stark, 1975). Thus a 'normal' saccade of a certain amplitude will have predictable qualities along the other three parameters; saccade duration, saccade magnitude and peak velocity. Though this 'main sequence' of a saccade is said to be constant, the trajectories of a saccade have been found to be variable (Smeets & Hooge, 2003). It will be important during this thesis to allow for the differences in saccadic trajectories as well as ensuring that saccades admitted into analysis represent saccades from a 'normal' population. By applying too stringent saccade exclusion criteria there is a chance that the resulting analyses will not be representative of a 'normal' sample of saccadic trajectories.

Experiment 1

Using empirically collected data saccade exclusion criteria were explored. In turn a consistent approach for qualifying saccades during this thesis was determined. Data was analysed to ascertain how exclusion criteria influences the measurement of saccade accuracy.

Method

Participants

Twelve participants took part in this study (8 female, 4 male, $M_{age} = 21.25$, $SD_{age} = 2.38$) All participants were recruited from Anglia Ruskin University and had normal or corrected colour vision. Informed consent was gained from participants and the study adhered to all relevant ethical guidelines. All participants self-reported as right-handed.

Apparatus

Experimental tasks were implemented using E-Prime (Psychology Software Tools, Pittsburgh, PA). An Acer monitor (17", spatial resolution: 1280 × 1024 pixels), positioned 57cm away from a chin/head rest, was used to present experimental stimuli. The SR Eyelink 1000 eye-tracker (SR Research, Osgoode ON, Canada) sampling the right eye at a temporal resolution of 2000Hz and a spatial resolution of $<.02^\circ$, was used to collect saccade trajectory data.

Stimuli

The stimuli consisted of a centre fixation cross (subtending 0.5°), a circular white target stimulus (subtending 1.5°), and distractor Gabor stimuli (subtending 1.5°). Gabor

stimuli were created at 1 to 8 cycles per degree (cpd) and were oriented vertically (0°). The centre fixation cross appeared in both red and green. The red fixation cross signalled to participants that they were required to maintain central fixation whereas the green fixation cross signalled to participants that they were required to make a saccade to a presented target stimulus. Target stimuli were presented at $\pm 6.76^\circ$ (visual angle) from the centre fixation and along the vertical meridian. Distractor stimuli were presented in four visual quadrants at $X = \pm 5.4^\circ$, $Y = \pm 4.9^\circ$. Stimuli were presented on a grey screen background.

Procedure

The experimental paradigm for this experiment was modelled on that of Theeuwes, Olivers, and Chizk (2005). Participants were required to maintain fixation on the central fixation cross whilst it remained red. A task-irrelevant distractor was presented 500msec after target onset and remained onscreen for 500msec. Participants were required to make a saccade to the target stimulus when they received the saccade initiation cue (the fixation cross changing to green). Participants performed 128 trials (see *fig. 3.2*).

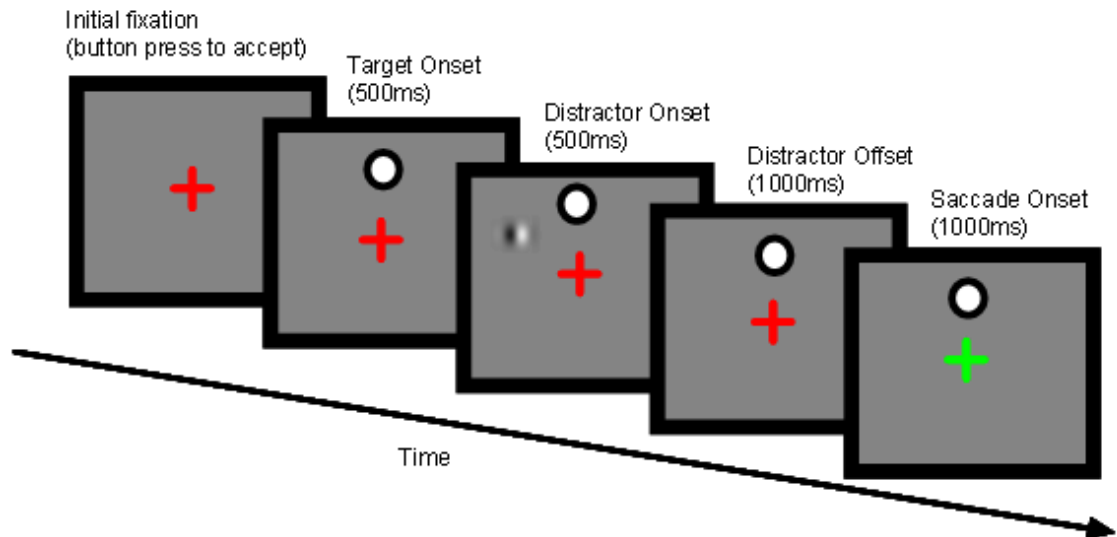


Fig. 3.2. Experiment 1- Experimental task sequence.

Design

Data collected formed a database of saccade trajectory data. This database was used to assess levels of each exclusion criteria. The aforementioned exclusion criteria were explored including: saccade latency, saccade amplitude, initial fixation position, final fixation position/angle.

Each exclusion criterion was assessed in order to ascertain the percentage number of excluded trials and how the measurement of saccadic accuracy was affected by the implementation of exclusion criteria. Saccadic accuracy was defined as the distance a saccade was initiated from with regards to the fixation cross, and the distance a saccade landed in relation to the target stimulus. Trials were excluded if there was a failure to initiate a saccade, if a participant blinked during saccade execution, or if there was an eye-tracker violation (for example, if the eye-tracker 'lost' the pupil during tracking). Trials were then excluded due to the violation of imposed exclusion criteria. The percentage number of excluded trials was calculated. Exclusion criteria

were then ranked according to percentage number of excluded trials and saccadic accuracy. Ranked criteria were then inputted into a ‘decision matrix’ which in turn enabled the identification on the most appropriate level of the exclusion criteria for use throughout the thesis.

Final Fixation Exclusion Criteria

Final fixation exclusion criteria levels can be seen in *Table 3.2* with references included for authors who have employed a given level.

Final Fixation Exclusion Criteria	Exclusion Description	Authors
1	If the final fixation angle is more than 30° (Eq. 3.4)	Godijn & Theeuwes (2004).
2	If the final fixation angle is more than 22.5° (Eq. 3.4)	van Zoest, Van der Stigchel, & Barton (2008) Van der Stigchel, Mulckhuyse, & Theeuwes (2009)
3	If the final fixation angle is more than 15° (Eq. 3.4)	McSorley, Haggard, & Walker (2004) McSorley, Haggard, & Walker (2005) Walker, McSorley, & Haggard (2006)
4	If the final fixation position is more than 2° from the target (Eq. 3.3)	Ludwig & Gilchrist (2003)
5	If the final fixation position is more than 4° from the target (Eq. 3.3)	Godijn & Theeuwes (2004).

Table 3.2. Final fixation exclusion criteria levels. Table also shows examples of authors who have used that level of exclusion criteria.

Results

Percentage Excluded

Final fixation exclusion criterion 4 excluded the highest percentage of trials whilst final fixation criterion 1 excluded the least. Exclusion criteria were ranked from most excluded trials to least excluded trials. The percentage number of excluded trials can be seen *Table 3.3* along with the ranks assigned to each exclusion criterion. Saccades excluded and accepted into analysis for exclusion criteria can be seen in *Fig. 3.3*.

	Final Fixation 1	Final Fixation 2	Final Fixation 3	Final Fixation 4	Final Fixation 5
mean	10.61%	12.63%	17.25%	32.42%	19.73%
std error	1.28	1.05	1.38	2.29	1.48
Rank	5	4	3	1	2

Table 3.3. Percentage number of excluded trials for final fixation exclusion criteria. Target exclusion criteria ranks can also be seen for this measure.

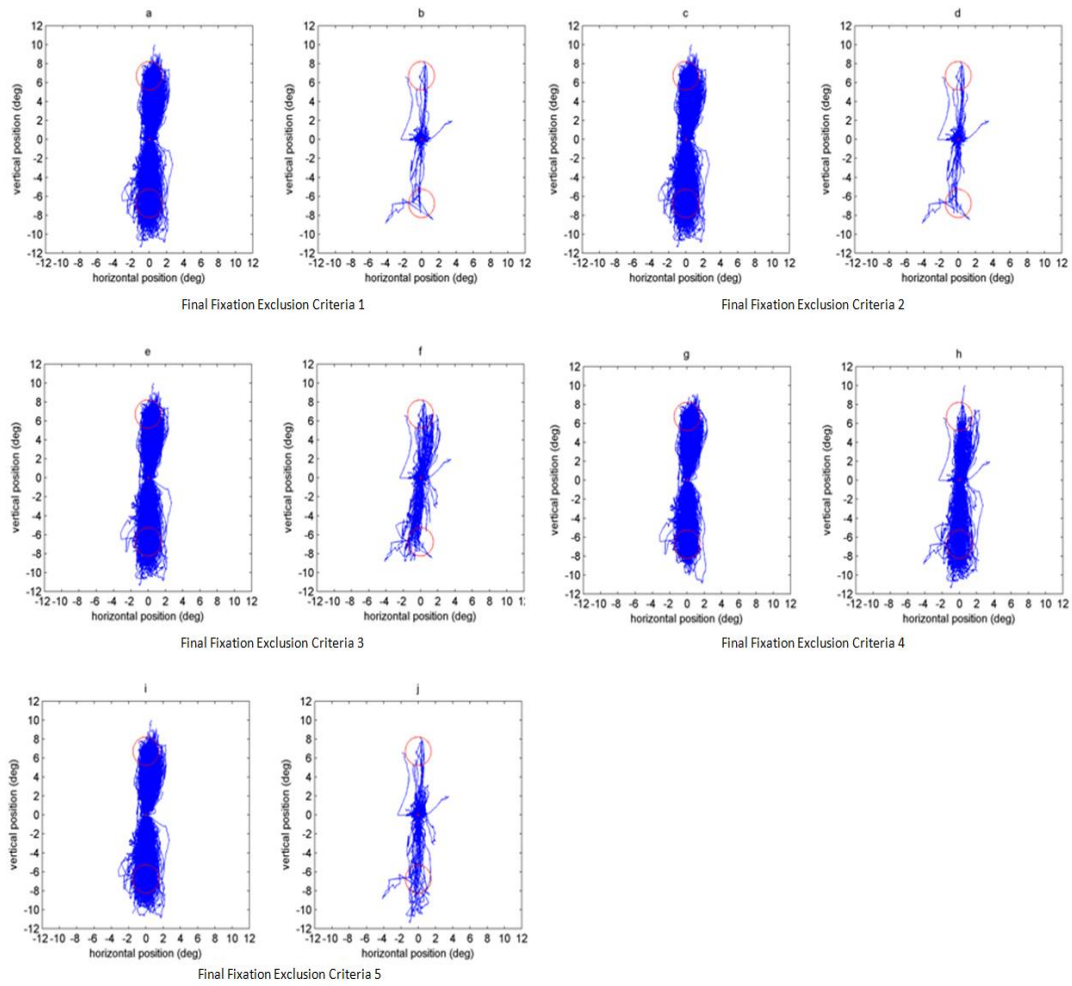


Fig. 3.3. Saccades excluded or accepted into analysis after the employment of final fixation criteria. Plots ‘a’, ‘c’, ‘e’, ‘g’, and ‘i’ show accepted saccades. Plots ‘b’, ‘d’, ‘f’, ‘h’ and ‘j’ show excluded saccades. Red circles show position of target stimulus.

Initial Fixation Distance

Final fixation exclusion criterion 4 resulted in saccades with an initial fixation distance closest to the central fixation cross whilst final fixation exclusion criterion 1 resulted in saccades that were initiated furthest from the central fixation cross. Initial fixation distances can be seen in *Table 3.4* along with the ranks assigned to each exclusion criterion.

	Final Fixation 1	Final Fixation 2	Final Fixation 3	Final Fixation 4	Final Fixation 5
mean	0.83	0.82	0.81	0.79	0.81
std error	0.03	0.02	0.03	0.05	0.02
Rank	1	2	3.5	5	3.5

Table 3.4. Initial fixation distance from centre fixation cross for final fixation exclusion criteria. Final fixation exclusion criteria ranks can also be seen for this measure.

Final Fixation Distance

Final fixation exclusion criterion 4 resulted in saccades that had a final fixation distance closest to the saccade target stimulus whilst final fixation exclusion criterion 1 resulted in saccades that had a final fixation furthest from the target. Final fixation distances can be seen in *Table 3.5*. Final fixation exclusion criteria ranks are also included.

	Final Fixation 1	Final Fixation 2	Final Fixation 3	Final Fixation 4	Final Fixation 5
mean	1.83	1.73	1.59	1.08	1.34
std error	0.24	0.20	0.15	0.32	0.25
Rank	1	2	3	5	4

Table 3.5. Final fixation distance from saccade target for final fixation exclusion criteria. Target exclusion criteria ranks can also be seen for this measure.

Decision Matrix

Final fixation exclusion criteria ranks were compiled into the final fixation exclusion criteria decision matrix (see *Table. 3.6*). Saccadic accuracy was computed as the average rank obtained between the initial fixation rank and the final fixation rank. Total rank was the sum rank of percentage excluded trials and saccadic accuracy.

The most appropriate final fixation exclusion criterion from this analysis is final fixation criteria 3 (if the final fixation angle is more than 15° from the target stimulus) as highlighted by ranks gained across saccadic accuracy measures and the percentage number of excluded trials.

Ranks	Final Fixation 1	Final Fixation 2	Final Fixation 3	Final Fixation 4	Final Fixation 5
Percentage errors	5	4	3	1	2
Initial Fixation Position	1	2	3.5	5	3.5
Final Fixation Position	1	2	3	5	4
Saccade Accuracy	1	2	3.25	5	3.75
Total Rank	6	6	6.25	6	5.75

Table 3.6. Final fixation exclusion criteria decision matrix

Initial Fixation Exclusion Criteria

Initial fixation exclusion criteria levels are shown in *Table 3.7* with references included for authors who have employed a given level.

Initial Fixation Exclusion Criteria	Exclusion Description	Authors
1	If the saccade start position is more than 1° from the centre fixation (Eq. 3.1)	Van der Stigchel (2010), Ludwig & Gilchrist (2003), Van der Stigchel, Meeter, & Theeuwes (2007),
2	If the saccade start position is more than 2° from the centre fixation (Eq. 3.1)	Van der Stigchel (2010), Ludwig & Gilchrist (2003), Van der Stigchel, Meeter, & Theeuwes (2007),
3	If the saccade start position is more than 2° from the centre fixation along the vertical plane and more than 1° from the centre fixation along the horizontal plane (Eq. 3.2)	van Zoest, Van der Stigchel, & Barton (2008), Van der Stigchel, Mulckhuysen, & Theeuwes (2009).

Table 3.7. Initial fixation exclusion criteria levels. Table also shows examples of authors who have used that level of exclusion criteria.

Results

Percentage Excluded

Initial fixation exclusion criterion 1 excluded the highest percentage of trials. Initial fixation criterion 3 excluded the lowest percentage of trials. Exclusion criteria were ranked from most excluded trials to least excluded trials. The percentage number of excluded trials can be seen *Table 3.8* as well as exclusion criteria ranks. Saccades excluded and accepted into analysis for exclusion criteria can be seen in *Fig. 3.4*.

	Initial Fixation 1	Initial Fixation 2	Initial Fixation 3
mean	28.45%	2.28%	0.46%
std error	5.46	2.49	3.02
Rank	1	2	3

Table 3.8. Percentage number of excluded trials for initial fixation exclusion criteria. Initial fixation exclusion criteria ranks can also be seen for this measure.

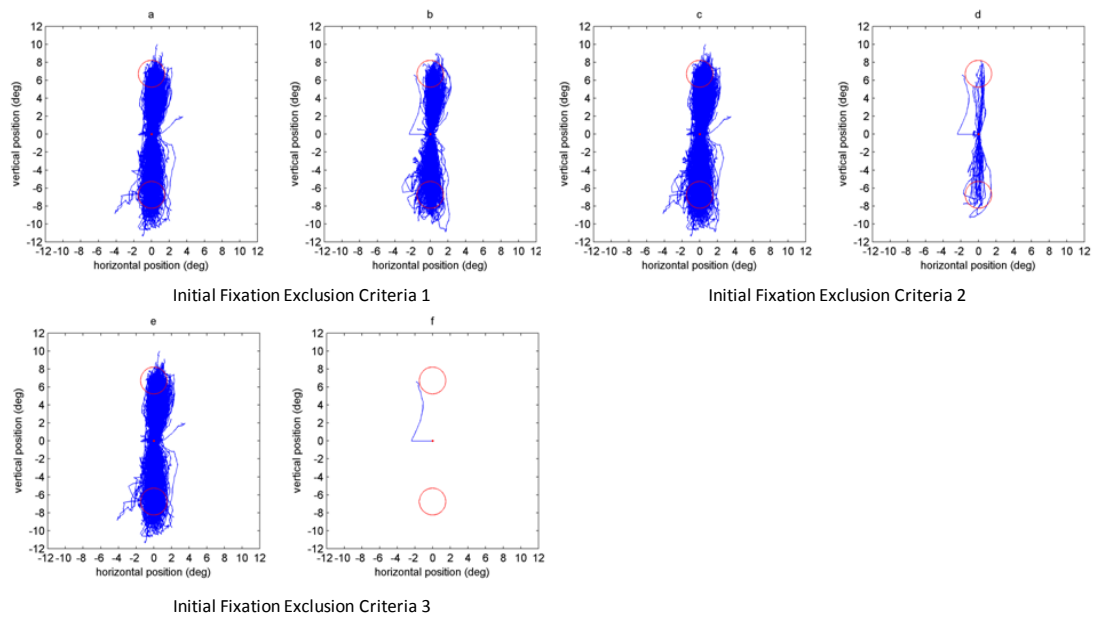


Fig. 3.4. Saccades excluded or accepted into analysis after the employment of initial fixation criteria. Plots 'a', 'c', 'and 'e' show accepted saccades. Plots 'b', 'd', and 'f' show excluded saccades. Red circles show position of target stimulus.

Initial Fixation Distance

Initial fixation exclusion criteria 1 resulted in saccades with an initial fixation distance closest to the central fixation cross. Initial fixation exclusion criteria 2 resulted in saccades that were initiated furthest from the central fixation cross. Initial fixation distances and ranks can be seen in *Table 3.9*.

	Initial Fixation 1	Initial Fixation 2	Initial Fixation 3
mean	0.57	0.77	0.72
std error	0.04	0.02	0.02
Rank	3	1	2

Table 3.9. Initial fixation distance from central fixation cross for initial fixation exclusion criteria. Initial fixation exclusion criteria ranks can also be seen for this measure.

Final Fixation Distance

Initial fixation exclusion criterion 1 resulted in saccades that had a final fixation distance closest to the saccade target stimulus. Employment of initial fixation criteria 2 and 3 resulted in the same degree of distance from the saccade target. Initial fixation distances can be seen in *Table 3.10*. Initial fixation exclusion criteria ranks can also be included.

	Initial Fixation 1	Initial Fixation 2	Initial Fixation 3
mean	2.25	2.30	2.30
std error	0.05	0.03	0.03
Rank	3	1.5	1.5

Table 3.10. Final fixation distance to saccade target for initial fixation exclusion criteria. Initial fixation exclusion criteria ranks can also be seen for this measure.

Decision Matrix

Initial fixation exclusion criteria ranks were compiled into the initial fixation exclusion criteria decision matrix (see *Table. 3.11*). Saccadic accuracy was computed as the average rank obtained between the initial fixation rank and the final fixation rank. Total rank was the sum rank of percentage excluded trials and saccadic accuracy.

Ranks	Initial Fixation 1	Initial Fixation 2	Initial Fixation 3
Percentage errors	1	2	3
Initial FixationPosition	3	1	2
Final Fixation Position	3	1.5	1.5
Saccade Accuracy	3	1.25	1.75
Total Rank	4	3.25	4.75

Table 3.11. Initial fixation exclusion criteria decision matrix

The most appropriate initial fixation exclusion criterion from this analysis is initial fixation criteria 3 (If the saccade start position is more than 2° from the centre fixation along the vertical plane, and more than 1° from the centre fixation along the horizontal plane) as highlighted by ranks gained across saccadic accuracy measures and the percentage number of excluded trials.

Latency Exclusion Criteria

Latency exclusion criteria levels can be seen in *Table 3.12* with references included for authors who have employed a given level.

Latency Exclusion Criteria	Exclusion Description	Authors
1	If the saccade latency is less than 80msecs (Eq. 3.6)	Ludwig & Gilchrist (2003), Van der Stigchel (2010), Van der Stigchel, Meeter, & Theeuwes (2007), van Zoest, Van der Stigchel, & Barton (2008).
2	If the saccade latency is less than 100msecs (Eq. 3.6)	Walker, McSorley, & Haggard (2006).
3	If the saccade latency is more or less than the mean +/- 2.5 times the standard deviation of a participant's latencies (Eq. 3.6)	Van der Stigchel, Meeter, & Theeuwes (2007), van Zoest, Van der Stigchel, & Barton (2008), Van der Stigchel, Mulckhuyse, & Theeuwes (2009).
4	If the saccade latency is more than 500msecs (Eq. 3.6)	Walker, McSorley, & Haggard (2006)
5	If the saccade latency is more than 600msecs (Eq. 3.6)	Godijn & Theeuwes (2004), Theeuwes & Godijn (2004), Van der Stigchel, Meeter, & Theeuwes (2007), van Zoest, Van der Stigchel, & Barton (2008).

Table 3.12. Latency exclusion criteria levels. Table also shows examples of authors who have used that level of exclusion criteria.

Results

Percentage Excluded

Latency exclusion criterion 4 excluded the highest percentage of trials whilst latency exclusion criterion 3 excluded the lowest percentage of trials. Exclusion criteria were ranked from most excluded trials to least excluded trials. The percentage number of excluded trials can be seen in *Table 3.13* as well as exclusion criteria ranks. Saccades excluded and accepted into analysis for exclusion criteria are indicated in *Fig. 3.5*.

	Latency 1	Latency 2	Latency 3	Latency 4	Latency 5
mean	5.47%	7.10%	2.08%	12.04%	6.25%
std error	1.57	1.86	1.24	2.77	1.41
Rank	4	2	5	1	3

Table 3.13. Percentage number of excluded trial for latency exclusion criteria. Latency exclusion criteria ranks can also be seen for this measure.

Initial Fixation Distance

Latency exclusion criterion 3 resulted in saccades with an initial fixation distance closest to the centre fixation cross. Latency exclusion criteria 1, 2, and 5 resulted in saccades that were initiated furthest from the centre fixation cross. Latency fixation distances and ranks are shown in *Table 3.14*.

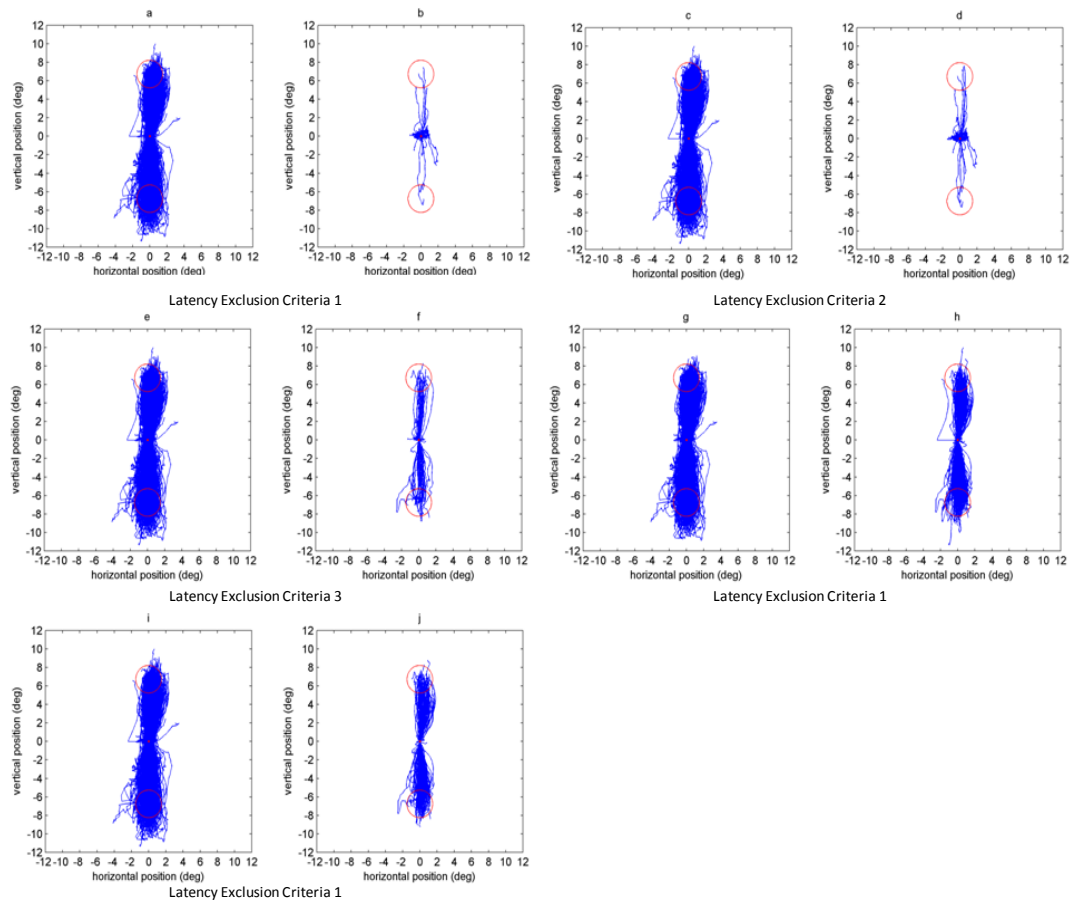


Fig. 3.5. Saccades excluded or accepted into analysis after the imposition of latency exclusion criteria. Plots ‘a’, ‘c’, ‘e’, ‘g’, and ‘i’ show accepted saccades. Plots ‘b’, ‘d’, ‘f’, ‘h’ and ‘j’ show excluded saccades. Red circles show position of target stimulus.

	Latency 1	Latency 2	Latency 3	Latency 4	Latency 5
mean	0.85	0.85	0.77	0.83	0.85
std error	0.01	0.01	0.06	0.02	0.02
Rank	2	2	5	4	2

Table 3.14. Initial fixation distance from the central fixation for latency exclusion criteria. Latency exclusion criteria ranks can also be seen for this measure.

Final Fixation Distance

Latency exclusion criterion 2 resulted in saccades that had a final fixation distance closest to the saccade target stimulus. Employment of latency fixation criteria 1 and 3 resulted in the same degree of distance from the saccade target. Latency exclusion

criterion 4 resulted in saccades that landed furthest from the target. Final fixation distances and ranks can be seen in *Table 3.15*.

	Latency 1	Latency 2	Latency 3	Latency 4	Latency 5
mean	2.13	2.06	2.13	2.42	2.36
std error	0.10	0.08	0.42	0.13	0.12
Rank	3.5	5	3.5	1	2

Table 3.15. Final fixation distance for latency exclusion criteria. Latency exclusion criteria ranks can also be seen for this measure.

Decision Matrix

Latency exclusion criteria ranks were compiled into the latency exclusion criteria decision matrix (see *Table. 3.16*). Saccadic accuracy was computed as the average rank obtained between the initial fixation rank and the final fixation rank. Total rank was the sum rank of percentage excluded trials and saccadic accuracy.

Ranks	Latency 1	Latency 2	Latency 3	Latency 4	Latency 5
Percentage errors	4	2	5	1	3
Initial FixationPosition	2	2	5	4	2
Final Fixation Position	3.5	5	3.5	1	2
Saccade Accuracy	2.75	3.5	4.25	2.5	2
Total Rank	6.75	5.5	9.25	3.5	5

Table 3.16. Latency exclusion criteria decision matrix

The most appropriate latency exclusion criterion from this analysis is latency criteria 3 (If a saccade's latency was more than 2.5 standard deviations from a participant's mean saccade latency) as highlighted by ranks gained across saccadic accuracy measures and the percentage number of excluded trials.

Amplitude Exclusion Criteria

Amplitude exclusion criteria used by previous studies are based on the total distance a saccade was required to travel or the mean amplitude of a participant. Due to differences in the length a saccade was expected to travel across different studies it is not possible to examine the specific amplitude criteria used in previous research. For instance, in a study by Walker, McSorley, and Haggard (2006), saccades were excluded if they had an amplitude of less than 5°. In this experiment, saccade targets are presented at 6.75° away from the centre fixation cross. Saccades in this study could have an amplitude of 4.9° and result in a final fixation point of less than 2° from the target stimulus. It has previously been seen that the most stringent final fixation exclusion criteria excluded saccades that landed above 2° from the target. Thus, it would be inappropriate to utilise this exact amplitude criteria. In this analysis, two levels of amplitude exclusion criteria will be used. These criteria will be based on the total distance a saccade is required to travel in this experiment, and the mean amplitude of participant's saccades. Amplitude exclusion criteria levels can be seen in *Table 3.17*.

Amplitude Exclusion Criteria	Exclusion Description
1	If the saccade amplitude is less or more than 3° from the target stimulus (Eq. 3.5)
2	If the saccade amplitude is less or more than the mean +/- 2.5 times the standard deviation of a participants mean saccade amplitude (Eq. 3.5)

Table 3.17. Amplitude exclusion criteria levels.

Percentage Excluded

Amplitude exclusion criterion 1 excluded the highest percentage of trials whilst amplitude exclusion criterion 2 excluded the lowest percentage of trials. Exclusion criteria were ranked from most excluded trials to least excluded trials. The percentage number of excluded trials can be seen *Table 3.18*. Saccades excluded and accepted into analysis for exclusion criteria can be seen in *Fig. 3.6*.

	Amplitude 1	Amplitude 2
mean	20.12%	3.06%
std error	2.53	2.53
Rank	1	2

Fig. 3.18. Percentage number of excluded trials for amplitude exclusion criteria. Amplitude exclusion criteria ranks can also be seen for this measure.

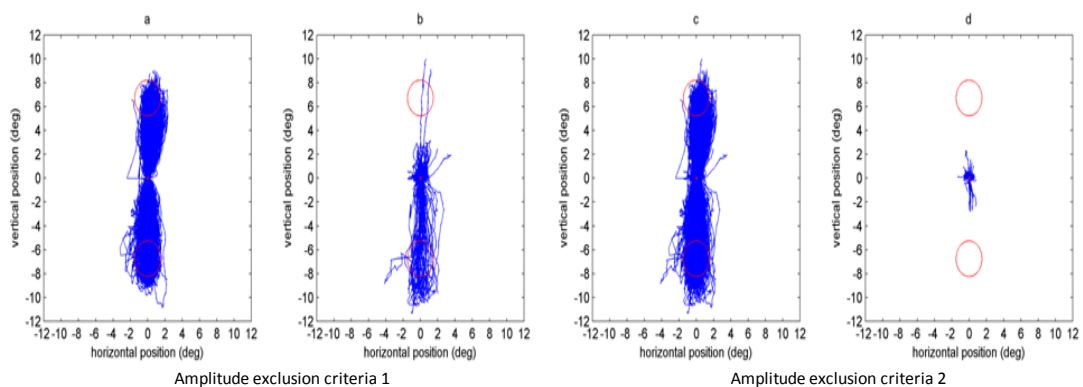


Fig. 3.6. Saccades excluded or accepted into analysis after the imposition of initial fixation criteria. Plots 'a' and 'c' show accepted saccades. Plots 'b' and 'd' show excluded saccades. Red circles show position of target stimulus.

Initial Fixation Distance

Amplitude exclusion criterion 2 resulted in saccades with an initial fixation distance closest to the centre fixation cross whilst amplitude exclusion 1 resulted in saccades

with an initial fixation distance furthest from the centre fixation cross. Amplitude fixation distances and ranks can be seen in *Table 3.19*.

	Amplitude 1	Amplitude 2
mean	0.86	0.85
std error	0.01	0.01
Rank	1	2

Table. 3.19. Initial fixation distance for amplitude exclusion criteria. Amplitude exclusion criteria ranks can also be seen for this measure.

Final Fixation Distance

Amplitude exclusion criteria 1 resulted in saccades that had a final fixation distance closest to the saccade target stimulus. Imposition of amplitude exclusion criteria 2 resulted in saccades that landed furthest from the target stimulus. Final fixation distances and ranks can be seen in *Table 3.20*.

	Amplitude 1	Amplitude 2
mean	1.38	2.20
std error	0.12	0.12
Rank	2	1

Table. 3.20. Final fixation distance for amplitude exclusion criteria. Amplitude exclusion criteria ranks can also be seen for this measure.

Decision Matrix

Amplitude exclusion criteria ranks were compiled into the amplitude exclusion criteria decision matrix (see *Table. 3.21*). Saccadic accuracy was computed as the average rank obtained between the initial fixation rank and the final fixation rank. Total rank was the sum rank of percentage excluded trials and saccadic accuracy.

Ranks	Amplitude 1	Amplitude 2
Percentage errors	1	2
Initial FixationPosition	1	2
Final Fixation Position	2	1
Saccade Accuracy	1.5	1.5
Total Rank	2.5	3.5

Table 3.21. Amplitude exclusion criteria decision matrix

The most appropriate amplitude exclusion criterion from this analysis is amplitude criteria 2 (If a saccade's amplitude was more than 2.5 standard deviations from a participant's mean saccade amplitude) as highlighted by ranks gained across saccadic accuracy measures and the percentage number of excluded trials.

Discussion

This experimental analysis was designed to ascertain the most appropriate saccade exclusion criteria for use in the experimental chapters of this thesis. The different levels of each exclusion criterion were based on exclusion criteria presented in previous studies. Saccade exclusion criteria included the initial and final fixation of a saccade, the latency of a saccade and the amplitude of a saccade. Formulae and definitions have been presented for these exclusions.

Data was inputted into 'decision matrices' which ranked exclusion criteria on the percentage of trials excluded and saccadic accuracy after the imposition of that criteria. The most appropriate exclusion criteria to be used are as follows: Final fixation exclusion criteria 3 (if the final fixation angle is more than 15° from the target stimulus), initial fixation exclusion criteria 3 (If the saccade start position is more than 2° from the centre fixation along the vertical plane, and more than 1° from the centre fixation along the horizontal plane), latency exclusion criteria 3 (If a saccade's latency

was more than 2.5 standard deviations from a participant's mean saccade latency), and amplitude exclusion criteria 2 (If a saccade's amplitude was more than 2.5 standard deviations from a participant's mean saccade amplitude). These exclusion criteria will be used throughout this thesis to qualify an accurate saccade.

MEASURING A SACCAD

The next section of this chapter will define measurements used throughout this thesis to measure a saccade trajectory. Saccade measurements are based on the initial deviation of a saccade trajectory, the mean deviation of a saccade trajectory, the mean direction of a saccade trajectory, the latency of a saccade, and the accuracy of a saccade in relation to a saccade target stimulus (notably different to saccadic accuracy defined in the previous section of this chapter).

Initial Deviation and Saccade Deviation

The initial deviation of a saccade is defined, in this thesis, as the mean deviation of a saccade within a given period of time (20 samples/ 10msec) after saccade onset (Eq. 3.7).

$$\theta = \frac{1}{20} \sum_{i=1}^{20} \left(\tan^{-1} \frac{opp_i}{adj_i} \right)$$

$$opp_i = x_i - Fx \quad adj_i = y_i - Fy$$

where x_i = x coordinate of sample number i ,

y_i = y coordinate of sample number i ,

Fx = fixation x coordinate,

Fy = fixation y coordinate.

(Eq. 3.7)

Saccade deviation is defined as the mean deviation of the whole saccade trajectory (Eq. 3.8).

$$\theta = \frac{1}{n} \sum_{i=1}^n \left(\tan^{-1} \frac{opp_i}{adj_i} \right)$$

$$opp_i = x_i - Fx \quad adj_i = y_i - Fy$$

where x_i = x coordinate of sample number i ,

y_i = y coordinate of sample number i ,

Fx = fixation x coordinate,

Fy = fixation y coordinate.

(Eq. 3.8)

Two theories have previously been highlighted relating to the deviation of saccades: the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá. 1987; Rizzolatti, Riggio, & Sheliga, 1994), and the population coding theory (Tipper, Howard, & Houghton, 2000). The premotor theory of attention stipulates that attentional capture, due to the presentation of a distractor, will result in corresponding neuronal activation in the SC and the subsequent deviation of goal-directed saccades. In turn, the population coding theory suggests that the presentation of a distractor will result in a shift in neuronal activation in the SC and subsequent deviation in the trajectories of saccades.

By measuring the initial deviation of a saccade, the influence of attentional capture on the trajectory of a saccade can be observed and it has been suggested that the initial deviation of a saccade is able to highlight the effect of two competing saccade

programmes (Ludwig and Gilchrist, 2002); as such it is a valuable measurement when exploring oculomotor inhibition. Saccade deviation, by measuring the mean deviation of a saccade, will be able to determine how a shift in neuronal activation influences the entire trajectory of a saccade.

Furthermore, McSorley, Haggard, and Walker (2004) have suggested that saccade deviation is the result of oculomotor inhibition in the SC whereas deviation back towards a saccade target is underpinned by an additional drive signal from the CB. In turn, this model suggests the possibility of different levels of deviation for the initial deviation of a saccade and the mean deviation of a saccade trajectory.

Saccade trajectories have been found to be differentially influenced by VF (for e.g., Zhou & King, 2002). Moreover separable vision pathways have been hypothesised to process information in the upper and lower (Previc, 1990) and left and right (D'Esposito et al., 1998; Köhler et al. 1995) VFs. Thus, in this thesis, VFs were not collapsed in order to compute the deviation of a saccade. By not collapsing across the VFs both positive and negative values of saccade deviation can be observed dependent on the VF a target is presented. If the centre fixation is always taken as the value $x = 0$, $y = 0$ then the upper left quadrant will be $x = n-$, $y = n+$ (where n = a given number along the given axis) and the overall deviation value for the upper left quadrant will be negative. In turn the deviation value for the upper right quadrant will be positive, the lower left quadrant positive, and the lower right quadrant will be negative.

Mean Direction

The mean direction of a saccade is defined as the mean direction along the axis a saccade travels (see Eq. 3.9). This measure is used to simply quantify the overall direction a saccade travels. The degree of directional deviation will also be very simply observed by this measure.

$$\frac{1}{n} \sum_{i=1}^n (x_i - Fx)$$

where x_i = x coordinate of sample number i ,

Fx = fixation x coordinate.

(Eq. 3.9)

Saccade Latency and Saccade Accuracy

Saccade latency has been defined in the previous section of this chapter as the time it takes to initiate a saccade after the receipt of the saccade cue (see Eq. 6). Saccade accuracy to a target can also be described as the final fixation point of a saccade. To calculate this measure Eq. 3.3 will be used.

SUMMARY

This chapter has justified and defined saccade exclusion criteria and saccade measures that will be used throughout this thesis. This will enable a consistent approach to measuring and qualifying a saccade to be reached. The exclusion criteria used throughout this thesis will be as follows: if the final fixation angle of a saccade is more than 15° from the target stimulus, if the saccade start position is more than 2° from the centre fixation along the vertical plane, and more than 1° from the centre fixation

along the horizontal plane, if saccade latency is more than 2.5 standard deviations from a participant's mean saccade latency, and if saccade amplitude is more than 2.5 standard deviations from a participant's mean saccade amplitude. Furthermore measures used to explore saccade characteristics in this thesis have been given as follows: initial deviation, saccade deviation, saccade latency, saccade accuracy, and mean direction.

The next chapter is the first experimental chapter. It explores the extent of saccade deviation when VWM is occupied with a concurrent saccade task. In this way it attempts to understand the extent of VWM involvement during the deviation of saccades.

Chapter 4

Extent of visual working memory

involvement during saccade generation

A dual paradigm experiment

This thesis is concerned with the involvement of VWM in the generation of saccades; thus this experimental chapter attempts to clarify this level of involvement. Research indicates that saccades deviate away from information presented in peripheral vision and stored in VWM (Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Olivers, 2006). König (2010) suggested that deviation away from memorised stimuli in peripheral vision could be due to prolonged IOR at the corresponding neuronal site in the SC. In this chapter, a dual paradigm experiment is conducted in order to investigate whether saccade trajectories are influenced when VWM and saccade tasks are run concurrently. The concurrent running of cognitive tasks utilising comparable systems should reduce performance levels of both tasks. Participants were presented with three conditions: 1. a saccade-only condition, 2. a memory-only condition, and 3. a dual-task condition (combining condition 1 and 2). VWM facilitation of oculomotor inhibition was observed during the saccade-only condition; however, this inhibition was not apparent during the dual-task condition. Moreover, results suggest that deviation was reduced during the dual-task condition in comparison to the saccade-only condition.

EXTENT OF VISUAL WORKING MEMORY- OCULOMOTOR INTERACTION

The nature and extent of VWM involvement during saccade execution remains unresolved. In studies conducted by Theeuwes and colleagues (Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Chizk, 2006) saccades were found to deviate away from spatial locations briefly presented in peripheral vision. Moreover, Theeuwes, Van der Stigchel, and Chizk (2006) found that saccadic deviation due to holding spatial locations in VWM was a separable effect to IOR. This conclusion is

supported by evidence of separable mechanisms for attentional IOR and saccadic IOR (Godijn & Theeuwes, 2004; Sumner et al., 2004) and also evidence suggesting that attentional IOR may mediate the extent of saccadic IOR and saccade deviations (Dorris et al., 2002; Theeuwes & Van der Stigchel, 2009). Belopolsky and Theeuwes (2011) also found that saccades deviated away from spatial information held in VWM. Moreover, these researchers found that saccade latencies to spatial locations held in VWM were also shorter than the saccadic latencies expressed when spatial locations were not held in VWM.

Saccade deviation, in the presence of a peripheral distractor, has been linked to competitive inhibition in neurons in the SC (Rizzolatti, Riggio, & Sheliga, 1994), or a shift in activation in the spatially coded map of neurons in the SC (Tipper, Howard, and Houghton, 2000). According to these theories, oculomotor inhibition of neurons coding for the spatial location of a distractor leads to saccade trajectory deviation from a presented distractor location. For example, if participants attend to a spatial location, and are then required to suppress the initiation of a saccade programme linked to that spatial location, saccades made to a location in close proximity to the initial and suppressed location will curve away due to neuronal inhibition in the SC. In a study by Van der Stigchel, Meeter, and Theeuwes (2007), saccades were found to deviate away from cued locations in close proximity to saccade targets.

In a dual-task paradigm, Van der Stigchel (2010) found evidence highlighting reduced saccade performance when saccade and VWM tasks were run concurrently. Van der Stigchel (2010) added a secondary verbal working memory task to a saccade execution task. Participants made more saccadic errors during the condition with the added

verbal working memory component than during a condition requiring just the saccade. The aim of this chapter will be to enhance current knowledge of how saccade trajectories are influenced when VWM and saccade tasks are run concurrently.

Dual paradigm experiments have been employed to increase understanding of a range of neurological and cognitive functions including working memory and postural control (Dault, Frank, & Allard, 2001), arithmetic and working memory (Lee & Kang, 2002), executive dysfunction (Baddeley, Della Sala, Pagano, & Spinnler, 1997), verbal working memory (Gruber, 2001), domain specificity in working memory (Cocchini, Logie, Della Sala, MacPherson, & Baddeley, 2002), and the relationship between visual search and VSWM (Woodman & Luck, 2004). Dual paradigm experiments advantageously exploit a deficit in cognitive performance during activities utilising common cognitive components in order to make inferences regarding the neuropsychological nature of the functions under consideration.

Van der Stigchel (2010) explored the influence of verbal working memory during a saccade execution task. Initial saccade errors towards a distractor stimulus, as opposed to towards a target stimulus, increased during a dual-task (involving the generation of a saccade and a further verbal working memory task) in comparison to a singular saccade-only task. Van der Stigchel (2010) concludes that these results indicate working memory involvement during oculomotor inhibition of distractor stimuli. However, the results reported by Van der Stigchel (2010) could be described as showing the distraction effect of a secondary, working memory, task on the oculomotor system. In a study by Kowler, Anderson, Doshier & Blaser (1995) it was found that saccades to targets were facilitated by directing perceptual attention to the

likely location of the saccade goal. Kowler et al. (1995) suggest that the endpoint of saccades, and thus saccade accuracy, is reliant on perceptual attention at the locus of a saccade target. It is possible that an alternative explanation for Van der Stigchel's (2010) results could be that during the dual-task, perceptual attention was directed away from the locus of the saccade target. In order to draw conclusions of dual-task interference on the oculomotor system, and in turn highlight a VWM component during oculomotor inhibition, it is argued that Van der Stigchel (2010) would be required to report working memory behavioural data.

In the study by Woodman and Luck (2004), dual-task impairment inferred VSWM involvement during visual search tasks. In a dual-task condition participants expressed slower reaction times during a visual search task and reduced percentage accuracy during a VSWM task in comparison to single task conditions. Reduced task performance in dual-task conditions being indicative of common neural mechanisms involved in visual search and VSWM tasks.

Cocchini et al. (2002) highlighted separable systems for the storage of verbal and visual working memory using a dual paradigm experiment. Performance on a verbal working memory task was not affected by an additional VWM task when tasks were run concurrently. However, when participants performed a concurrent articulatory suppression task and verbal memory task there was a marked performance deficit. These studies highlight a need to present behavioural results from both single task performances to be contrasted with performance during dual tasks. Moreover, Cocchini et al. (2002) highlights dissociable systems within working memory for the processing of verbal working memory and VWM. A VWM task had no discernable

effect on a verbal working memory task but an articulatory suppression task did have a significant effect on the verbal working memory task. This chapter will require a VWM task to be performed concurrently with a saccade task in an attempt to further understanding of how the oculomotor system is influenced by working memory.

If remembering an object in peripheral vision results in deviation away from that object, then in a condition in which VWM is preoccupied a decreased amount of deviation may be expected. It is therefore expected that greater deviation will be apparent during a saccade when the VWM system is available in comparison to occasions when this system is occupied by running a concurrent task.

The current study aims to extend the work by Van der Stigchel (2010) in order to understand the extent of VWM and oculomotor system interaction. It employs a dual paradigm method in order to ascertain how saccade generation is impacted by a loaded VWM system. Thus, three conditions will be presented to participants: 1. a saccade-only condition, 2. a memory-only condition, and 3. a dual-task condition. It is thought that if there is a relationship between the oculomotor system and the VWM system, performance during the dual-task condition will be reduced in comparison to the performance during the first two single conditions.

Experiment 2

Method

Participants

Twelve participants were recruited for this study; four male and eight female ($M_{\text{age}} = 22.75$, $SD_{\text{age}} = 4.71$). Ten participants classed themselves as right-handed, two

participants were left-handed. All participants had normal or corrected colour vision. All participants gave informed consent; the study conformed to all applicable ethical guidelines.

Apparatus

The apparatus used to implement the experimental conditions was identical with that reported in Chapter 3 of this thesis.

Stimuli

The stimuli in this experiment were also similar to that presented in chapter 3. Stimuli comprised of a central fixation cross, subtending 0.5° visual angle, presented in either green or red, along with a target and distractor stimuli presented in white and measuring 1.5° . Stimuli were presented on a grey background. Target stimuli were presented at $\pm 6.76^\circ$ along the vertical plane. The distractor stimuli were presented at $x = \pm 5.4^\circ$, $y = \pm 4.9^\circ$. These locations were also used in Theeuwes et al. (2005) study. Gabor memory stimuli were created vertically at 0° rotation and frequencies of 1 to 8 cpd (cycles per degree) and subtended at 1.5° ; see *fig. 4.1*.

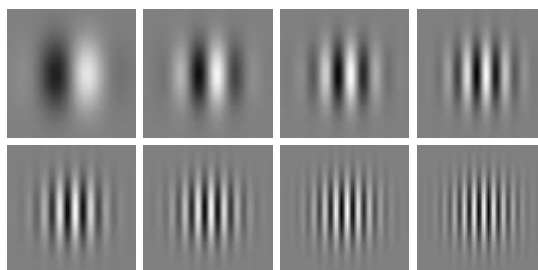


Fig. 4.1. Gabor memory stimuli.

Procedure

The experiment comprised of three conditions. Participants completed a nine-point calibration routine before the start of each condition. Prior to the presentation of each condition, participants also completed 15 practice trials. In condition 1 a saccade-only task was completed, in condition 2 a memory-only task was completed, and in condition 3 both memory and saccade tasks were completed (i.e. a dual-task condition). Conditions were counterbalanced across participants. Participants completed 128 randomised trials in each condition.

Condition 1 (Saccade-only)

In the saccade-only condition (see *fig. 4.2*) participants were instructed to make an accurate eye movement towards a target stimulus. Participants were instructed to fixate on a red central fixation cross until it turned green (the saccade 'go' signal). The target stimulus remained on screen from the beginning of the trial until after saccade initiation and completion. Target stimuli were presented in either the upper or lower section of the visual field (VF). After 500ms a distractor stimulus would appear in one of the four aforementioned positions for 500ms. Distractor stimuli would appear in either the same hemifield as the target object (close proximity), or the opposite hemifield (far proximity) as the target object, with an equal likelihood of appearing in either of these proximal locations. After 2000ms participants received the 'go' signal to make a saccade towards, and fixate upon, the target stimulus. Participants were not instructed on the presence of the distractor stimulus.

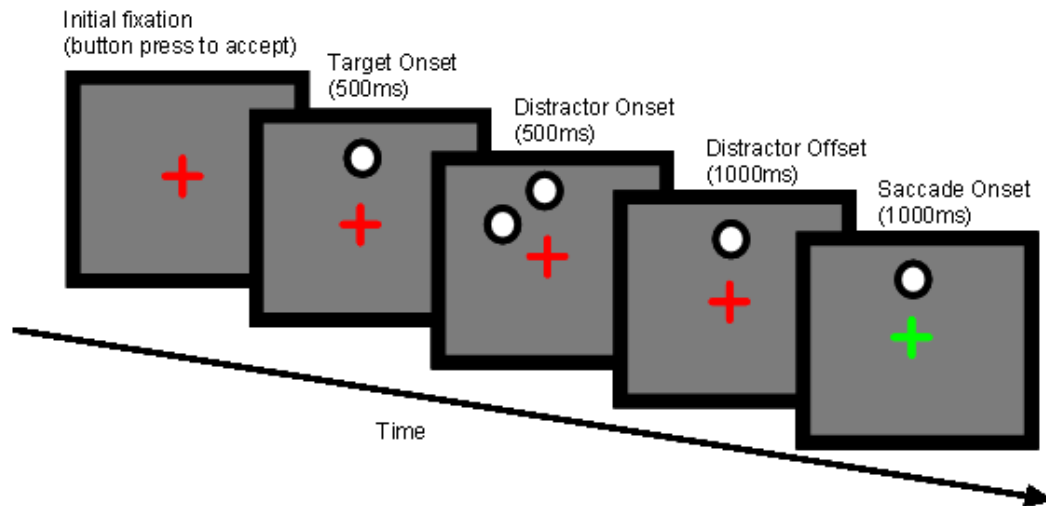


Fig. 4.2. Saccade-only condition.

Condition 2 (Memory-only)

In the memory-only condition (see *figure 4.3.*) participants were presented with a set of three Gabor stimuli presented against a grey background. These Gabor stimuli persisted on screen during the retention phase of the trial for 1500ms, after which they would disappear for 3000ms. Next, participants were presented with a single Gabor stimulus and were required to state whether this stimulus was originally presented within the initial set of three Gabors by pressing the appropriate response box button. In half of the presented trials the Gabor image would have been previously presented, and in the remaining 50% of trials they had not been previously seen.

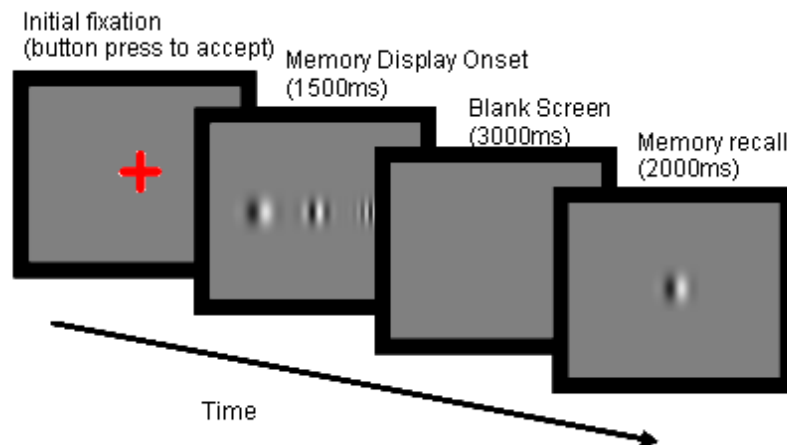


Fig. 4.3. Memory-only condition

Condition 3 (Dual-task)

The dual task condition combined the saccade-only task and the dual-task conditions. The saccade task was introduced into the memory-task during the 3000ms blank period. This dual-task procedure is illustrated in *fig. 4.4*.

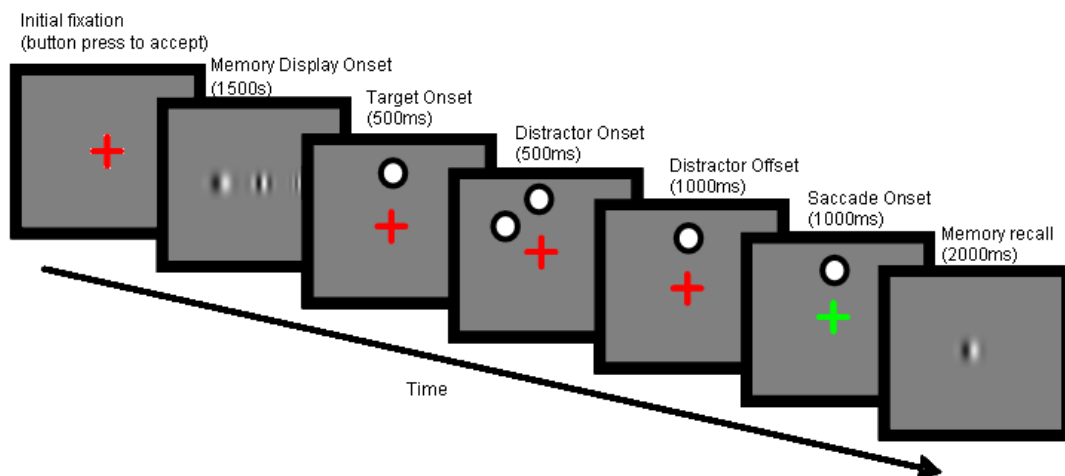


Fig. 4.4. Dual-task condition.

Design

Data were filtered using MATLAB (R2010a, Mathworks, Natick, MA) using the same methods and exclusion criteria justified in chapter 3. Saccade measures explored were: saccade deviation, initial deviation, saccade accuracy, and saccade latency. These measures formed the dependent variables for the saccade portion of this experiment. A 2×2 repeated measures design was implemented to ascertain whether the dependent variables were influenced by the proximity of a distractor in relation to a target (close proximity vs. far proximity) or target VF (upper VF vs. lower VF) in both the saccade-only and dual-task conditions. A further $2 \times 2 \times 2$ repeated measures analysis was used to ascertain whether there was a difference across conditions with proximity, target VF, and condition (saccade-only vs. dual-task) as the independent variables. Planned comparisons will explore any significant interactions between the independent variables.

To ascertain differences between the behavioural working memory data, a paired-samples design was implemented comparing the total percentage errors (dependent variable) for the memory-only and dual-task conditions.

Results

Initial Deviation

A 2 (distractor proximity to target: 1. close proximity, 2. far proximity) $\times 2$ (target VF: 1. upper VF, 2. lower VF) repeated measures ANOVA reported no significant main effects for distractor proximity to target [$F(1, 11) = 1.87, p = .20, \eta p^2 = .20$] or for target VF [$F(1, 11) = 1.27, p = .28, \eta p^2 = .10$] on the initial deviation of a saccade. However, a significant interaction between these two variables was highlighted; $F(1, 11) = 15.53, p$

$< .005$, $\eta p^2 = .59$. Planned comparisons indicated a significant ($p = < .05$) decrease in initial deviation for saccades that were directed to the upper VF after the presentation of close proximity distractors ($M = -11.64$, $SE = 4.54$) in comparison to far proximity distractors ($M = -17.58$, $SE = 3.59$); a result not replicated in saccades directed to the lower VF. In this hemifield, a slightly reduced level of initial deviation was found after the presentation of far proximity distractors ($M = -7.98$, $SE = 3.88$) in comparison to close proximity distractors ($M = -9.13$, $SE = 3.56$); though planned comparisons did not find that this reduction was significant ($p > .05$); see *fig. 4.5*

A 2×2 repeated measures ANOVA revealed no significant main effects during the dual-task condition for distractor proximity to target [$F(1, 11) = 0.02$, $p = .90$, $\eta p^2 = .00$] or target VF [$F(1, 11) = 1.80$, $p = .21$, $\eta p^2 = .14$]. Moreover, no interaction effect was observed during the dual-task condition contrary to that found during the saccade-only condition.

A further 2 (condition: 1. saccade-only, 2. dual-task) $\times 2$ (distractor proximity to target: 1. close proximity, 2. far proximity) $\times 2$ (target VF: 1. upper VF, 2. lower VF) repeated measures ANOVA found no significant main effects for distractor proximity [$F(1, 11) = 0.83$, $p = .38$, $\eta p^2 = .07$] or target VF [$F(1, 11) = 1.85$, $p = .20$, $\eta p^2 = .14$]. A trend towards significance was found for condition [$F(1, 11) = 4.05$, $p = .07$, $\eta p^2 = .27$] indicating that the initial deviation of a saccade tended to be greater during the saccade-only ($M = -11.59$, $SE = 1.97$) in comparison to the dual condition ($M = -0.85$, $SE = 1.93$); see *fig 4.6*.

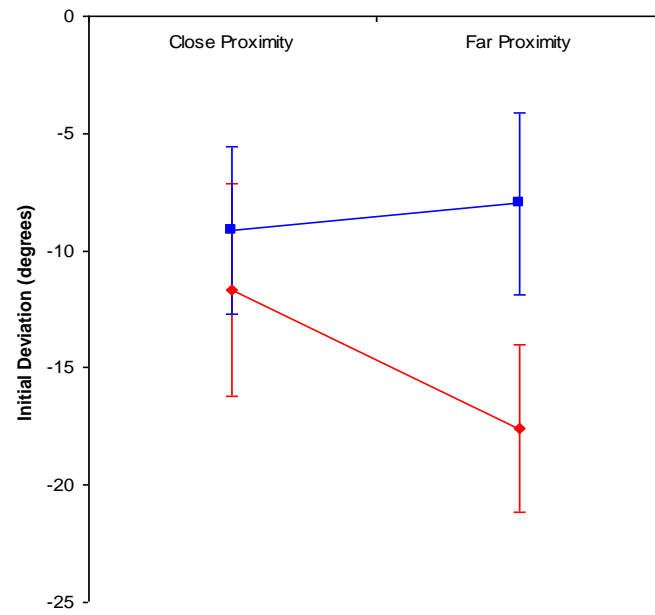


Fig. 4.5. Distractor proximity to a target \times target VF interaction during the saccade-only condition. Red line denotes saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

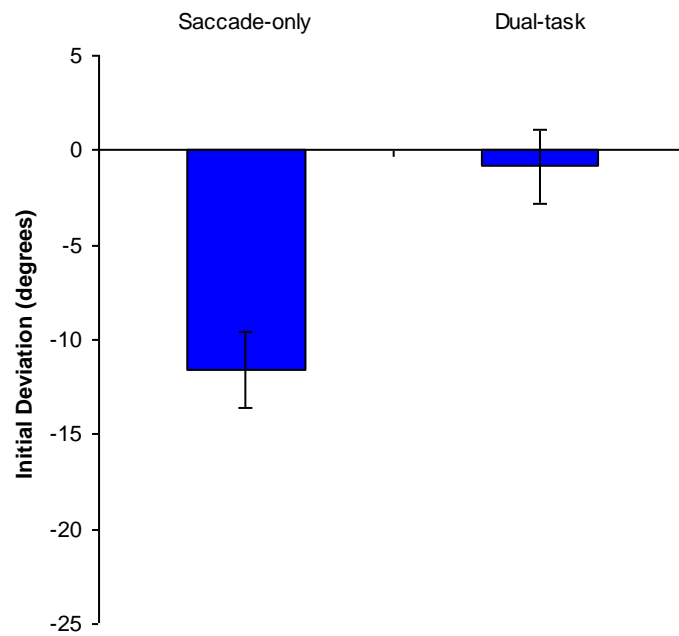


Fig. 4.6. Mean initial deviation for conditions. Error bars represent ± 1 SE.

A three-way interaction across all independent variables was also observed [$F(1, 11) = 7.89$, $p < .05$, $\eta p^2 = .42$]. As aforementioned, during the saccade-only condition, saccades to the upper VF yielded a significantly reduced degree of initial deviation after the presentation of close proximity distractors in comparison to after the presentation of far proximity distractors ($p < .05$); a result not found during the dual-task condition. Further planned comparisons also indicate a significantly ($p < .05$) reduced degree of initial deviation for saccades directed to the upper VF after the presentation of far proximity distractors during the dual-task condition ($M = -3.49$, $SE = 2.96$) in comparison to the saccade-only condition ($M = -17.58$, $SE = 3.59$); see *fig. 4.7*. This result was also not replicated in the initial deviation of saccades after the presentation of close proximity distractors.

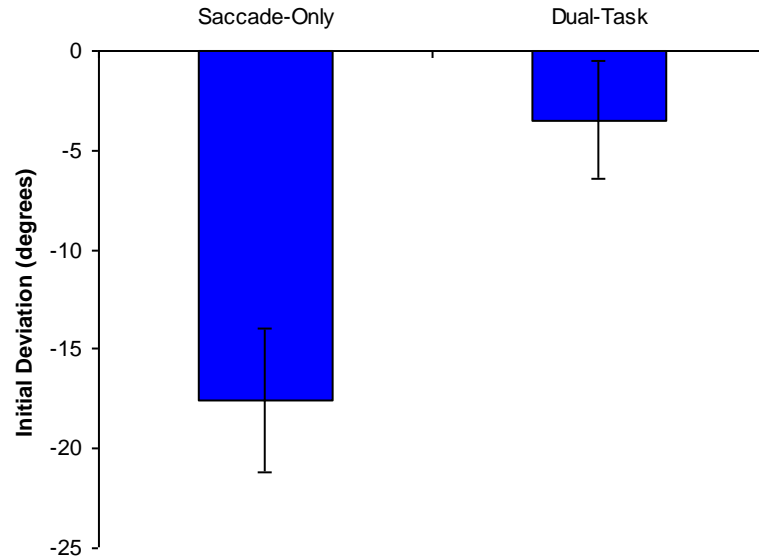


Fig. 4.7. Initial deviation for saccades directed to the upper VF after the presentation of far proximity distractors during dual-task and saccade-only conditions. Error bars represent ± 1 SE.

Saccade Deviation

A 2×2 repeated measures ANOVA found no significant main effects on saccade deviation for target VF during the saccade-only condition [$F(1, 11) = 0.03, p = .87, \eta p^2 = .00$] or dual-task condition [$F(1, 11) = 0.76, p = .40, \eta p^2 = .06$]. Moreover no significant main effect was found for distractor proximity to target during the dual-task condition [$F(1, 11) = 2.06, p = .18, \eta p^2 = .16$] though a trend towards significance was found during the saccade-only condition [$F(1, 11) = 3.94, p = .08, \eta p^2 = .25$]. This trend indicated that saccades tended to deviate to a lesser degree when distractors were presented in close proximity to a target ($M = 0.08, SE = 1.12$) in comparison to far proximity distractors ($M = 0.45, SE = 1.24$). No interaction effects were observed for either condition.

A $2 \times 2 \times 2$ repeated measures ANOVA revealed no significant main effect for target VF [$F(1, 11) = 0.38, p = .55, \eta p^2 = .03$] or condition [$F(1, 11) = 2.80, p = .12, \eta p^2 = .20$]. A significant main effect for distractor proximity was found; $F(1, 11) = 6.63, p < .05, \eta p^2 = .38$. Saccades deviated to a significantly greater extent when distractors were presented in close proximity to a target ($M = 0.91, SE = 0.79$) in comparison to when distractors were presented further away from a target ($M = 0.42, SE = 0.80$); see *fig 4.8*. No significant interactions were observed.

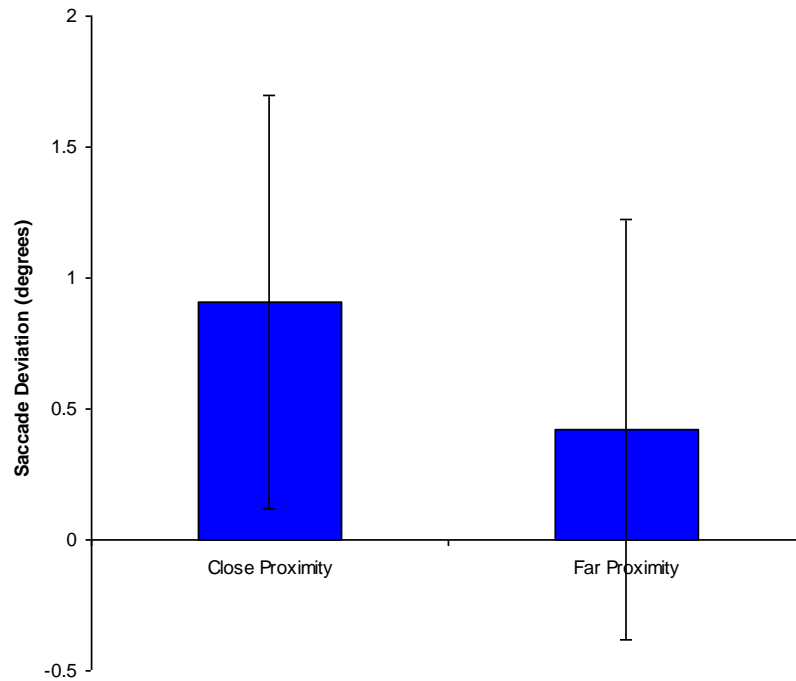


Fig. 4.8. Mean saccade deviation for distractor proximity to a target. Error bars represent ± 1 SE.

Saccade Accuracy

No significant results were found for the saccade accuracy measure during either the saccade-only condition (distractor proximity to target: $F(1, 11) = 0.01$, $p = .92$, $\eta p^2 = .00$, target VF: $F(1, 11) = 1.43$, $p = .26$, $\eta p^2 = .12$), the dual-task condition (distractor proximity to target: $F(1, 11) = 2.84$, $p = .12$, $\eta p^2 = .21$, target VF: $F(1, 11) = 1.19$, $p = .30$, $\eta p^2 = .10$), or indeed across the two conditions (condition: $F(1, 11) = 2.48$, $p = .14$, $\eta p^2 = .18$, distractor proximity to target: $F(1, 11) = 1.23$, $p = .29$, $\eta p^2 = .10$, target VF: $F(1, 11) = 0.32$, $p = .58$, $\eta p^2 = .03$).

Saccade Latency

No significant results were found for saccade latency during the saccade-only condition (distractor proximity to target $F(1, 11) = 0.93$, $p = .36$, $\eta p^2 = .08$, target VF: $F(1, 11) =$

0.81, $p = .39$, $\eta p^2 = .07$), the dual-task condition (distractor proximity to target: $F(1, 11) = 1.58$, $p = .24$, $\eta p^2 = .24$, target VF: $F(1, 11) = 1.61$, $p = .23$, $\eta p^2 = .13$), or across the two conditions (condition: $F(1, 11) = 0.60$, $p = .46$, $\eta p^2 = .05$, distractor proximity to target: $F(1, 11) = 2.00$, $p = .19$, $\eta p^2 = .15$, target VF: $F(1, 11) = 1.59$, $p = .23$, $\eta p^2 = .13$).

Memory Data

A paired-sample t-test revealed a significant difference between the percentage of correct memory trials between the memory-only condition and the dual-task condition; $t(11) = -3.72$, $p < .005$. Results suggests that performance levels deteriorated during the dual-task condition in comparison to the memory-only condition (see *fig. 4.9.*); participants scored significantly lower during the dual-task condition ($M = 59.05$, $SD = 6.94$) than the memory-only task ($M = 63.65$, $SD = 5.76$).

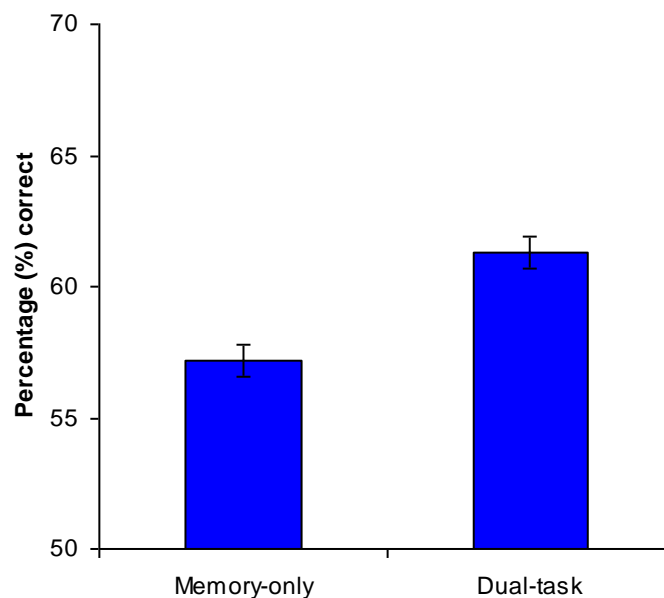


Fig. 4.9. Mean percentage correct trials during the memory-only and dual-task conditions.

Discussion

This study explored how a dual-task paradigm influenced the saccade trajectory characteristics. In this way the interaction between the oculomotor system and VWM could be examined. König (2010) has suggested that the deviation of saccades, after the brief presentation of a distractor, is consequent on prolonged oculomotor inhibition. In this study, the deviation of saccades was explored in conditions running concurrent VWM and saccade tasks after the brief presentation of distractor stimuli in peripheral vision. It was thought that if VWM facilitates saccade deviation as proposed by Belopolsky and Theeuwes (2011), reduced VWM performance and a reduced degree of deviation in saccades would be evident.

Three main findings were observed in this experiment: 1. memory performance decreased as a product of the concurrent running of saccade and VWM tasks, 2. deviation reduced during the dual-task condition in comparison to the saccade-only condition, and 3. increased initial deviation of saccade trajectories can be observed in conditions not involving the active rehearsal of briefly presented information. VF differences were also found to influence the deviation of saccades during the saccade-only condition.

Memory performance during concurrent VWM and saccade tasks

Memory performance deterioration was evident during the dual-task condition in comparison to the saccade-only condition. This result suggests that the VWM system was in concurrent use during the dual-task condition for both the memory component of the task and the saccade component of the task. This result supports conclusions by Belopolsky and Theeuwes (2011) of a VWM facilitation of oculomotor inhibition by the

maintenance of visual information during oculomotor preparation. If memory performance did not suffer during the dual-task condition this would imply that this cognitive faculty was not in 'dual' use and thus would lead to the conclusion that VWM was not being used during oculomotor preparation.

During a dual-task paradigm, it is thought that when one cognitive system is utilised to perform two concurrent tasks, performance on those tasks will be reduced in relation to when a cognitive system is required to perform only one task. For instance, when a secondary articulatory suppression task was added to a verbal working memory task, verbal working memory performance was reduced (Cocchini et al., 2002). In experiment 1 of this thesis a reduction in VWM ability suggests that the VWM system is utilised during the generation of saccadic eye movements.

This experiment also supports findings by Van der Stigchel (2010) who reported evidence of working memory recruitment during saccade execution. In this study, Van der Stigchel (2010) reported that saccade accuracy deteriorated as a function of the concurrent running of a verbal working memory task and a saccade execution task. A finding of memory deterioration in this experiment, as well as to be discussed deviation in the trajectories of saccades, supports the findings by Van der Stigchel (2010). Moreover, this experiment further specifies VWM as being particularly recruited by the oculomotor system as opposed to the working memory system as a whole. The remainder of this discussion will focus on the influence of this VWM recruitment during saccade execution.

VWM facilitation of oculomotor inhibition

The deviation of saccades was reported by two measures during this experiment: initial deviation and saccade deviation. In this way the influence of a briefly presented distractor could be discerned from the initial and the mean impact on a saccade trajectory. Results differed across the two measures; the degree of initial deviation appeared contingent on condition and VF whilst the degree of saccade deviation appeared to differ due to the proximity of presented distractors.

During the saccade-only condition, a significant interaction indicated that in the upper VF the proximity of a distractor in relation to a target influenced the degree of initial deviation. This influence was not observed in the lower VF which reported a more consistent, though very slightly reduced, degree of initial deviation after the presentation of far proximity distractors in comparison to close proximity distractors. Separable visual processing streams are theorised to be active for the upper and lower VFs. The upper VF, being superior in the processing of visual object stimuli, is thought to rely on the ventral visual pathway. The lower VF, by way of contrast, is thought to rely on the dorsal visual pathway (Previc, 1990). The interaction between VF and distractor proximity suggests that the visual processing pathways may contribute in different ways to the deviation of saccades.

No significant main effects, and no significant interactions, were found for initial deviation during the dual-task condition contrary to that found during the saccade-only condition. This suggests that oculomotor inhibition was, to some extent, influenced by the concurrent running of the memory task and the saccade task. This conclusion is corroborated by a three way interaction across condition, distractor

proximity, and target VF. This interaction highlighted a reduced degree of initial deviation during the dual-task condition, in comparison to the saccade-only condition, for saccades made to the upper VF after the presentation of far proximity distractors. These results, as well as the behavioural results from the memory-only and dual-task conditions, suggests that oculomotor inhibition of distractor information is reduced due to the concurrent running of a VWM and a saccade task. These results also support findings by Belopolsky and Theeuwes (2011) who suggested that VWM facilitates oculomotor inhibition via the preservation of saccade programmes and further extends these findings to VWM being able to facilitate oculomotor inhibition in the absence of active rehearsal of visual information.

That active rehearsal was not necessary for oculomotor inhibition was concluded by König (2010) who also suggested that oculomotor inhibition after the brief presentation of a distractor was due prolonged oculomotor inhibition. However, the findings of this experiment suggest that though active rehearsal of distractor information is unnecessary for oculomotor inhibition, the VWM system is utilised to facilitate oculomotor inhibition via short-term storage of visual information. When the VWM system is less available due to concurrent running of a memory-specific task, oculomotor inhibition is reduced.

Saccade deviation results, highlighting the mean deviation of a saccade trajectory, however did not replicate the results found for initial deviation. Reduced saccade deviation was not found in the dual-task condition relative to the saccade-only task condition; though the proximity of a distractor in relation to a target was found to have some affect on the trajectories of saccades. It has already been theorised that

non-active rehearsal of information, leading to short-term storage in VWM, facilitated deviation evidenced in the initial deviation results. During the saccade-only condition, it is possible that decay in the memory representations held in VWM resulted in the graduating reduction of competitive neuronal activation in the oculomotor map. Mean saccade deviation therefore being similar across the saccade-only and dual-task conditions. Subsiding neuronal inhibition has previously been theorised to influence saccade characteristics, particularly in that saccade landing points are not modulated by distractor location (McSorley, Cruickshank, & Inman, 2009).

No significant results were found in relation to saccade latency or saccade accuracy. Theeuwes, Van der Stigchel and Olivers (2006) found that VWM facilitated oculomotor inhibition and resultant saccade deviations were separate to the affects of attentional IOR. Thus the absence of saccade latency results may be suggestive of a lack of goal-directed attentional inhibition. Furthermore, McSorley, Haggard and Walker (2004), suggest that saccades are influenced by two mechanisms: an initial mechanism that is responsible for the deviation of saccades away from distractors, and a secondary mechanism which is responsible for directing a saccade back towards a target stimulus. In their theory, the initial mechanism responds to the activation and inhibition of neurons in the SC. A lack of distractor-induced modularity in saccade endpoints is suggestive of the aforementioned secondary mechanism. The secondary mechanism in their model is theorised to be underpinned by the cerebellum. These researchers suggest that the cerebellum provides directional drive back towards a saccade target location. The current results suggest that initial deviation is underpinned by the SC and that this deviation is subject to VWM facilitation. In contrast cerebellar influenced

deviation back toward a saccade target stimulus is not influenced by information held in VWM.

SUMMARY

This study presents evidence of reduced oculomotor inhibition and memory performance during the concurrent running of VWM and saccade generation tasks. These results suggest that the VWM system facilitates oculomotor inhibition in support of Belopolsky and Theeuwes (2011). This facilitation of oculomotor inhibition was found after the presentation of a task-irrelevant distractor. König (2010) also found that task-irrelevant information induces saccade deviation during conditions not requiring the active rehearsal of information. König (2010) suggested that saccade deviation after briefly presented distractors was indicative of prolonged inhibition. However, evidence from this experiment suggests that prolonged inhibition after briefly presented distractors is underpinned and facilitated by VWM.

Theeuwes and colleagues (2005, 2006) found evidence of saccade deviation for goal-directed saccades after the presentation of task-relevant distractor stimuli. It has yet to be established how saccade deviation is influenced during conditions involving the active rehearsal of task-relevant distractor stimuli, and conditions not requiring the rehearsal of task-irrelevant distractor information. If both conditions are underpinned by VWM facilitation of oculomotor inhibition, the extent of deviation may be the only observable difference in saccade characteristics. The next chapter will explore the influence of task-relevant and task-irrelevant information stored in VWM on the facilitation of saccade deviation.

Chapter 5

Non-active and active rehearsal VWM-
oculomotor interactions

In the previous chapter, saccade trajectories were shown to deviate due to briefly presented task-irrelevant distractor stimuli in peripheral vision. An interaction between the VWM system and the oculomotor system was such that, when VWM was occupied with concurrent tasks, the initial deviation of a saccade was reduced. These results suggested that the deviation of saccades is able to occur when distractor stimuli are not actively rehearsed. This result partially supports results presented by König (2010) who also found that the active rehearsal of information was not necessary to induce saccade deviations away from distractors. Previous studies have found saccade deviation differences for actively maintained distractor stimuli (Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Olivers, 2006). In this study, saccade deviations were measured under two conditions: 1. a non-active rehearsal VWM condition that did not require the maintenance of presented peripheral distractor information and 2. an active rehearsal VWM condition requiring the active maintenance of distractor information in VWM. Differential saccadic deviations and latencies were observed across the two conditions. Results are discussed in relation to how bottom-up and top-down processing influences the trajectories of saccades.

VISUAL WORKING MEMORY AND SACCADIC DEVIATIONS

Studies by Theeuwes and colleagues (2005, 2006) suggest that saccades deviate away from the location of stimuli held in VWM. The interaction between the VWM system and the oculomotor system was explored in the previous chapter. It was found that when VWM was occupied by a dual processing task, the initial deviation of saccades was reduced. This result supported that of Van der Stigchel (2010) who found that

reduced saccade accuracy was observable during dual processing tasks involving the oculomotor system and the VWM system.

König (2010) found that active rehearsal was not necessary for saccades to deviate away from previously presented distractor stimuli. Thus, König (2010) theorised that differential saccade deviation found when spatial locations were held in VWM could better be described as the result of prolonged inhibition and was not necessarily the influence of VWM on the oculomotor system. This conclusion is disputed by the findings of the previous chapter. Though the briefly presented distractor stimuli in that experiment were not subject to active rehearsal, when VWM was occupied by a concurrent task, the initial deviation of a saccade was reduced. This finding supports Belopolsky and Theeuwes (2011) who suggest that saccade deviation is facilitated by information held in VWM.

The working memory model suggests that visual information is temporarily stored in the visuospatial sketchpad from where it is accessible to other cognitive systems (Baddeley & Hitch, 1974). On occasions where active rehearsal is not performed, temporarily stored information is subject to decay. However, active rehearsal allows information to be maintained. Visual information is theorised to be maintained in memory by the reorienting of spatial attention (Awh et al. 1999; Awh & Jonides, 2001). Spatial attention directed to visual information in the environment generates neuronal activity in the oculomotor map corresponding to attended spatial regions (Repovš & Baddeley, 2006). In this way, active rehearsal of attended to spatial locations leads to memory maintenance. Evidence suggests that visual storage systems may be localised to the posterior parietal region (Todd & Marois, 2004), whilst maintenance of working

memory representations across delay periods may be localised to the prefrontal regions (D'Esposito, 2007).

It may be that VWM interaction with the oculomotor system is possible under two separable conditions: an active rehearsal condition whereby task-relevant information is attended to, and a condition where task-irrelevant information is temporarily stored and is subject to decay. In both conditions VWM facilitates oculomotor inhibition. The previous chapter presents evidence supporting the existence of a 'non-active' VWM facilitation of oculomotor inhibition; evidence presented by König (2010) also supports this theory. Temporarily held information in VWM results in prolonged oculomotor inhibition. Active VWM facilitation of oculomotor inhibition is supported by Theeuwes and colleagues (2005, 2006) with the rehearsal of task-relevant information resulting in deviation away from memorised stimuli. Top-down processing leads to saccade deviation away from briefly presented distractors.

In this chapter, the extent of oculomotor inhibition will be explored in a condition involving the active rehearsal of visual information, and a 'non-active' rehearsal VWM condition. In this way, VWM facilitation of oculomotor inhibition and resultant saccade deviations can be explored under two states; a state presenting task-irrelevant distractor stimuli and a state presenting task-relevant distractor stimuli. It is predicted that saccade deviation across these two conditions will support the development of a theory in which separable components (storage and maintenance) of VWM consequently interact with the oculomotor system to facilitate the generation of saccades. The mean direction of a saccade trajectory in relation to a distractor stimulus will also be explored. This measure will allow further insight into top-down and

bottom-up processing during VWM interaction with the oculomotor system. Previous research has suggested that top-down processing results in deviation away from a distractor whilst deviation toward a distractor is indicative of bottom-up processing (McSorley, Haggard, & Walker, 2006). Researchers have presented evidence of top-down VWM facilitation of saccade deviation (Theeuwes and colleagues, 2005, 2006). It is hypothesised that prolonged oculomotor inhibition facilitated by non-active VWM may be underpinned by bottom-up neuronal processing; a shift in activation in the oculomotor map, after the presentation of task-irrelevant stimuli, inducing saccadic deviation. Comparatively, the active rehearsal of information to be stored in VWM may be seen to facilitate saccade deviations under-pinned by top-down processing.

Experiment 3

Method

Participants

Twelve participants ($M_{\text{age}} = 21.08$, $SE_{\text{age}} = 1.93$) with normal or corrected-to-normal colour vision consented to take part in this study. Four participants were male, eight participants were female. All participants classed themselves as right-handed. All participants gave informed consent; the study conformed to all applicable ethical guidelines.

Apparatus

The apparatus used was identical to that used in previous chapters (see chapter 3 for details).

Stimuli

The centre fixation stimuli (presented in red/green, subtending 0.5°) and target stimuli (white circular discs subtending 1.5°) used were consistent with previous chapters. Two Gabor images, like those used in chapter 4, served as distractors. Both Gabor images were vertically oriented; one had a spatial frequency of 3 cpd, and the other 5 cpd. Both Gabor images subtending 1.5° of visual angle were presented peripherally at $x = \pm 5.4^\circ$, $y = \pm 4.9^\circ$ (the same spatial locations used in previous chapters). Stimuli were presented on a grey background.

Procedure

Participants completed two conditions: 1. a non-active rehearsal VWM condition, and 2. an active rehearsal VWM condition. In the non-active VWM condition participants were required to make a saccade to a target stimulus after the brief presentation of a distractor stimulus. The active VWM condition, by contrast, required participants to remember the frequency (3 or 5cpd) of distractor stimuli in order to complete a yes-no discrimination task presented at the end of the saccade portion of the trial. Participants completed a calibration routine and 15 practice trials before the commencement of experimental conditions. Each condition consisted of 128 randomised trials. Conditions were counterbalanced across participants.

Condition 1 – Non-active rehearsal VWM

The non-active VWM condition in this experiment was similar to the saccade-only condition in the previous chapter. However, in this chapter Gabor images were presented as distractors. Participants were not informed as to the nature of the peripherally presented distractor stimuli; thus the distractors in this condition were

task-irrelevant and did not require active rehearsal (see *fig. 5.1*). Participants made a saccade to a presented target after the presentation of a distractor.

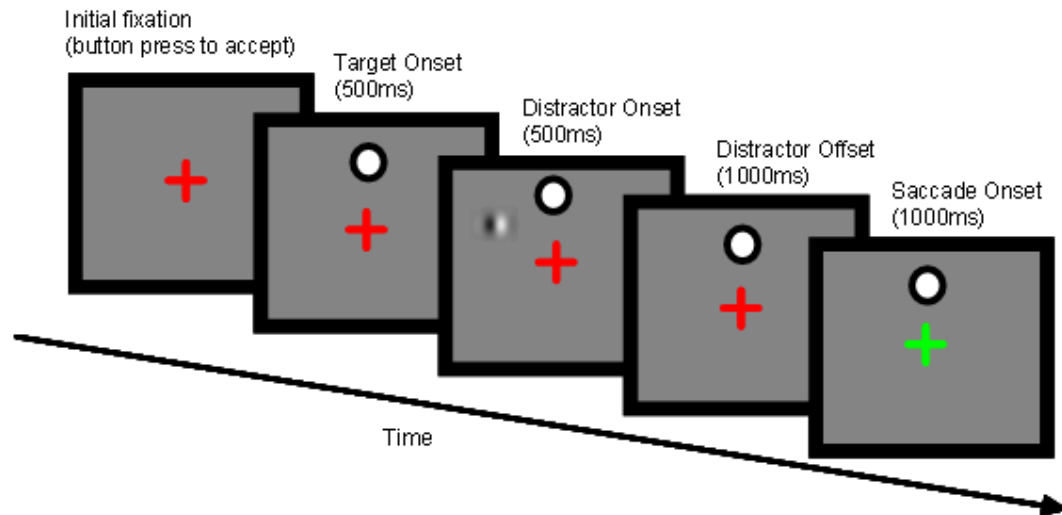


Fig. 5.1. Non-active rehearsal VWM condition.

Condition 2 – Active rehearsal VWM

The active VWM condition was identical to that of the non-active VWM condition. However, after participants had made a saccade to the presented target stimulus, a yes-no recognition memory task was completed in which participants were required to state whether a single probed stimulus was the same Gabor image, or a different Gabor image, relative to the Gabor shown in the saccade portion of the trial (see *fig. 5.2*). In 50% of trials, the Gabor image shown in the test display matched that shown in the saccade display.

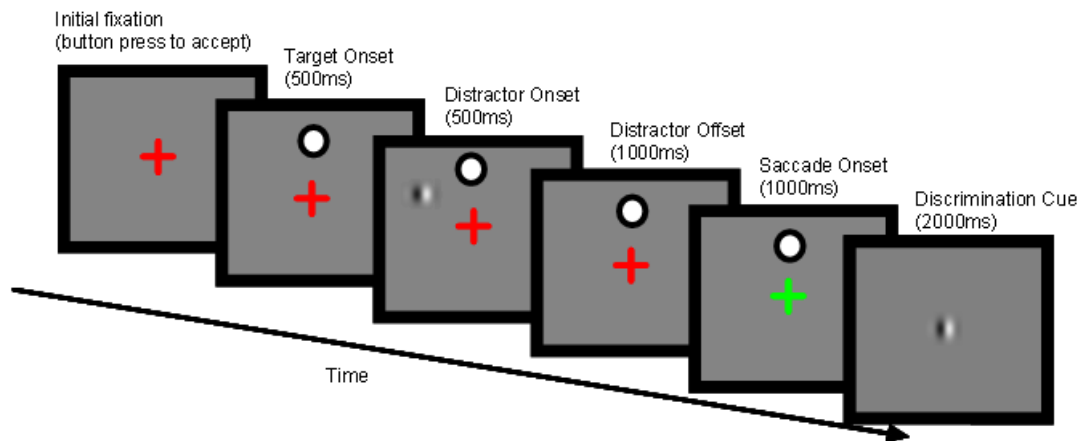


Fig. 5.2. Active rehearsal VWM condition.

Design

Data was filtered through MATLAB (R2010a, Mathworks, Natick, MA) using the same methods and exclusion criteria justified in chapter 3. Saccade measures were also equivalent to those used in chapter 4; saccade deviation, initial deviation, saccade accuracy and saccade latency were explored.

A 2×2 repeated measures design was implemented on saccade data from both conditions with the independent variables being the distractor proximity in relation to a target (close proximity vs. far proximity), and target visual field (upper VF vs. lower VF). A further $2 \times 2 \times 2$ repeated measures design was used to ascertain whether there was a difference between conditions with distractor proximity, target VF and condition being the independent variables.

In order to explore the mean direction of a saccade, a 2×2 repeated measures ANOVA was run with distractor proximity and distractor VF (left vs. right VF) as the

independent variables. A further 2 x 2 x 2 repeated measures ANOVA was used to compare mean direction across the two conditions; the variables being distractor proximity, distractor VF, and condition.

Planned comparisons will explore any significant interactions found across the independent variables.

Results

Initial Deviation

2 × 2 repeated measures ANOVA's revealed no significant main effects during the non-active rehearsal VWM condition (distractor proximity to a target: $F(1, 11) = 0.01$, $p = .91$, $\eta p^2 = .00$, target VF: $F(1, 11) = 2.95$, $p = .11$, $\eta p^2 = .21$), or the active rehearsal VWM condition (distractor proximity to target: $F(1, 11) = 0.40$, $p = .54$, $\eta p^2 = .04$, target VF: $F(1, 11) = 0.88$, $p = .37$, $\eta p^2 = .07$) on the initial deviation of a saccade. However, a significant interaction between the two independent variable was revealed during the non-active rehearsal VWM condition; $F(1, 11) = 12.89$, $p < .005$, $\eta p^2 = .54$. Planned comparisons indicated a significant reduction ($p < .05$) in initial deviation for saccades directed to the upper VF after the presentation of close proximity distractors ($M = -9.61$, $SE = 3.40$) in comparison to far proximity distractors ($M = -13.27$, $SE = 2.80$). This result was not replicated in the lower VF. In the lower VF a non-significant, slightly reduced level of initial deviation was found after the presentation of far proximity distractors ($M = -1.29$, $SE = 5.01$) in comparison to close proximity distractors ($M = -4.53$, $SE = 4.01$); see *fig. 5.3*. In contrast no significant interaction was revealed during the active rehearsal VWM condition.

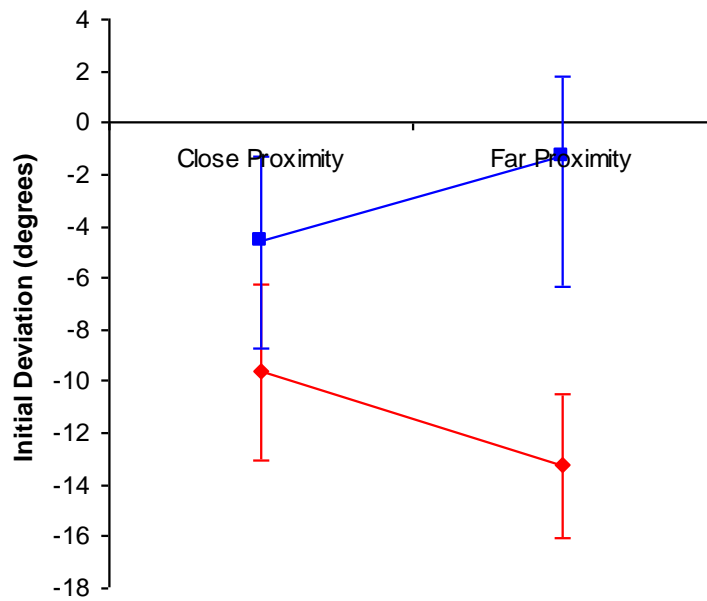


Fig. 5.3. Distractor proximity to a target \times target VF interaction during the non-active rehearsal VWM condition for initial deviation. Red lines denote saccades made to the upper target VF. Blue line denotes saccades made to the lower target VF. Error bars represent ± 1 SE.

Furthermore, a $2 \times 2 \times 2$ repeated measures ANOVA revealed no significant main effects for distractor proximity to target [$F(1, 11) = 0.12, p = .73, \eta p^2 = .01$], target VF [$F(1, 11) = 2.65, p = .13, \eta p^2 = .19$], or condition [$F(1, 11) = 0.14, p = .72, \eta p^2 = .01$] and no significant interaction was found.

Saccade Deviation

A 2×2 repeated measures ANOVA revealed no significant main effect on saccade deviation during the non-active rehearsal VWM condition for distractor proximity to a target [$F(1, 11) = 0.73, p = .41, \eta p^2 = .06$] or target VF [$F(1, 11) = 0.14, p = .71, \eta p^2 = .01$]. A significant interaction between these two variables was found; $F(1, 11) = 11.96, p < .01, \eta p^2 = .52$. Planned comparisons indicated a significantly ($p < .05$) reduced degree of saccade deviation for saccades made to the lower VF after the presentation

of close proximity distractors ($M = 0.11$, $SE = 1.52$) in comparison to after the presentation of far proximity distractors ($M = 2.00$, $SE = 1.68$). Furthermore planned comparisons also revealed a trend towards significance ($p = .05$) indicating directional differences for saccades made to the upper VF. Close proximity distractors elicited saccades with a rightwards deviation (as borne out by a positive saccade deviation, $M = 0.63$, $SE = 1.17$) and far proximity distractors eliciting saccades with a leftwards deviation (as borne out by a negative saccade deviation, $M = -0.49$, $SE = 1.17$); see *fig. 5.4*.

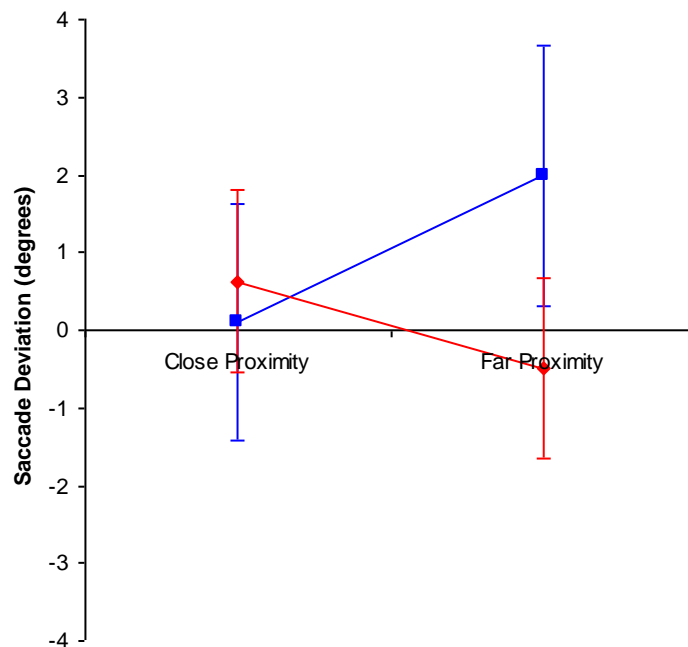


Fig. 5.4. Distractor proximity \times target VF interaction during the non-active VWM condition for saccade deviation. Red line denotes saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

During the active rehearsal VWM condition, no significant main effects were found for distractor proximity to a target [$F(1, 11) = 1.41$, $p = .26$, $\eta p^2 = .11$] or target VF [$F(1, 11) = 0.09$, $p = .78$, $\eta p^2 = .01$]. Moreover, during this condition, no significant

interactions were found contrary to the interaction found during the non-active VWM condition.

A $2 \times 2 \times 2$ repeated measures ANOVA revealed no significant main effects for distractor proximity to a target [$F(1, 11) = 2.08, p = .18, \eta p^2 = .16$], target VF [$F(1, 11) = 0.00, p = .98, \eta p^2 = .00$], or condition [$F(1, 11) = 0.42, p = .53, \eta p^2 = .04$]. However, a significant three way interaction was found; $F(1, 11) = 7.13, p < .05, \eta p^2 = .39$. During the non-active rehearsal VWM condition, the aforementioned degree of saccade deviation contingent on distractor proximity to a target was found in the lower VF as well as directional deviation differences contingent on distractor proximity to target in the upper VF. During the active rehearsal VWM condition, saccade trajectories did not appear to be modulated by a distractor proximity to a target and target VF interaction and a slightly reduced, non-significant, reduction in saccade deviation was observed after close proximity distractors (upper VF: $M = 1.00, SE = 1.96$, lower VF: $M = 0.54, SE = 1.44$) were presented in comparison after far proximity distractor (upper VF: $M = 2.08, SE = 1.60$, lower VF: $M = 0.76, SE = 1.40$) presentation; see *fig. 5.5*.

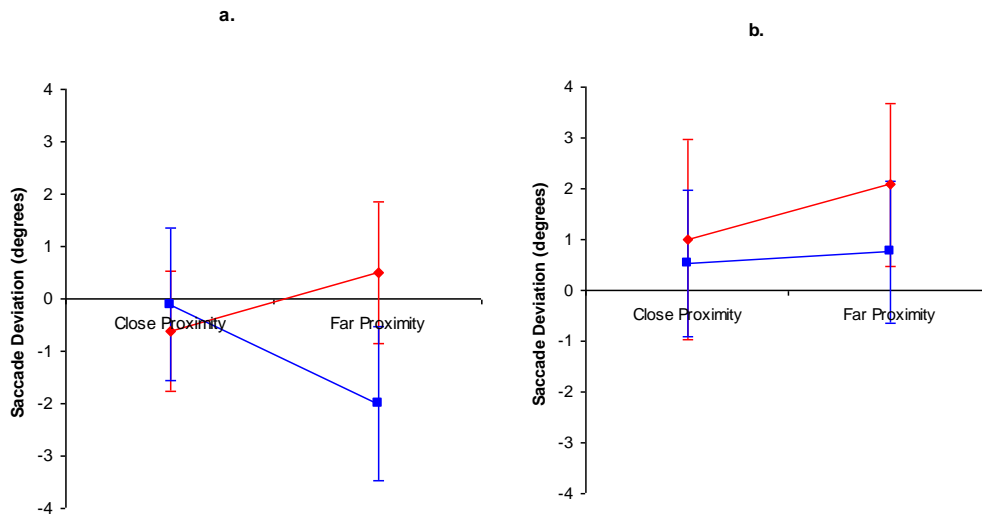


Fig. 5.5. Three-way interaction for saccade deviation. a. shows non-active VMW condition. b. shows active VWM condition. Red lines denote saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

Saccade Accuracy

No significant results were found for saccade accuracy during either the non-active VWM condition (distractor proximity to target: $F(1, 11) = 0.85$, $p = .38$, $\eta p^2 = .07$, target VF: $F(1, 11) = 2.26$, $p = .16$, $\eta p^2 = .17$), active VWM condition (distractor proximity to target: $F(1, 11) = 1.62$, $p = .23$, $\eta p^2 = .13$, target VF: $F(1, 11) = 0.53$, $p = .48$, $\eta p^2 = .05$), or across the conditions (condition: $F(1, 11) = 1.16$, $p = .30$, $\eta p^2 = .10$, distractor proximity to target: $F(1, 11) = 0.00$, $p = .99$, $\eta p^2 = .00$, target VF: $F(1, 11) = 1.51$, $p = .24$, $\eta p^2 = .12$).

Saccade Latency

During the non-active rehearsal VWM condition, a 2×2 repeated measures ANOVA found no significant main effect for distractor proximity to target [$F(1, 11) = 0.79$, $p = .39$, $\eta p^2 = .07$] for saccade latency, however a main effect was found for target VF [$F(1, 11) = 18.00$, $p < .005$, $\eta p^2 = .62$]. Saccades made to the upper VF had shorter latencies

($M = 283.48$, $SE = 5.70$) than saccades made to the lower VF ($M = 304.35$, $SE = 5.64$).

No significant interactions were revealed.

A 2×2 repeated measures ANOVA for the active rehearsal VWM condition did find a significant main effect for distractor proximity [$F(1, 11) = 7.52$, $p < .05$, $\eta p^2 = .41$] contrary to results during the non-active rehearsal VWM condition. The latency of saccades made after the presentation of close proximity distractors ($M = 272.03$, $SE = 6.15$) were shorter than saccade latencies made after the presentation of far proximity distractors ($M = 289.10$, $SE = 5.66$); see *fig. 5.6*. Furthermore, a significant main effect was also found for target VF; $F(1, 11) = 5.39$, $p < .05$, $\eta p^2 = .33$. Corresponding with results found in the non-active rehearsal VWM condition, saccade latencies made to the upper VF ($M = 270.99$, $SE = 5.77$) were significantly shorter than saccades made to the lower VF ($M = 290.15$, $SE = 5.91$).

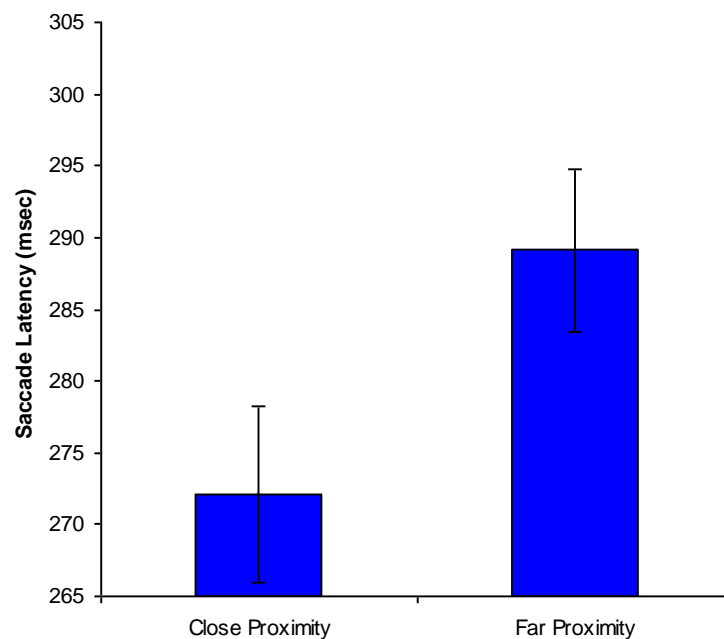


Fig. 5.6. Saccade latencies for distractor proximities for the active rehearsal VWM condition. Error bars represent ± 1 SE.

A further $2 \times 2 \times 2$ repeated measures ANOVA across the two conditions found no significant main effect for condition; $F(1, 11) = 1.53$, $p = .24$, $\eta p^2 = .12$. However, a significant main effect was observed for distractor proximity; $F(1, 11) = 9.03$, $p < .05$, $\eta p^2 = .45$ and target VF; $F(1, 11) = 15.07$, $p < .005$, $\eta p^2 = .59$. Saccade latencies made after the presentation of close proximity saccades were shorter than saccade latencies made after the presentation of far proximity saccades (see *fig. 5.7*). Furthermore, saccades made to the upper VF ($M = 277.23$, $SE = 4.11$) had significantly shorter latencies than saccades made to the lower VF ($M = 297.25$, $SE = 4.17$); see *fig. 5.8*.

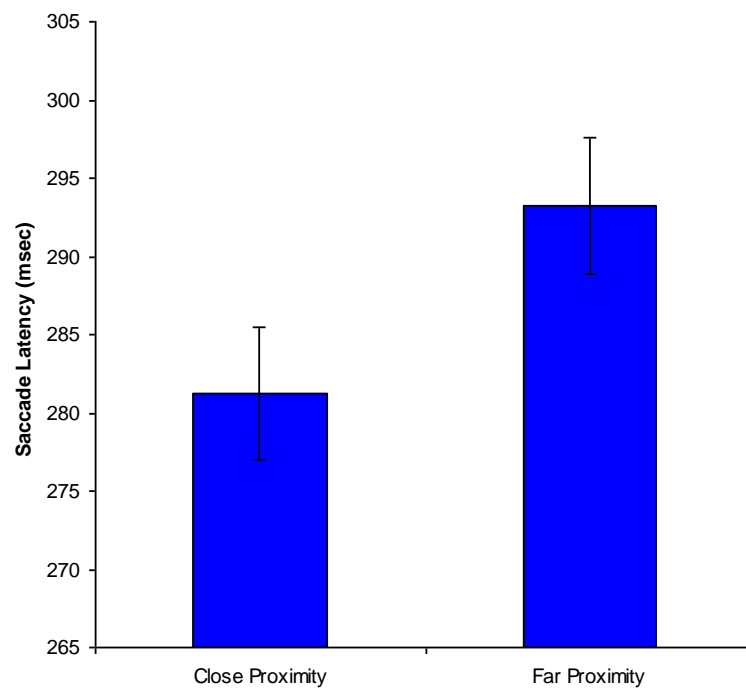


Fig. 5.7. Saccade latencies for distractor proximities across the non-active and active rehearsal conditions. Error bars represent ± 1 SE.

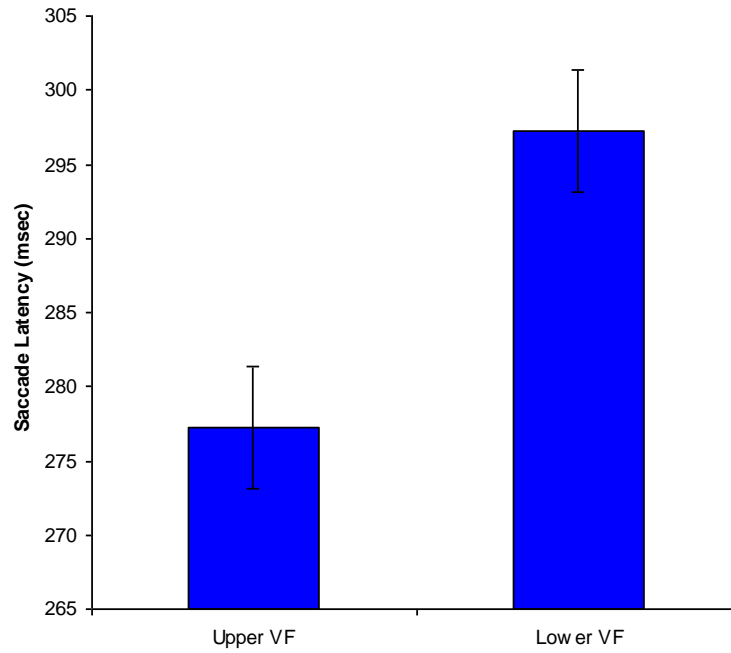


Fig 5.8. Saccade latencies for target VF across the non-active and active rehearsal conditions. Error bars represent ± 1 SE.

Mean Direction

2×2 repeated measures ANOVA's for mean direction found no significant main effects for distractor proximity to a target during the non-active rehearsal VWM condition [$F(1, 11) = 2.01, p = .18, \eta p^2 = .16$] or the active rehearsal VWM condition [$F(1, 11) = 0.39, p = .54, \eta p^2 = .03$]. A trend towards a main effect was found for distractor VF [$F(1, 11) = 4.05, p = .07, \eta p^2 = .27$] during the non-active rehearsal VWM condition. This trend suggested that saccades made after the presentation of a left VF distractor deviated rightwards to a greater extent ($M = 0.05, SE = 0.03$) than saccades made after a right VF distractor ($M = 0.00, SE = 0.03$). Furthermore, a significant main effect was found for distractor VF [$F(1, 11) = 6.41, p < .05, \eta p^2 = .37$] during the active rehearsal VWM condition. Following the same pattern as the trend found in the non-active rehearsal VWM condition, saccades made after the presentation of a left VF distractor deviated rightwards to a greater extent ($M = 0.10, SE = 0.03$) than saccades made after

a right VF distractor ($M = 0.05$, $SE = 0.03$); see *fig 5.9*. No significant interactions were found for either condition.

A further $2 \times 2 \times 2$ repeated measures ANOVA across both conditions revealed no significant main effects for distractor proximity [$F(1, 11) = 0.60$, $p = .46$, $\eta p^2 = .05$], or condition [$F(1, 11) = 0.38$, $p = .54$, $\eta p^2 = .04$]. A significant main effect was found for distractor VF; $F(1, 11) = 13.94$, $p < .005$, $\eta p^2 = .56$. Saccades made after the presentation of a left VF distractor deviated to a greater extent rightwards ($M = 0.07$, $SE = 0.02$) than saccades made after a right VF distractor ($M = 0.03$, $SE = 0.02$); see *fig 5.10*. No significant interactions were found.

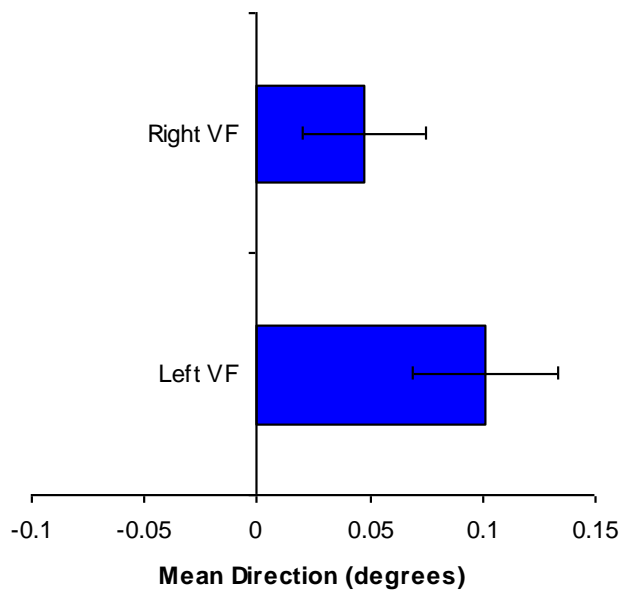


Fig. 5.9. Mean direction during the active rehearsal VWM condition for distractor VF. Error bars represent ± 1 SE.

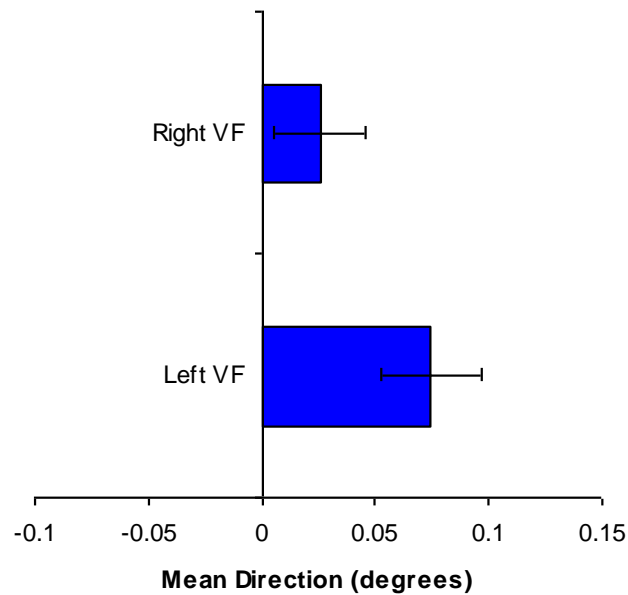


Fig. 5.10. Mean direction for distractor VF across the non-active and active rehearsal VWM conditions. Error bars represent ± 1 SE.

Discussion

This chapter explored saccade characteristics during two different conditions: a non-active VWM condition and an active VWM condition. Three main findings will be discussed: 1. saccade trajectory deviations during the non-active rehearsal VWM condition seem to be preferentially influenced by target VF and distractor proximity interactions in contrast to the active rehearsal VWM condition; 2. saccade latencies were found to be shorter after the presentation of close proximity distractors in the active rehearsal VWM condition; and 3. saccades were found to deviate away from the distractor in both conditions (though more so in the active rehearsal VWM condition). It was also found that saccade latencies were shorter to upper VF targets in comparison to lower VF targets.

The previous chapter found that when concurrent VWM and saccade tasks were completed, VWM ability was reduced and oculomotor inhibition was limited. Those results indicated that active rehearsal of information in VWM was not necessary for the oculomotor system to be influenced by memory traces. König (2010) also found that active rehearsal was unnecessary to elicit saccade deviations away from briefly presented task-irrelevant visual information; prolonged oculomotor inhibition facilitated by VWM resulting in saccade deviation.

Research by Theeuwes and colleagues (2005, 2006) has illustrated that saccades deviate away from task-relevant information presented in peripheral vision and held in VWM. In this chapter it was proposed that VWM facilitation of oculomotor inhibition after the non-active rehearsal of task-irrelevant visual information may be characterised by bottom-up processing. In comparison, VWM facilitation of oculomotor inhibition after the active rehearsal of task-relevant visual information was theorised to be characterised by top-down processing.

VWM facilitation of oculomotor inhibition (bottom-up and top-down processing)

The degree of saccade trajectory deviation was reported by the initial deviation and saccade deviation measures. The further measure, mean deviation, was also used during this chapter, to ascertain the direction a saccade travelled (left or right) along the horizontal axis.

The non-active rehearsal VWM condition found that the deviation of saccades were influenced significantly by an interaction between target VF and distractor proximity to target; this interaction supports that found in chapter 4. In the upper VF, the initial

deviation of saccades was significantly increased after far proximity distractors in comparison to close proximity distractor. This result was not replicated in the lower VF. Furthermore, the upper and lower VF appeared to be influenced by a distractors proximity to a target for the saccade deviation measure; though a trend towards significance indicated that directional differences could be observed in the upper VF. Close proximity distractors appeared to express saccades that predominantly deviated rightwards whilst far proximity distractors appeared to express saccades that deviated predominantly leftwards. In the lower VF, saccade deviation was significantly reduced after the presentation of close proximity distractors in comparison to far proximity distractors.

This thesis has previously discussed separable visual processing streams being theorised as being active during the upper and lower VF's. The upper VF has been associated with the ventral visual pathway and thus has been linked to visual object processing. Conversely, the lower VF has been associated with the dorsal visual pathway and thus has been linked to visuospatial processing (Previc, 1990). The results of the current experiment suggest possible differential processing streams as being active at different temporal stages along the saccade trajectory. Results from the initial deviation of a saccade highlighting possible processing along the ventral stream (as indicated by distractor proximity to target effects in the upper VF), and results from the saccade deviation results highlighting the possible subsiding of activation along the ventral pathway (as indicated by a trend towards significance in distractor proximity to target effects in the upper VF) and possible activation along the dorsal stream (as indicated by distractor proximity effects in the lower VF). This thesis will not be concerned with the temporal stages of saccade trajectories and any associated

processing streams; however, more in depth research on this point may be able to provide further insight.

The initial deviation, and saccade deviation, results do provide supportive evidence of results from chapter 4 and also results by König (2010). Task-irrelevant information does not need to be actively rehearsed in order to induce saccade deviation. Thus, a form of bottom-up, neuron-driven activation can be ascribed for saccade deviation during non-active rehearsal VWM condition characterised by an interaction between the altitudinal VF a saccade is made to (either the upper or the lower VF) and the proximity a presented task-irrelevant distractor in relation to a saccade target. No such interaction was observed during the active rehearsal VWM condition suggesting that saccade deviation characterised by this neuron-driven, bottom-up processing is to some extent negated after the presentation of task-relevant distractor stimuli.

Results relating to the mean direction of a saccade provide evidence of top-down processing of information stored in VWM. These mean direction results indicate that, in this experiment, saccades appeared to have a greater tendency to deviate rightwards than leftwards. However, saccades were also found to deviate to a greater extent rightwards after the presentation of left VF distractors in comparison to right VF distractors. Thus saccades had a greater propensity to deviate away from a presented. Previously it has been found that top-down processing induces saccade that deviates away from distractor stimuli (McSorley, Haggard, & Walker, 2006). In this study, during the non-active rehearsal VWM condition, a trend towards significance was found for distractor VF and the mean direction of a saccade. This main effect was found to be significant during the active rehearsal VWM condition. These results suggest that top-

down influences are more prevalent during active rehearsal VWM conditions comparative to non-active rehearsal VWM conditions. However these results suggest that both conditions, according to current research, employ a degree of top-down processing to inhibit distractor locations.

Saccade latency effects

The active rehearsal VWM condition found that saccade latencies expressed after the brief presentation of close proximity distractors were shorter than the latencies expressed after the presentation of far proximity distractors. These results support and extend that of McSorley, Haggard, & Walker (2005) who also found reduced saccade latencies after the presentation of close proximity distractors for voluntary saccades. These researchers suggest that distractors in close proximity to a target may provide a saccade trigger facilitating saccade onsets. In contrast, far proximity distractors may act a 'remote distractor inhibitor'. The results from the current experiment indicate that distractor modulation of saccade latencies is not dependent on a distractor being onscreen at the time of saccade initiation during active rehearsal VWM conditions. However, during the non-active rehearsal VWM condition this distractor modulation of saccade latencies is not apparent.

Saccade latencies to upper VF targets were shorter than latencies to lower VF targets; this finding supports that of Zhou & King (2002). The upper VF has been associated with specialised visual object processing whilst the lower VF has been associated with visuo-spatial processing (Previc, 1990). The results of this chapter highlighting shorter latencies for upper VF saccades support this theory.

SUMMARY

This chapter has been concerned with how saccade deviations, and in turn oculomotor inhibition, are influenced by the presence of task-irrelevant and task-relevant distractor stimuli. The previous chapter suggested that task-irrelevant stimuli held in VWM but not actively rehearsed leads to VWM facilitated prolonged inhibition in the oculomotor saccade map. Task-relevant, actively rehearsed and maintained, stimuli in VWM have also been found to influence the trajectories of saccades (Theeuwes, Olivers, & Chizk, 2005; Theeuwes, Van der Stigchel, & Olivers, 2006). Saccade trajectory deviation results, the results observed for saccade latency, and the mean direction results suggest that during active rehearsal VWM conditions, top-down processing influences oculomotor inhibition for the facilitation of goal-directed saccades. During the non-active rehearsal VWM condition, a form of bottom-up deviation has been theorised to occur expressed in the modulation of saccade trajectories by the interaction between distractor proximity to a target and target VF. However, mean direction results also suggest that some level of top-down processing is present during non-active rehearsal VWM conditions. It is possible that parallel, top-down and bottom-up, processing underpins VWM facilitation during non-active rehearsal VWM conditions. The results from this chapter have supported differential VWM-oculomotor interaction for stimuli maintained and stored (active rehearsal VWM condition), and passively stored (non-active rehearsal VWM condition), in VWM.

In the next chapter, dorsal and ventral pathway interactions during VWM facilitation of oculomotor inhibition will be explored. Theeuwes and colleagues (2005, 2006) have found that saccades deviate to a greater extent after the presentation of to-be-

remembered distractor stimuli. The results from this chapter have supported differential activation for stimuli maintained, and stored, in VWM. In studies by Theeuwes and colleagues (2005, 2006), a VSWM was presented to participants. In contrast, the active rehearsal VWM condition contained a NS-VWM task. It has been postulated that VSWM and NS-VWM are processed separately along the dorsal and the ventral pathways (Ungerleider & Haxby, 1994). Thus, differences in results between Theeuwes and colleagues (2005, 2006) and the present study may be characterised as differences in the manner of interaction between the oculomotor system and the dorsal and ventral visual pathways.

Chapter 6

The dorsal and ventral visual pathways
and saccade generation

Visual working memory subsystems

Chapter 4 and 5 of this thesis demonstrated VWM facilitation of saccade trajectory deviations. A possible dissociable influence regarding the dorsal and ventral visual pathways has also been highlighted. The upper and lower VF have been theorised as being processed by the ventral and dorsal visual pathways respectively. In the previous two chapters the proximity of presented distractor stimuli was seen to influence saccades made to the upper and lower VF differently. Theeuwes and colleagues (2005, 2006) have presented evidence suggesting that the active rehearsal of VSWM induces saccades with greater deviation. Furthermore, the two previous chapters have presented evidence of VWM (both active rehearsal NS-VWM and non-active rehearsal VWM) interaction with the oculomotor system. NS-VWM and VSWM have been related to the ventral and dorsal visual pathways respectively. Thus, there is evidence that the ventral and dorsal pathways may influence oculomotor inhibition and that this influence may be characterised by differential saccade trajectories. In this chapter, three conditions were presented to participants: 1. a non-active rehearsal VWM condition, 2. a VSWM condition, and 3. a NS-VWM condition. Comparable VSWM and non-active VWM interactions with the oculomotor system were found. NS-VWM had a dissociable influence on the oculomotor system in comparison to the other two conditions. The results are discussed in relation to a dorsal and ventral pathway separable interaction with the oculomotor system.

VISUO-SPATIAL, AND NON-SPATIAL, VISUAL WORKING MEMORY AND SACCADIC

TRAJECTORIES

It has been argued that there is a functional separation between the dorsal and ventral pathways although the nature of this separation has been debated. Research has

suggested that the dorsal stream, from the primary visual cortex projecting to the DLPFC and along the occipito-parietal pathway, is responsible for visuo-spatial processing. In contrast the ventral stream, from the primary visual cortex projecting to the VLPFC and along the occipito-temporal stream, is responsible for visual object processing (for example, Ungerleider & Haxby, 1994).

Research by Goodale and Milner (1992), however, suggests that the 'what' and 'where' pathways can be better characterised as the 'what' and 'how' pathways. The ventral pathway is thought to be responsible for vision perception and the dorsal pathway is thought to be responsible for visual action. In this model the perception, or 'what', ventral pathway is responsible for conscious and unconscious perception of objects or events. It is also claimed that the ventral pathway does not govern action responses. This pathway perceives target objects allowing for appropriate actions to be undertaken by other cognitive systems. By way of contrast the action, or 'how', dorsal pathway is responsible for the implementation of actions. This pathway is posited to employ visual information in order to programme movements needed to complete an action (Milner & Goodale, 2008). In support, Kravitz et al. (2013) suggests a recurrent stream of processing along the ventral pathway concerned with object quality that communicates with six or more distinct cortical and subcortical regions; including regions involved in learning and memory. Furthermore, Kravitz et al. (2011) identified three pathways emerging from the dorsal pathway concluding that this pathway is responsible for both conscious and unconscious visuo-spatial processing.

In VWM research it has been suggested that the dorsal/ventral divide may be consistent with a manipulation or maintenance separation of function. The ventral

pathway is responsible for the maintenance of visual information whilst the dorsal pathway is responsible for the manipulation of information. D'Esposito et al. (1999) found evidence that the DLPFC is preferentially activated during trials requiring 'transformation' or manipulation, as opposed to trials involving maintenance.

Increased activation in the DLPFC has been noted during VSWM tasks, as well as increased activation in the posterior parietal cortex and the anterior cingulate cortex (Ricciardi et al., 2006). In contrast NS-VWM has been seen to preferentially activate regions along the ventral stream including the inferotemporal cortex (Tanaka, 1996). In a study by Jackson et al. (2011), a reliable dorsal/ventral neuroanatomical divide for VSWM and NS-VWM was found. These researchers also reported interplay between the DLPFC and the VLPFC for combined VSWM and NS-VSWM tasks. Tasks requiring both spatial and object working memory resulting in increased activation in the DLPFC and VLPFC relative to activation found in the DLPFC after VSWM task presentation or activation in the VLPFC after NS-VWM task presentation.

Clinical populations have been found to support a VSWM and NS-VWM divide in the storage and manipulation of visual information. For instance, reduced performance in VSWM tasks, as opposed to NS-VWM, has been noted in early stage Parkinson's disease. Medicated sufferers of Parkinson's disease with mild symptoms suffered decreased VSWM ability relative to control subjects, but did not suffer from NS-VWM deficits. In contrast, medicated sufferers of Parkinson's disease with severe symptoms expressed deficits on both NS-VWM and VSWM tasks (Owen et al., 2007). Patients with Huntington's disease have also been shown to VSWM, as opposed to NS-VWM, deficits (Lawrence et al., 2000).

Comparable neural cortices and subcortices sub-serve both VWM and saccade execution. Specifically the DLPFC is thought to play an important role in the suppression of task-irrelevant saccades (Johnston & Everling, 2006) via a direct pathway from the DLPFC to the SC (Munoz & Everling, 2004). This suppression is thought to be due to an excitatory effect from the DLPFC on saccade related neurons in the ipsilateral SC resulting in the facilitation of task relevant saccades (Johnston, Koval, Lomber, & Everling, 2013). Antisaccade tasks also demonstrate this DLPFC mediated suppression of task irrelevant saccades. Increased activation in the DLPFC has been noted during the execution of antisaccades (Ford, Goltz, Brown, & Everling, 2005; Matsuda et al., 2004).

Irwin & Brockmole (2004) have noted that response times to spatial tasks were adversely effected by saccade amplitude. Conversely this effect was not noted during tasks of visual object processing. These researchers suggested that these findings were the result of dual processing along the dorsal pathway and that the dorsal, spatial, pathway is integral during the generation of saccades. Moreover, the framework put forward by Godijn & Theeuwes (2004) integrates several cortical areas associated with dorsal pathway processing including the LIP (Powell & Goldberg, 2000) and the DLPFC (D'Esposito et al., 1999). The ventral pathway has also been theorised to interact with the oculomotor system via top-down communication allowing the execution of rapid saccades (Buffalo, Fries, Landman, Liang, & Desimone, 2010). This ventral pathway interaction with the oculomotor system can be observed in the shorter latencies of saccades made the upper VF (e.g. Zhou and King, 2002). Corbetta et al. (1998) have suggested that ventral pathway extrastriate areas interact with frontoparietal areas to

promote efficient visual processing. Thus both the dorsal and ventral pathways have been theorised to interact with the oculomotor system differently during saccade execution.

In this chapter, VSWM, and NS-VWM, interaction with the oculomotor system will be explored. In this way the contributions of the dorsal and ventral pathway in the interaction between VWM and the oculomotor system can be observed. Tasks will be presented that will require peripherally presented information to be held in VSWM or NS-VWM and the execution of a goal-directed saccade. Thus, the relationship between VWM and the oculomotor system along the dorsal/ventral divide can be examined and theoretical inferences regarding neuronal communication between areas involved in VWM and the generation of saccades can be made. It is predicted that differential saccade deviations for target VF and distractor proximity may be discernable across conditions. The upper VF having been associated with the ventral visual pathway may result in increased saccade efficiency, accuracy, or differential saccade deviation during the NS-VWM condition. In contrast the lower VF, associated with processing along the dorsal pathway may show the opposite pattern during saccade generation.

Experiment 4

Method

Participants

Twelve participants were recruited for this study; five male and seven female ($M_{\text{age}} = 22$, $SD_{\text{age}} = 4.07$). Eleven participants classed themselves as right-handed, one participant was left-handed. All participants had normal or corrected colour vision. All

participants gave informed consent; the study conformed to all applicable ethical guidelines.

Apparatus

Apparatus used was identical to that of previous chapters.

Stimuli

Stimuli were identical to that presented in the previous chapter.

Procedure

Participants took part in three conditions; a non-active rehearsal VWM condition, a condition requiring VSWM, and a condition requiring NS-VWM. Participants completed a nine-point calibration routine before completing each condition. Participants completed 15 practice trials for each condition. Conditions were counterbalanced across participants. Participants completed 128 randomised trials in each condition.

Condition 1 – non-active VWM

The non-active VWM condition was identical to that of the previous chapter (see *fig. 6.1*). Participants made a saccade to a presented target after the presentation of a distractor.

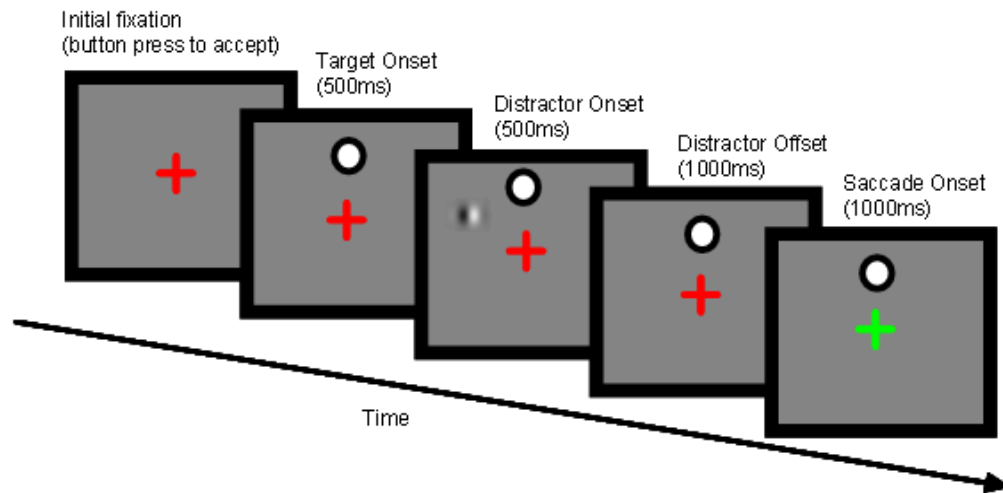


Figure 6.1. Non-active condition.

Condition 2 – VSWM

In this condition the presentation of experimental paradigm did not differ from the non-active rehearsal VWM condition. However, participants were instructed to remember the spatial location of peripherally presented ‘distractor’ stimuli. Participants were required to make a saccade to a target stimulus. A yes-no spatial recognition task was completed in which participants were required to state whether a single probed stimulus was in the same spatial location as the previously presented distractor stimulus. In 50% of trials the probed stimulus was in the same spatial location as the previously presented distractor. In 50% of the trials the probed stimulus was in a different spatial location. Different spatial locations were presented at $\pm 2^\circ$ horizontally from the original peripherally presented distractor stimulus (see *fig, 6.2*).

Condition 3 – NS-VMM

In this condition the experimental paradigm was identical to the active rehearsal VWM condition in the previous chapter. Participants were required to make a saccade to a

target stimulus. A yes-no recognition memory task was completed in which participants were required to state whether a single probed stimulus was the same Gabor image, or a different Gabor image, relative to the Gabor shown in the saccade portion of the trial (see *fig. 6.3*). In 50% of trials, the Gabor image shown in the test display matched that shown in the saccade display.

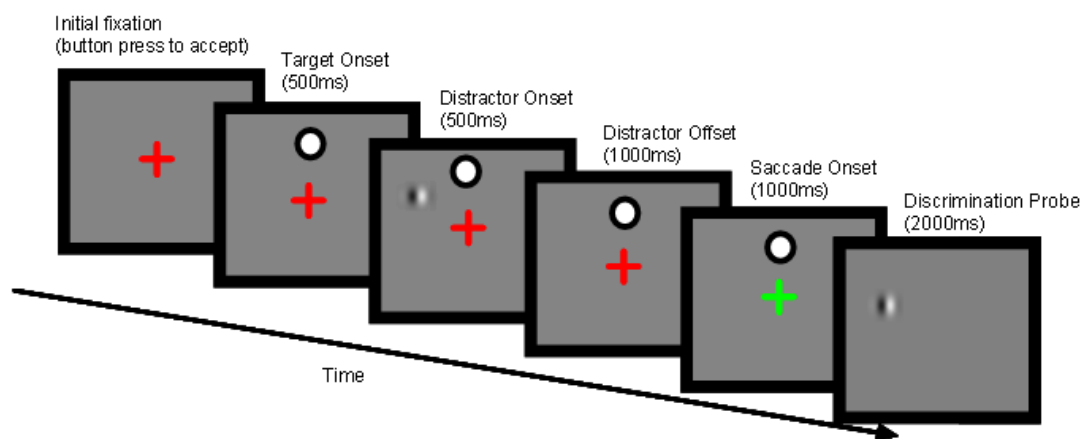


Fig. 6.2. The VSWM condition

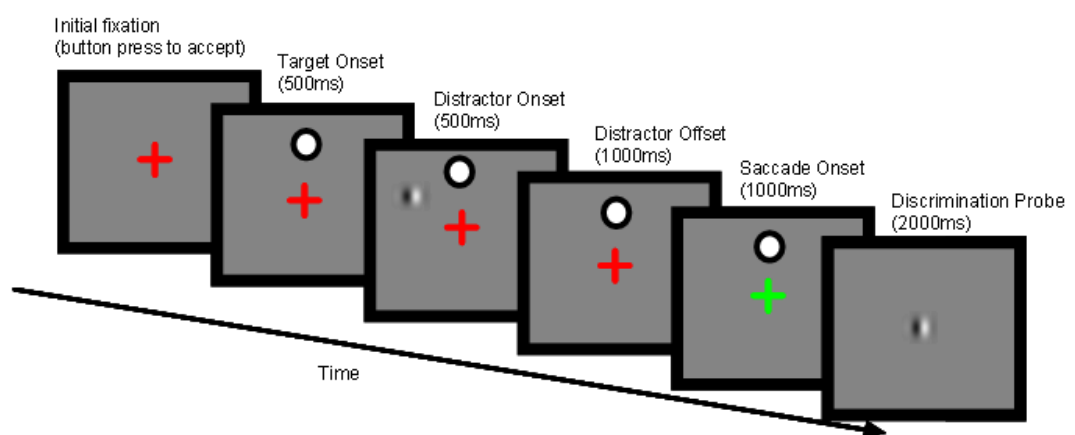


Fig 6.3. NS-VWM condition

Design

Data was filtered in the same way as previous chapters using MATLAB (R2010a, Mathworks, Natick, MA) and previously defined exclusion criteria were used (see chapter 3). Saccade measures used were the same as described in the chapter 5; thus saccade deviation, initial deviation, saccade accuracy, saccade latency, and mean direction were calculated as dependent variables for analysis.

A 2×2 repeated measures design was implemented on the saccade data from the conditions with the independent variables being the distractor proximity to a target (close proximity vs. far proximity), and target VF (upper VF vs. lower VF). A further $2 \times 2 \times 3$ repeated measures design was used to ascertain whether there was a difference between conditions with distractor proximity, target VF and condition being the independent variables.

When analysing the mean direction of a saccade, target VF was replaced by distractor VF (left vs. right VF). A 2×2 repeated measures ANOVA was run with distractor proximity and distractor VF as the independent variables computed across the three previously stated conditions. A $2 \times 2 \times 3$ repeated measures ANOVA explored differences within and across these conditions.

Planned comparisons will examine any significant interactions found across the independent variables.

A paired-samples design was used to analyse the behavioural data in order to ascertain whether there was a difference in task difficulty across the VSWM and the NS-VWM

conditions. The percentage number of correct memory trials was used as the dependent variable.

Results

Initial Deviation

Initial deviation 2×2 repeated measures ANOVA's revealed no significant results during the non-active rehearsal VWM condition (distractor proximity to a target: $F(1, 11) = 1.02, p = .34, \eta p^2 = .09$, target VF: $F(1, 11) = 0.02, p = .90, \eta p^2 = .00$) or the VSWM condition (distractor proximity to target: $F(1, 11) = 1.50, p = .25, \eta p^2 = .12$, target VF: $F(1, 11) = 0.59, p = .46, \eta p^2 = .05$). Moreover, no significant main effect was found for initial deviation for the NS-VWM condition for target VF; $F(1, 11) = 0.11, p = .75, \eta p^2 = .01$. A trend towards significance, however, was found for distractor proximity to a target during the NS-VWM condition proximity [$F(1, 11) = 3.70, p = .08, \eta p^2 = .25$]. The initial deviations of saccades was reduced after the presentation of close proximity distractors ($M = -7.73, SE = 2.38$) in comparison to far proximity distractors ($M = -9.86, SE = 2.36$); see *fig. 6.4*. No other significant results were found during the NS-VWM condition.

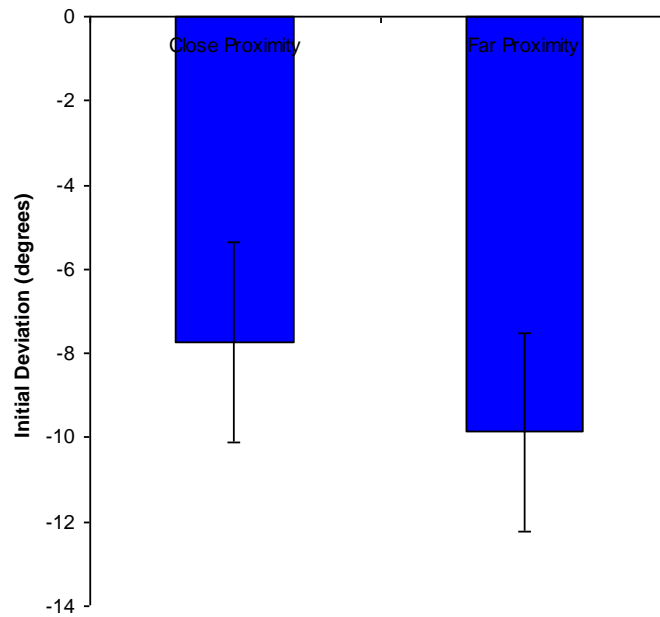


Fig. 6.4. Initial deviation for NS-VWM condition for distractor proximity to a target. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effects for target VF [$F(1, 11) = 0.09, p = .77, \eta p^2 = .01$] or condition [$F(2, 22) = 0.28, p = .76, \eta p^2 = .03$]. A trend towards a significance was found for distractor proximity to a target [$F(1, 11) = 3.59, p = .09, \eta p^2 = .25$]. Close proximity distractors elicited a reduced amount of initial deviation ($M = -9.50, SE = 1.70$) in comparison to far proximity distractors ($M = -11.47, SE = 1.78$). No significant interactions were found.

Saccade Deviation

During the non-active rehearsal VWM condition, a 2×2 repeated measures ANOVA revealed no significant main effects for distractor proximity to a target [$F(1, 11) = 0.08, p = .79, \eta p^2 = .01$] or target VF [$F(1, 11) = 0.32, p = .59, \eta p^2 = .03$] for the saccade deviation measure. A significant interaction was found for these two variables; $F(1, 11) = 6.41, p < .05, \eta p^2 = .37$. A reduced degree of saccade deviation was observed in

the lower VF after the presentation of close proximity distractors ($M = -2.51$, $SE = 1.82$) in comparison to after the presentation of far proximity distractors ($M = -1.68$, $SE = 2.12$). In contrast, in the upper VF more comparable, though apparently directionally different (as borne out by both positive and negative values) levels of saccade deviation were observed (close proximity distractors: $M = -0.58$, $SE = 1.97$, far proximity distractors: $M = 0.56$, $SE = 1.84$). However, planned comparisons did not indicate any significant difference for saccades directed to either upper or lower VF after the presentation of close or far proximity distractors; see *fig 6.5*.

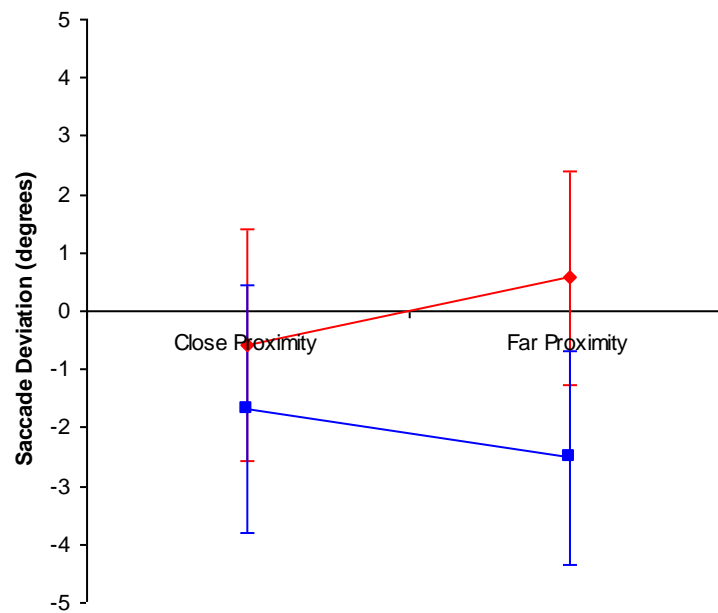


Fig. 6.5. Distractor proximity to a target \times target VF interaction during the non-active VWM condition for saccade deviation. Red lines denote saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

No significant results were found for either the VSWM (distractor proximity to target: $F(1, 11) = 0.09$, $p = .77$, $\eta p^2 = .01$, target VF: $F(1, 11) = 0.01$, $p = .92$, $\eta p^2 = .00$) or the NS-VWM conditions (distractor proximity to target: $F(1, 11) = 1.85$, $p = .20$, $\eta p^2 = .14$, target VF: $F(1, 11) = 0.52$, $p = .48$, $\eta p^2 = .05$) after the completion of 2×2 repeated

measures ANOVA's. A trend towards significance was found for the interaction between distractor proximity to a target and target VF during the VSWM [$F(1, 11) = 3.21, p = .10, \eta p^2 = .23$]. The lower VF yielded saccades with a reduced degree of saccade deviation after the presentation of close proximity ($M = -0.43, SE = 1.55$) distractors in comparison to after the presentation of far proximity distractors ($M = -1.39, SE = 1.84$). The opposite pattern of results was observed for saccades directed to the upper VF (close proximity distractors: $M = -0.83, SE = 1.89$, far proximity distractors: $M = -0.26, SE = 1.95$); see *fig. 6.6*. Planned comparisons, again, did not find any significant differences across these independent variables.

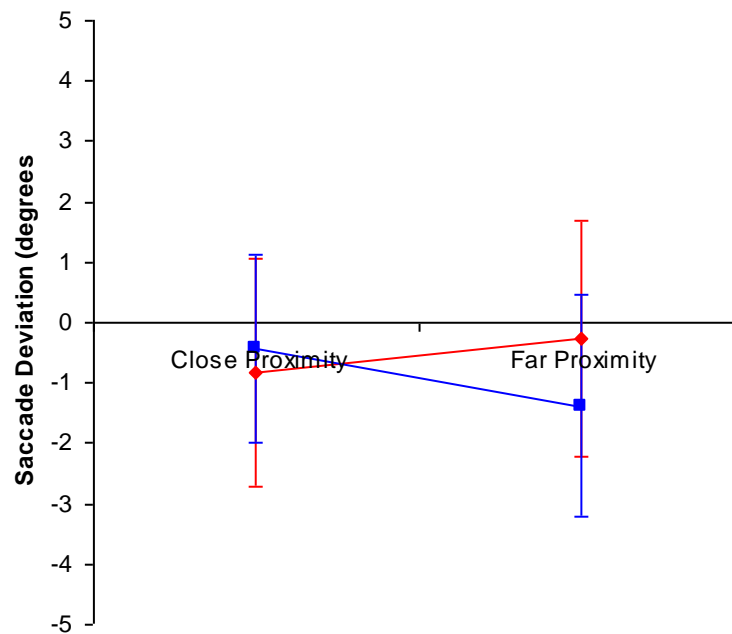


Fig. 6.6. Distractor proximity to a target \times target VF interaction during the VSWM condition for saccade deviation. Red lines denote saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effects for distractor proximity [$F(1, 11) = 0.36, p = .56, \eta p^2 = .03$], target VF [$F(1, 11) = 0.67, p =$

.43, $\eta p^2 = .06$], or condition [$F(2, 22) = 0.43$, $p = .66$, $\eta p^2 = .04$] across the three conditions. A significant interaction was observed between distractor proximity and target VF [$F(1, 11) = 7.41$, $p < .05$, $\eta p^2 = .40$]; see *fig. 6.7*. Planned comparisons revealed that saccades directed to the lower VF were subject to a significantly ($p < .05$) reduced degree of saccade deviation after the presentation of close proximity distractors in comparison to after the presentation of far proximity distractors. Directional deviation differences appeared to influence saccade deviation in saccades directed to the upper VF (close proximity distractors: $M = -1.05$, $SE = 0.99$, far proximity distractors: $M = -2.00$, $SE = 1.03$); though planned comparisons did not find that these differences were significant.

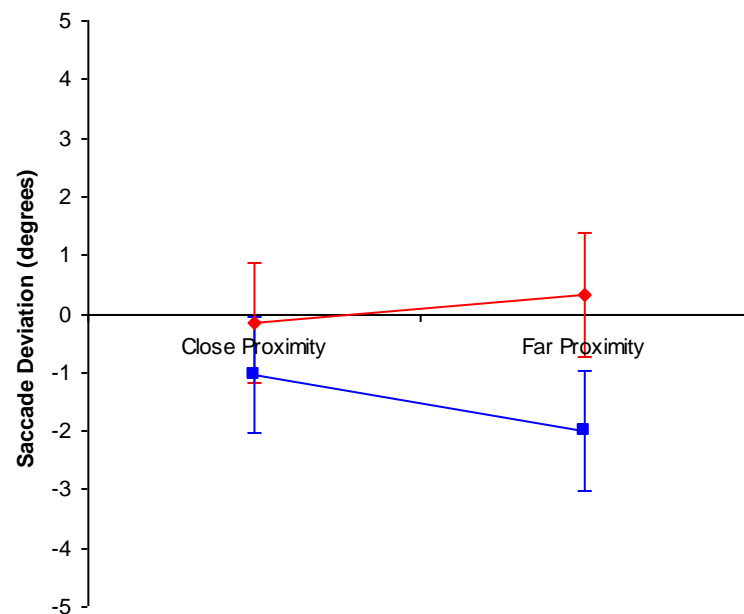


Fig. 6.7. Distractor proximity to a target \times target VF interaction for saccade deviation across conditions. Red lines denote saccades directed to the upper VF. Blue line denotes saccades directed to the lower VF. Error bars represent ± 1 SE.

Saccade Accuracy

During the non-active rehearsal VWM condition, a 2×2 repeated measures ANOVA found no significant main effect for target VF [$F(1, 11) = 0.01, p = .94, \eta p^2 = .00$] for saccade accuracy. A trend towards significance was found for distractor proximity to a target [$F(1, 11) = 3.93, p = .07, \eta p^2 = .26$]. Saccades made after the presentation of close proximity distractors ($M = 1.20, SE = 0.05$) tended to land closer to the target than saccades made after the presentation of far proximity distractors ($M = 1.31, SE = 0.52$); see *fig. 6.8*. No significant interactions were found.

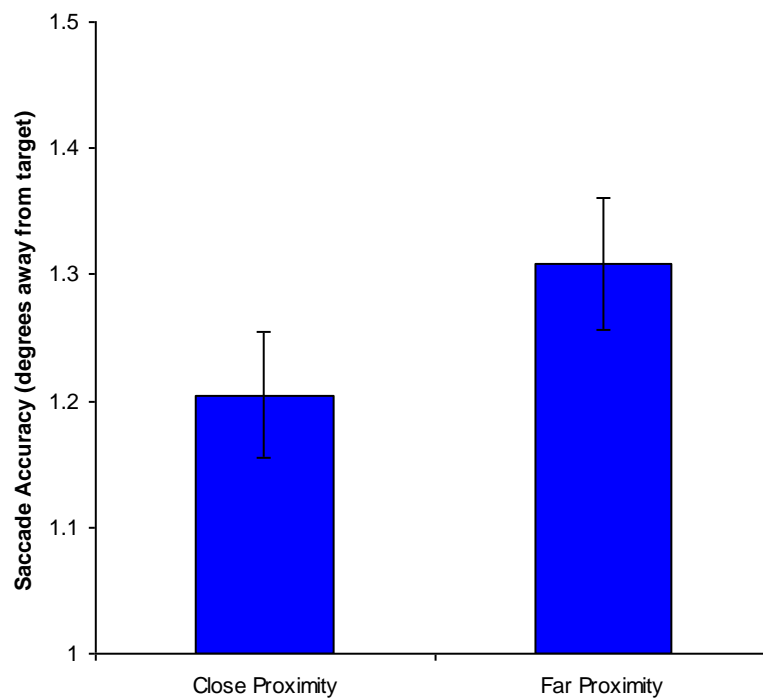


Fig. 6.8. Saccade accuracy for distractor proximity during the non-active rehearsal condition. Error bars represent ± 1 SE.

In contrast, a 2×2 repeated measures ANOVA found no significant main effects during the VSWM condition (distractor proximity to a target: $F(1, 11) = 0.75, p = .40, \eta p^2 = .06$, or target VF: $F(1, 11) = 0.14, p = .72, \eta p^2 = .01$) or the NS-VWM condition

(distractor proximity to a target: $F(1, 11) = 0.00$, $p = .99$, $\eta p^2 = .00$, target VF: $F(1, 11) = 0.52$, $p = .48$, $\eta p^2 = .05$). However, during the NS-VWM condition, a trend towards a significant interaction was found across the two variables; $F(1, 11) = 4.77$, $p = .05$, $\eta p^2 = .30$. Planned comparisons found a trend towards significance ($p = .10$) suggesting that for saccades made to the lower VF were less accurate after the presentation of close proximity distractors ($M = 1.36$, $SE = 0.07$) in comparison to after the presentation of far proximity distractors ($M = 1.27$, $SE = 0.06$). In the upper VF the opposite result was observed (close proximity distractors: $M = 1.21$, $SE = 0.08$, far proximity distractors: $M = 1.30$, $SE = 0.05$) though planned comparisons found that this result was not significant; see *fig. 6.9*.

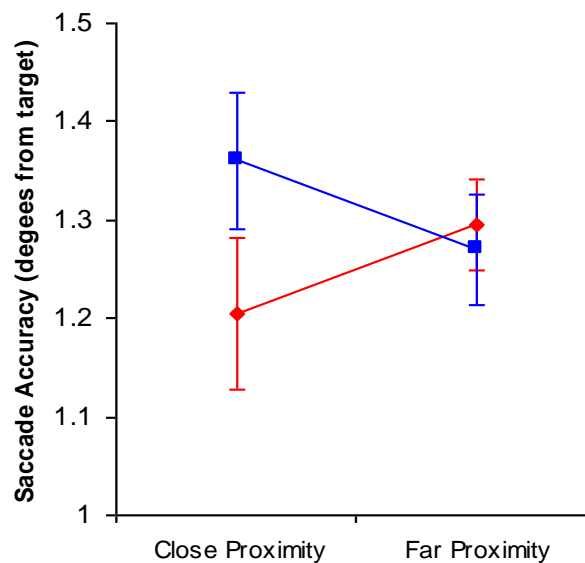


Fig. 6.9. Saccade accuracy for distractor proximity to target vs. target VF interaction during the NS-VWM condition. Red line denotes upper target VF. Blue line denotes saccades lower target VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA found no significant main effects for distractor proximity [$F(1, 11) = 1.48$, $p = .25$, $\eta p^2 = .12$], target VF [$F(1, 11) = 0.02$, $p =$

.89, $\eta p^2 = .00$], or condition [$F(2, 22) = 0.72$, $p = .50$, $\eta p^2 = .06$] across the three conditions. A trend towards significance was found for the three-way interaction; $F(2, 22) = 2.94$, $p = .07$, $\eta p^2 = .21$. The aforementioned trend towards significance was found for the interaction between distractor proximity to a target and target VF during the NS-VWM condition. Moreover, an additional planned comparison highlighted a further trend towards significance ($p = .06$) suggesting that saccades made to the lower VF after the presentation of close proximity distractors were more accurate during the non-active rehearsal VWM condition ($M = 1.16$, $SE = 0.09$) in comparison to the NS-VWM condition ($M = 1.36$, $SE = 0.07$); see *fig. 6.10*. No other significant planned comparisons were revealed.

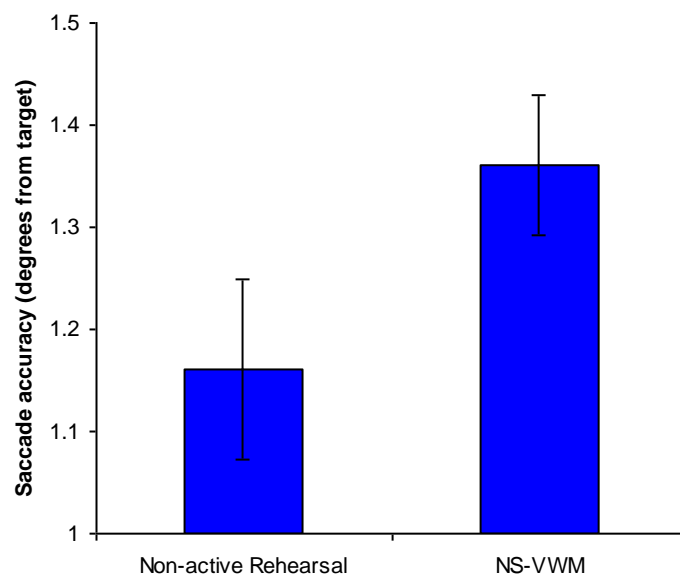


Fig. 6.10. Saccade accuracy for saccades directed to the lower VF after the presentation of close proximity distractors for the non-active rehearsal and NS-VWM conditions. Error bars represent ± 1 SE.

Saccade Latency

For saccade latency, all conditions presented a similar pattern of results. 2×2 repeated measures ANOVA's revealed no significant main effects for distractor proximity to a target (non-active rehearsal VWM: $F(1, 11) = 0.32, p = .58, \eta p^2 = .03$, VSWM: $F(1, 11) = 0.01, p = .93, \eta p^2 = .00$, NS-VWM: $F(1, 11) = 1.87, p = .20, \eta p^2 = .15$). However, for target VF a trend towards significance was found for during the non-active rehearsal VWM condition [$F(1, 11) = 4.57, p = .06, \eta p^2 = .29$] whilst significant main effects were found across the other two conditions (VSWM: $F(1, 11) = 13.62, p < .005, \eta p^2 = .55$, NS-VWM: $F(1, 11) = 31.39, p < .001, \eta p^2 = .74$). All conditions found that saccades made to the upper VF (non-active rehearsal VWM: $M = 295.56, SE = 7.16$, VSWM: $M = 282.28, SE = 8.34$, NS-VWM: $M = 287.38, SE = 8.58$) had shorter saccade latencies than saccades made to the lower VF (non-active rehearsal VWM: $M = 323.31, SE = 7.77$, VSWM: $M = 317.57, SE = 8.73$, NS-VWM: $M = 334.30, SE = 9.44$); see *fig 6.11*. for saccade latencies during the VSWM condition and *fig. 6.12*. for saccade latencies during the NS-VWM condition. No significant interactions were found for any of the conditions.

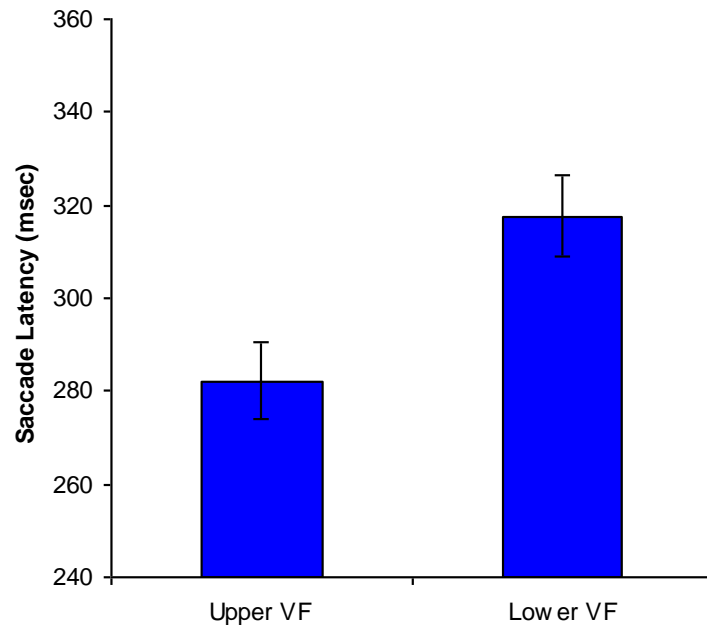


Fig. 6.11. Saccade latencies for target VF during VSWM condition. Error bars represent ± 1 SE.

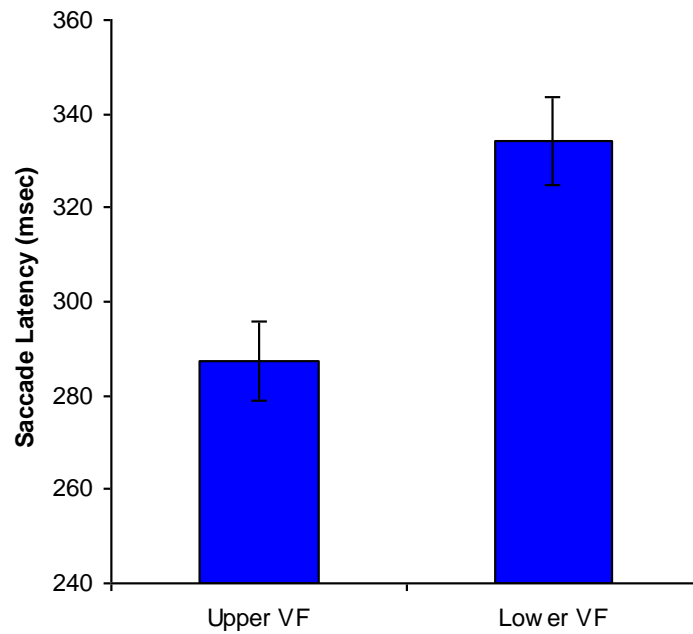


Fig. 6.12. Saccade latencies for target VF during NS-VWM condition. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effect for distractor proximity to a target [$F(1, 11) = 0.40$, $p = .54$, $\eta p^2 = .04$], or condition [$F(2,$

22) = 0.26, $p = .78$, $\eta p^2 = .02$] across the three conditions. A significant main effect was found for target VF; $F(1, 11) = 17.41$, $p < .005$, $\eta p^2 = .61$. Saccade latencies made to the upper VF ($M = 288.41$, $SE = 4.63$) were shorter than the latencies of saccades made to the lower VF ($M = 325.06$, $SE = 5.01$). No significant interactions were found.

Mean Direction

During the non-active rehearsal VWM condition, a 2×2 repeated measures ANOVA found a trend towards a significant main effect for distractor proximity to target for the mean direction measure; $F(1, 11) = 4.17$, $p = .07$, $\eta p^2 = .28$. Saccades were directed rightwards to a greater extent after the presentation of far proximity distractors ($M = 0.11$, $SE = 0.05$) in comparison to after the presentation of close proximity distractors ($M = 0.06$, $SE = 0.05$); see *fig. 6.13*.

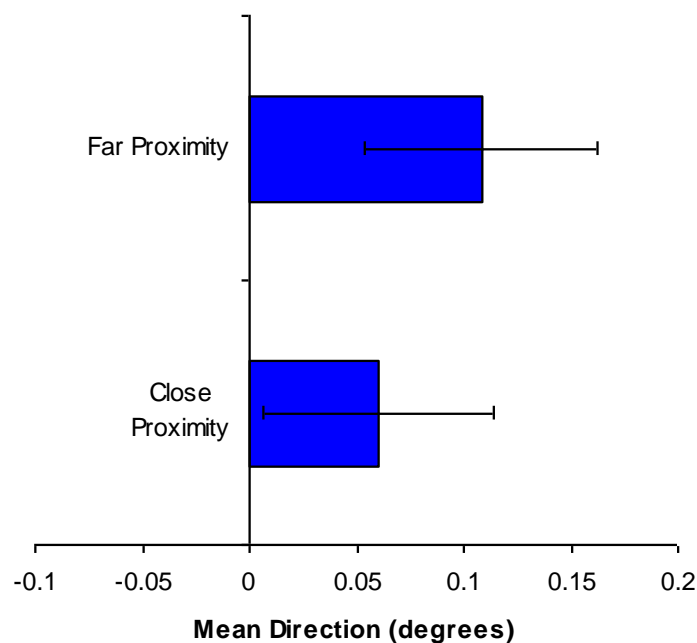


Fig. 6.13. Mean saccade direction for distractor proximity during the non-active condition. Error bars represent ± 1 SE.

A trend towards significance was also found for distractor VF; $F(1, 11) = 4.11, p = .07, \eta p^2 = .27$. Saccades made after the presentation of a left VF distractor tended to be directed rightwards ($M = 0.10, SE = 0.06$) to a greater extent than saccades made after the presentation of a right VF distractor ($M = 0.07, SE = 0.05$); see *fig 6.14*.

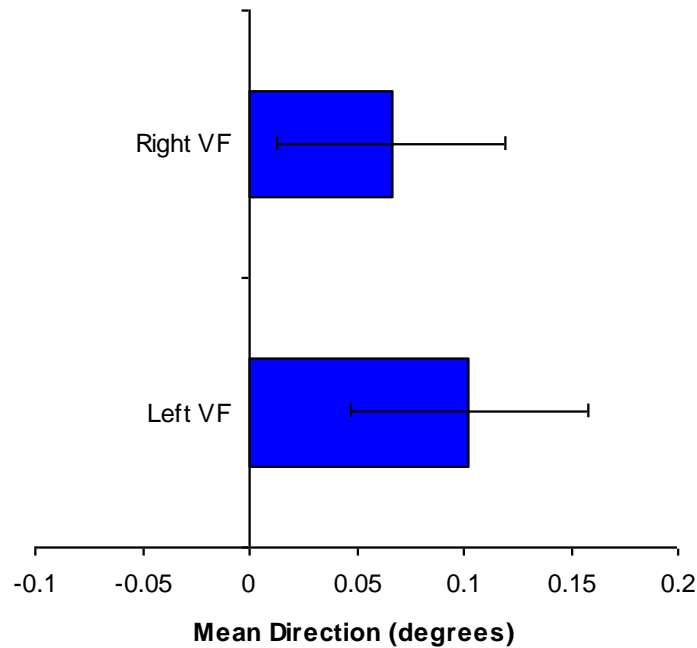


Fig. 6.14. Mean saccade direction for distractor VF during the non-active condition. Error bars represent ± 1 SE.

A trend towards significance was also found for the interaction between the two independent variables; $F(1, 11) = 3.49, p = .09, \eta p^2 = .24$. Planned comparisons revealed that saccades made after the presentation of left VF, close proximity distractors were directed rightwards to a significantly ($p < .05$) greater extent ($M = 0.08, SE = 0.08$) than saccades made after the presentation of right VF, close proximity distractors ($M = 0.03, SE = 0.07$). Furthermore, saccades made after the presentation of right VF distractors were significantly ($p < .05$) more likely to be directed to a greater extent rightwards after the presentation of far proximity distractors ($M = 0.09,$

$SE = 0.08$) in comparison to close proximity distractors ($M = 0.03$, $SE = 0.07$); see *fig. 6.15*.

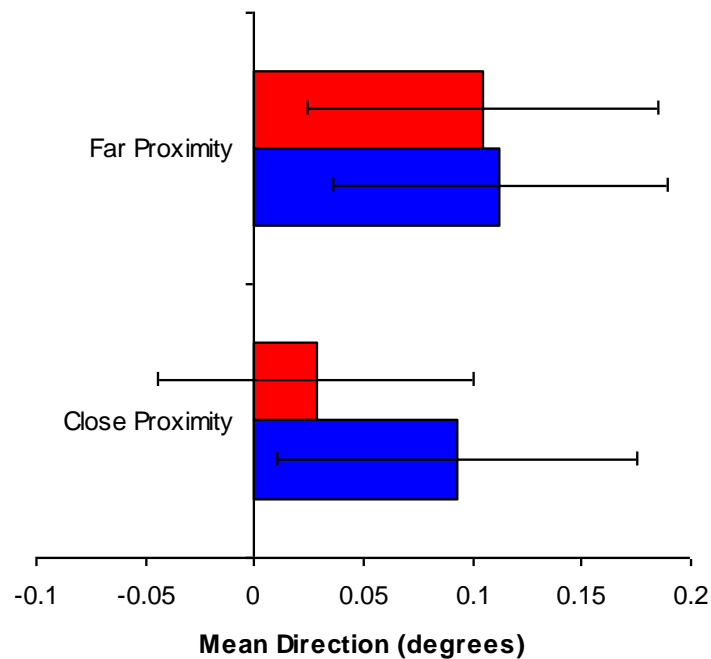


Fig. 6.15. Distractor proximity \times distractor VF interaction during the non-active condition for mean direction. Red bars represent the right VF. Blue bars represent the left VF. Error bars represent ± 1 SE.

In comparison, during the VSWM and the NS-VWM conditions 2×2 repeated measures ANOVA's revealed no significant main effect for distractor proximity to a target (VSWM: $F(1, 11) = 2.78$, $p = .12$, $\eta p^2 = .20$, NS-VWM: $F(1, 11) = 2.10$, $p = .18$, $\eta p^2 = .16$). A trend towards significance was found for distractor VF during the VSWM; $F(1, 11) = 4.49$, $p = .06$, $\eta p^2 = .29$. Saccades made after the presentation of left VF distractors exhibited a greater rightward deviation ($M = 0.10$, $SE = 0.04$) in comparison to saccades made after the presentation of right VF distractors ($M = 0.04$, $SE = 0.06$); see *fig. 6.16*. This effect was not found in the NS-VWM condition [$F(1, 11) = 2.50$, $p = .14$, $\eta p^2 = .19$]. No significant interactions were found in either condition.

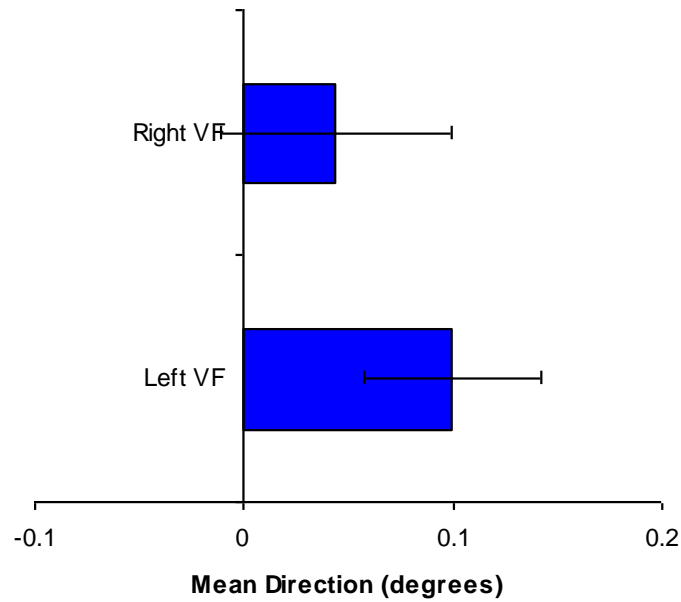


Fig 6.16. Mean saccade direction for distractor VF during the VSWM condition. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effect for condition; $F(1, 11) = 0.03$, $p = .97$, $\eta p^2 = .00$, however a significant main effect for distractor proximity was found; $F(1, 11) = 8.58$, $p < .05$, $\eta p^2 = .44$. Saccades made after the presentation of far proximity distractors elicited saccades with a greater degree of rightwards direction ($M = 0.09$, $SE = 0.03$) in comparison with saccades made after the presentation of close proximity distractors ($M = 0.05$, $SE = 0.03$); see *fig. 6.17*.

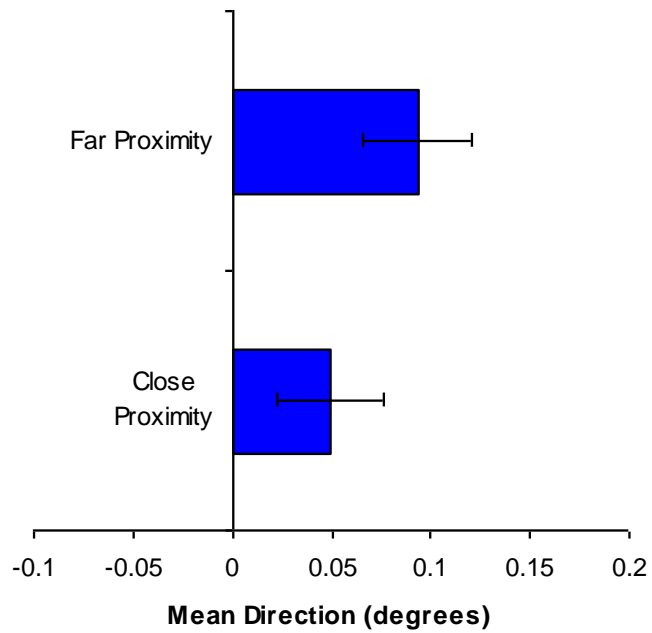


Fig. 6.17. Mean saccade direction for distractor proximity across conditions. Error bars represent ± 1 SE.

A significant main effect was also found for distractor VF; $F(1, 11) = 25.15$, $p < .001$, $\eta p^2 = .70$. Saccades made after the presentation of left VF distractors were more likely to be directed to the right ($M = 0.09$, $SE = 0.01$) to a greater extent than saccades made after the presentation of right VF distractors ($M = 0.05$, $SE = 0.03$); see fig 6.18. No significant interactions were found.

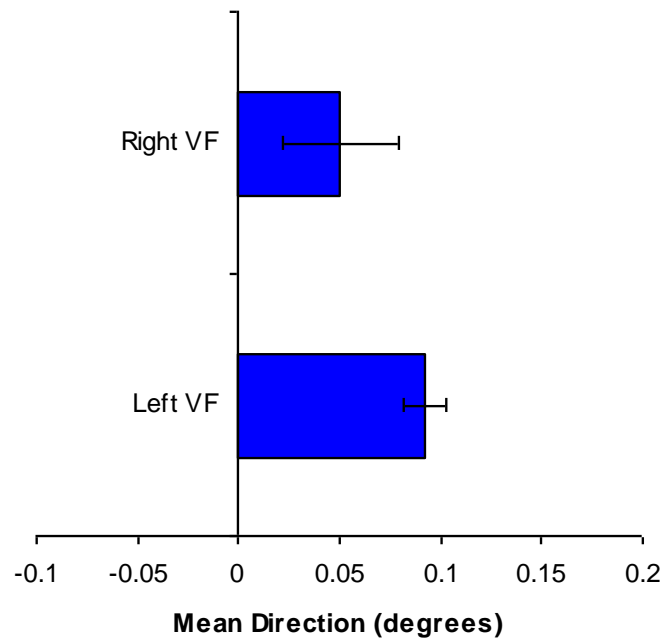


Fig. 6.18. Mean saccade direction for distractor VF across conditions. Error bars represent ± 1 SE.

Memory Data

A paired-sample t-test revealed no significant difference between the percentage of correct memory trials between the VSWM condition and the NS-VWM condition; $t(11) = -1.36, p < .20$.

Discussion

This study was designed to explore how the different visual processing pathways interact with the oculomotor system. Four main findings will be discussed: 1. differential saccade deviations were observed across conditions thought to be specialised for dorsal and ventral pathway processing; 2. saccade accuracy was influenced by distractor proximity and target VF; 3. Saccade latencies for upper VF targets were shorter in all three conditions in comparison to saccade latencies to lower VF targets; and 4. the mean direction of a saccade was influenced by distractor

proximity and distractor VF during dorsal pathway specialised conditions but not in the ventral pathway condition. The behavioural memory data results will firstly be briefly discussed.

Memory Data

No significant difference was found for the percentage correct trials across both active rehearsal VWM conditions (VSWM and NS-VWM conditions). This suggests that task difficulty was not a confounding factor in this experiment. Differences in task difficulty across the two conditions would suggest that observed changes in saccade trajectory characteristics could be better portrayed as a by-product of differential cognitive processing power. Thus, findings relating to saccade trajectory differences cannot be attributed, straightforwardly, to task difficulty.

Dorsal and ventral interactions with the oculomotor system

This experiment has been concerned with possible dorsal and ventral pathway interactions with the oculomotor system. Two active rehearsal VWM conditions designed to specifically recruit VSWM (dorsal pathway) and NS-VWM (ventral pathway) were presented to participants in order to draw inferences regarding any interaction with the oculomotor system. A further non-active rehearsal VWM condition was presented to participants. Unconscious processing of visual information has been attributed to processing along the dorsal pathway (Ro, 2008). Thus the non-active rehearsal VWM condition and the VSWM condition can both be arguably attributed to processing along the dorsal pathway and the NS-VWM condition can be arguably attributed to processing along the ventral pathway.

The interaction between the proximity of a distractor in relation to a target and the altitudinal VF a saccade was directed to (either upper or lower VF) appeared to be preferentially related to the dorsal visual processing stream. The overall mean saccade deviation measure found a significant interaction between these two variables during the non-active rehearsal VWM condition, and a trend towards significance for these variables in the VSWM condition. Measures observing the deviation of saccades in previous chapters also found this interaction during non-active rehearsal VWM conditions. That this interaction was not observed during the NS-VWM condition in this experiment, or in previous experiments, suggests that tasks recruiting the dorsal pathway are influenced to a greater extent by the spatial relationships between a visual target object and distractor, and by altitudinal VF properties.

These interaction results suggest that during dorsal pathway interactions with the oculomotor saccade map, a form of bottom-up processing is ongoing. During these conditions, neuronal inhibition in the oculomotor saccade map, facilitated by information stored and maintained in VWM, is influenced at a basic level by the specialised VFs. The spatial relationship between target stimuli and distractor stimuli, and the associated degree of deviation expressed, being dependent on the VF a target was presented in. In contrast, no such target VF sensitivity has been associated with VWM facilitation of oculomotor inhibition during the NS-VWM condition. This suggests that whilst the influences of bottom-up processing can be observed in non-active rehearsal VWM and VSWM (dorsal pathway) conditions, NS-VWM facilitation is primarily based on top-down, goal-directed, influences.

That NS-VWM facilitation of oculomotor inhibition is based on top-down influences is partially supported by results highlighting distractor proximity to a target effects during conditions recruiting this VWM sub-system. A trend towards significance found that close proximity distractors produced a smaller degree of initial deviation during the NS-VWM in comparison to far proximity distractors. This result was again not replicated within the VSWM or the non-active rehearsal VWM conditions. The dissociable nature of saccades facilitated by conditions specialised for the ventral or dorsal visual processing pathways is further illustrated.

Results relating to the degree of deviation expressed in saccades highlight a possible difference in the interaction between the dorsal and ventral processing streams and the oculomotor system. Findings indicate the possibility that ventral pathway influences on the trajectories of saccades is primarily driven by top-down processing. Moreover, bottom-up influences have been associated with dorsal pathway interactions with the oculomotor system. Mean direction results further elaborate on the appropriateness of these conclusions and further suggest that the dorsal pathway may be subject to both top-down and bottom-up influences.

In this study mean saccade direction was mainly represented in the right VF; however the extent of this rightward direction was somewhat mediated by distractor proximity to a target and distractor VF in the non-active rehearsal VWM condition, and by distractor VF in the VSWM condition. The extent of rightward direction was not found to be mediated by either of these two variables in the NS-VWM condition.

Distractors presented in close proximity to targets tended to generate a smaller degree of rightward direction in comparison to distractors presented further away from targets during the non-active rehearsal VWM condition. A trend towards significance also indicated that saccades made after the presentation of left VF distractors tended to elicit a greater degree of rightwards direction during the non-active rehearsal VWM condition in comparison to right VF distractors. In the VSWM condition, left VF distractors also elicited a greater rightward direction in saccades in comparison to right VF distractors. Furthermore, an interaction effect for the non-active rehearsal VWM condition suggests that this reduced rightward direction is also influenced by the spatial relationship between a distractor VF and a distractors proximity to target.

Mean direction results suggest that in both the non-active rehearsal VWM and VSWM conditions saccades trajectories are directed away from the location of a briefly presented distractor. These results support previous findings reported by Theeuwes and colleagues (2005, 2006) who found that saccades deviated away from spatial information held in VWM. The current results also suggest that this deviation away occurs during conditions not requiring the active rehearsal of information (consistent with the findings of König, 2010 and findings reported in previous chapters).

It has been suggested that deviation away from the location of a distractor is indicative of top-down influences, whereas deviation toward a distractor is indicative of bottom-up processes (McSorley, Haggard, and Walker, 2005; McSorley, Cruickshank, and Inman, 2009). In this study both the VSWM condition and the non-active rehearsal VWM condition resulted in saccades that deviated away from presented distractors.

These findings suggest that a degree of top-down influence is apparent in both VSWM and non-active VWM conditions.

Saccade latency effects and ventral pathway-oculomotor interaction

Saccade latencies to the upper VF were consistently shorter than saccade latencies made to the lower VF. These results support previous findings reported in chapter 5 and also previously published studies (e.g., Zhou and King, 2002). It has been suggested that shorter saccade latencies to upper VF targets are consequent of ventral pathway top-down interaction with the oculomotor system (Buffalo, Fries, Landman, Liang, & Desimone, 2010). The upper VF has been associated with the ventral stream processing (Previc, 1990). In the non-active rehearsal VWM condition a trend towards significance was found for target VF whilst a significant main effect was found during the other two conditions. Thus, it can be concluded that in active rehearsal VWM conditions (VSWM and NS-VWM) a degree of ventral pathway-oculomotor interaction for the production of rapid upper VF saccades can be observed independent of the pathway recruited during specific VWM tasks. In non-active rehearsal VWM tasks, this ventral pathway-oculomotor can be thought of as still intact, though less to a lesser extent influential.

Saccade accuracy effects

The final fixation point of a saccade has been attributed to an additional cerebellar drive back towards a target stimulus resulting in saccadic 'curvature' (McSorley, Haggard & Walker, 2004). Moreover, it has been found that perceptual attention at the locus of a saccade target stimulus facilitates the accuracy of saccades (Kowler, Anderson, Doshier, & Blaser, 1995). In the non-active rehearsal VWM condition, a trend

towards significance indicating a tendency for reduced saccade accuracy after the presentation of far proximity distractors can be attributed to perceptual attention being captured by stimuli in the opposite VF to the target VF. Hoffman and Subramaniam (1995) have presented evidence suggesting that saccades cannot be directed to one location whilst perceptual attention is directed to another location.

During the NS-VWM condition a trend towards significance indicated that saccades made to the lower VF tended to be more accurate after the presentation of far proximity distractors than after the presentation of close proximity distractors. Furthermore, a trend towards significance indicated a reduced degree of saccade accuracy during the NS-VWM condition in comparison to the non-active rehearsal VWM condition for saccades directed to the lower VF after the presentation of close proximity distractors. These results suggests that when saccades were made to the lower VF (thought to be a dorsal pathway specialised VF) during the completion of a task theorised to recruit the ventral pathway (NS-VWM), the brief presentation of close proximity distractors resulted in reduced saccade accuracy. This reduction in saccade accuracy may be indicative of attentional capture by close proximity distractors in the lower VF. In the upper VF, no significant difference in saccade accuracy was observed after the presentation of close or far proximity distractors. Upper VF specialism for the processing of visual object information may facilitate accurate saccades in the upper VF after the presentation of close proximity distractors; the lower VF being specialised for spatial information receives no such facilitation.

Previous experiments in this thesis (chapter 4 and 5) have not demonstrated saccade accuracy differences during non-active and NS-VWM conditions. In past experiments

saccade accuracy consistency was thought to display a lack of VWM interaction between the proposed cerebellar drive directing saccades to back towards a target stimulus after deviation induced by SC inhibition. However, saccade accuracy differences were found during this study. Experimental designs have been consistent throughout this thesis. Thus, it is unlikely that experimental design differences, across chapters, have influenced these results. It is suggested that as perceptual attention is proposed to influence the trajectories of saccades, factors influencing the degree of perceptual attention directed towards target and distractor stimuli will influence saccade accuracy results (e.g., participant fatigue and individual differences). For instance, participants with low VWM capacity are typically less accurate than high VWM capacity participants in antisaccade performance (Kane, Bleckley, Conway, & Engle, 2001). Intuitively such findings suggest that low VWM participants may be less able to suppress task-irrelevant saccades. Individual differences may have influenced saccade accuracy results in all experiments presented in this thesis. In the next chapter individual differences will be explored in relation to how saccade deviations are facilitated by VWM.

SUMMARY

In this chapter the results suggest that non-active rehearsal VWM conditions and VSWM conditions are sub-served by mutual pathways. The dorsal pathway, thought to be responsible for VSWM, has also been implicated by Irwin and Brockmole (2004) as being important during the generation of saccades. In their experiment, saccade amplitudes were seen to be moderated by spatial, as opposed to object, processing tasks. In this chapter, VSWM and non-active rehearsal VWM conditions appear to

mediate VWM facilitated prolonged inhibition oculomotor saccade map. Previous studies have found that the dorsal pathway is capable of 'unconsciously' processing information (for example Fang & He, 2005). Ro (2008) found that disruption to the primary visual cortex did not influence performance on a reaching task. It was suggested that projection to the dorsal pathway from the SC bypassed the primary visual cortex and allowed for the processing of unconscious information (Ro, 2008). The current results support unconscious processing of visual information, and visuo-spatial processing, along the same, dorsal, pathway.

A direct pathway from the PFC to intermediate layers in the SC has been implicated in the generation of saccades (Munoz & Everling, 2004). In particular, the DLPFC is thought to be involved in the facilitation of task relevant saccades (Johnston, Koval, Lomber, & Everling, 2013). DLPFC suppression has also been noted in the suppression of task-irrelevant saccades (Johnston & Everling, 2006) as evidenced by antisaccade studies (for example, Ford, Goltz, Brown, & Everling, 2005; Matsuda et al., 2004). The DLPFC has also been implicated as being active in the processing of VSWM (Ricciardi et al., 2006). A degree of top-down processing is evident during dorsal pathway specialised VWM subsystem facilitation of saccade deviations. It is also suggested that top-down ventral pathway processing mediates the generation of saccades during NS-VWM tasks. Reduced initial deviation for close proximity distractors during the NS-VWM condition supports a ventral pathway, top-down, inhibition of task-irrelevant stimuli presented in close proximity to targets.

In chapter 7 the temporal characteristics of VWM facilitated prolonged inhibition will be explored in an aim to understand the nature of bottom-up and top-down

processing during the deviation of saccades. Separate effects of attentional IOR and saccadic IOR have been noted (e.g. Godijn & Theeuwes, 2004). In this study attentional mechanisms appeared to have had a significant influence on the accuracy of saccades. By exploring top-down, attentional influences during VWM facilitation of saccades it is hoped that further insight can be gained into how VWM influences the bottom-up inhibition in the oculomotor system in contrast to how goal-directed attention influences oculomotor inhibition via information maintained in VWM. Chapter 7 will also explore how VWM performance influences the characteristics of saccades. Working memory has been associated with ability to suppress task-irrelevant information (McNab & Klingberg, 2008; Unsworth, Schrock, & Engle, 2004). It is possible that the ability to employ VWM efficiently influences the trajectories of saccades. These influences will be investigated in the next chapter and will inform the implications of VWM interaction with the oculomotor system.

Chapter 7

The implications of VWM facilitation of
saccade deviations

Assessing top-down and bottom-up processing and
visual working memory performance

This chapter was designed to explore the implications of oculomotor and VWM interaction. Two experiments are presented: experiments 5 and 6. Experiment 5 was designed to examine the theoretical implications of VWM-oculomotor interaction whilst experiment 6 was designed to examine the clinical implications of VWM-oculomotor interaction. Data collected from two previous experiments were re-analysed; thus the two experiments presented in this chapter should be assessed as post-hoc experiments. Two conditions were used: 1. a NS-VWM condition and 2. a non-active rehearsal VWM condition. Results from experiment 5 suggest that a form of parallel, top-down and bottom-up, processing can be observed during the non-active rehearsal VWM condition in contrast to the NS-VWM condition which displays saccade characteristic results indicative of top-down processing. These results are discussed in relation to models of saccade execution (e.g. Godijn & Theeuwes, 2004). Results from the experiment 6 suggest that VWM performance levels can influence the trajectories of saccades. These results are discussed in relation to how visual processing may differ across clinical groups.

IMPLICATIONS OF VWM-OCULOMOTOR INTERACTION

Oculomotor inhibition in the SC saccade map has been implicated in the deviation of saccades. Saccade trajectories are thought to deviate towards, or away, from distracting information presented in peripheral vision (for example, McSorley, Haggard, & Walker, 2006). Oculomotor neurons in the intermediate layers of the SC are organised topographically. Spatially adjacent stimuli presented in the VF are represented by spatially adjacent neurons within this map. Oculomotor inhibition of neurons coding for the spatial location of a distractor stimulus therefore leads to a

shift in activation in a spatially related population of neurons in the SC (Tipper, Howard, & Houghton, 2000). Saccade deviation is the behavioural outcome of oculomotor inhibition.

Saccades have also been found to deviate as a consequence of top-down influences. For instance, saccades have been found to deviate away from the location of an expected distractor (Van der Stigchel & Theeuwes, 2006) and from a cued location (Van der Stigchel, Meeter, & Theeuwes, 2007). It has also been found that target similarity influences the degree of saccade deviation towards or away from a target (Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). Thus, both dorsal, 'spatial', top-down influences, and ventral, non-spatial, top-down influences have previously been found to modulate saccade trajectories.

In this thesis, VWM facilitation of prolonged oculomotor inhibition has been demonstrated during conditions not requiring the active rehearsal of information stored in VWM. Deviation away from the spatial location of a distractor has previously been related to top-down processing; in contrast deviation towards a distractor has been related to bottom-up processing (McSorley, Haggard, & Walker, 2006). This thesis has suggested that parallel processing, in both a top-down and bottom-up fashion may be observable during VWM interaction with the oculomotor system. A VSWM condition presented comparable results to non-active rehearsal VWM conditions and it has been concluded that the dorsal visual pathway may drive both bottom-up and top-down interaction with the oculomotor saccade map. In contrast, ventral visual pathway interaction has appeared to interact with the oculomotor system in a primarily top-down fashion in order to facilitate saccades (chapter 6).

The PFC is thought to underpin top-down processing by the selection and integration of relevant information (Miller, Erikson, & Desimone, 1996). Regions along the dorsal visual processing pathway have been implicated in both the suppression of task-irrelevant information (Powell & Goldberg, 2000) and also in the generation of eye movements (Irwin & Brockmole, 2004). Evidence demonstrating a direct projection to the dorsal pathway from the SC during the processing of unconscious information (Ro, 2008) also supports theories highlighting two modes of processing (top-down and bottom-up) in the deviation of saccades along the dorsal pathway.

A framework developed by Godijn and Theeuwes (2004) proposes independent mechanisms accounting for attentional IOR and oculomotor inhibition (Godijn & Theeuwes, 2004) in the deviation of saccades. In their framework the SC invokes a tag for inhibition to an inhibitory control system located in the PFC (the DLPFC and FEF). In turn, afferents from the PFC to the SC and from the PFC to the LIP to the SC result in oculomotor inhibition and attentional IOR respectively. Activation in the LIP has been associated with visual attention and distractor presentation (Powell & Goldberg, 2000). In line with this framework it has been found that saccades made to inhibited spatial locations result in a reduced degree of saccade deviation (Theeuwes & Godijn, 2004). Moreover, saccade deviation is thought to occur after short delays between a cue and a saccade, whilst attentional IOR is thought to occur after longer delays between a cue and a saccade (Godijn & Theeuwes, 2004). Bottom-up processing, within this framework, would initiate from the SC as the aforementioned 'tag for inhibition'. In contrast top-down processing would be attributable to signals from the LIP to the SC.

As aforementioned (chapter 6), rapid saccades made to task-relevant stimuli have highlighted the rapid integration of information, in a top-down fashion, along the ventral visual pathway (Buffalo, Fries, Landman, Liang, & Desimone, 2010). Higher order processing of information along this pathway acts upon earlier visual centres to shorten the latencies of saccades made to relevant stimuli (Zhou & King, 2002). Moreover, it has been suggested that extrastriate areas along the ventral pathway may interact with frontoparietal cortices specialised for spatial attention in order to promote efficient visual processing (Corbetta et al., 1998). Shorter latency saccades after close proximity distractors have been found during NS-VWM conditions (chapter 5) and reduced saccade deviations have also been associated with processing along the ventral pathway after the presentation of close proximity distractors (chapters 5 and 6). It is suggested that NS-VWM, processed along the ventral pathway, does not facilitate saccade deviation via the bottom-up mediation of prolonged oculomotor inhibition and instead interacts with the oculomotor system in a purely top-down fashion via communication from cortical regions related to ventral pathway processing and the LIP.

In experiment 5 the extent, and the consequence, of bottom-up, VWM facilitated prolonged oculomotor inhibition will be explored. By exploring how the deviation of saccades is influenced by distractor stimuli presented at prior spatial locations across trials the extent of prolonged inhibition can be established. If the deviation of saccades is driven by parallel processing during non-active rehearsal VWM conditions, differential deviation and latency results should be apparent; VWM facilitation of prolonged inhibition should be reduced due to saccadic IOR. If bottom-up VWM

prolonged oculomotor inhibition is not facilitated during NS-VWM conditions, the degree deviation in saccades and saccade latencies would appear more consistent.

In experiment 6 the clinical implications of VWM-oculomotor interactions are explored. Differential saccade trajectories have been identified as a result of individual differences (McSorley, Haggard, & Walker, 2005). Participants have also been found to express distinguishable saccadic accuracy as a product of working memory ability (Kane, Bleckley, Conway, & Engle, 2001). Further evidence has found that working memory span is related to the suppression of task irrelevant information and the maintenance of goal information after the presentation of distracting information (Unsworth, Schrock, & Engle, 2004) during prosaccade and antisaccade tasks.

VWM capacity has been related to cortical activity (Vogel & Machizawa, 2004) illustrating that neuronal activation is causally related to behavioural responses. In experiment 6, VWM performance is assessed across a group of participants during a NS-VWM condition and participants subsequently separated into a 'high' performing VWM group and a 'low' performing VWM group. Saccade trajectory characteristics are explored across both groups of participants. In low VWM performance participants a smaller degree of top-down interaction with the oculomotor system is expected in comparison to high VWM performers (if low VWM participants are less able to suppress task-irrelevant information). It is also predicted that low VWM performers will be influenced to a greater extent by bottom-up oculomotor inhibitions.

Experiment 5

Method

Data was analysed from 24 participants; ($M_{\text{age}} = 21.83$, $SD_{\text{age}} = 3.21$). All participants had normal or corrected colour vision. All participants gave informed consent; the study conformed to all applicable ethical guidelines. One participant self-reported as left-handed, all other participants self-reported as right-handed.

Non-active rehearsal VWM and NS-VWM data from chapters 5 and 6 formed a database of saccade trajectory data. Memory data was also used from the NS-VWM conditions. In the non-active rehearsal VWM conditions, participants were required to make a saccade to a target stimulus after the brief presentation of a distractor stimulus. In the NS-VWM condition, participants were required to state whether a probed stimulus presented at the end of a trial was previously presented as the distractor stimulus. Details for these conditions can be seen in chapters 5 and 6.

Design

Data was filtered as in previous chapters using MATLAB (R2010a, Mathworks, Natick, MA) and previously defined exclusion criteria were used (chapter 3). Saccade measures used were the saccade deviation, initial deviation, saccade accuracy, saccade latency, and the mean direction of a saccade.

A 2×2 repeated measures design was implemented for both conditions with the independent variables being prior distractor presentation (previously presented in a preceding trial vs. newly presented distractor spatial locations) and distractor

proximity to a target (close proximity distractors vs. far proximity distractors). Previously presented distractors were defined as distractor stimuli that were shown in the same spatial location as the preceding trial. Newly presented distractors were defined as a distractor that was presented at a different location to that of a previous distractor from the A further $2 \times 2 \times 2$ repeated measures design was used to ascertain whether there was a difference between conditions with prior distractor presentation, distractor proximity, and condition (non-active VWM vs. NS-VWM) as the independent variables.

In order to analyse the mean direction of a saccade in relation to the VF of a presented, a further 2×2 repeated measures design was used. The independent variables for this analysis were prior distractor presentation and distractor VF (left VF vs. right VF). A further $2 \times 2 \times 2$ repeated measures ANOVA was run in order to establish whether there was a difference between conditions for the deviation of saccades towards or away from distractors; the independent variables being prior distractor presentation, distractor VF (left VF vs. right VF), and condition.

Planned comparisons will examine any significant interactions found between the independent variables.

Results

Initial Deviation

2×2 repeated measures ANOVA's found no significant difference for the degree of initial deviation for the prior presentation of a distractor during the non-active rehearsal VWM condition (prior presentation of a distractor: $F(1, 23) = 1.03, p = .32$,

$\eta p^2 = .04$, distractor proximity to a target: $F(1, 23) = 1.15$, $p = .29$, $\eta p^2 = .05$) or NS-VWM conditions (prior presentation of a distractor: $F(1, 23) = 2.57$, $p = .12$, $\eta p^2 = .10$, distractor proximity to a target: $F(1, 23) = 0.14$, $p = .72$, $\eta p^2 = .06$). No significant interactions in either condition were found.

A further $2 \times 2 \times 2$ repeated measures ANOVA found no significant difference for distractor proximity to a target [$F(1, 23) = 0.70$, $p = .41$, $\eta p^2 = .03$] or condition [$F(1, 23) = 0.87$, $p = .36$, $\eta p^2 = .04$]. A trend towards significance was indicated for the prior presentation of a distractor; $F(1, 23) = 3.03$, $p = .10$, $\eta p^2 = .12$. It was found that previously presented distractors tended to elicit a reduced degree of initial deviation ($M = -9.16$, $SE = 1.46$) in comparison to newly presented distractors ($M = -10.41$, $SE = 1.12$); see *fig 7.1*.

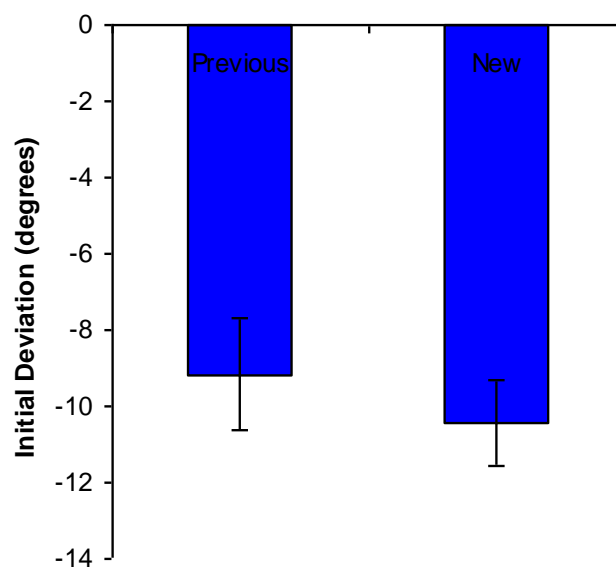


Fig. 7.1. Initial deviation across the two conditions. Error bars represent ± 1 SE.

A trend towards significance was also found for the three-way interaction across the variables; $F(1, 23) = 3.23$, $p = .09$, $\eta p^2 = .12$. Planned comparisons revealed a trend towards significance ($p = .07$) indicating a reduction in the degree of initial deviation expressed after the presentation of far proximity, previously presented distractors ($M = -5.59$, $SE = 2.16$) in comparison to after the presentation of far proximity, newly presented distractors ($M = -9.40$, $SE = 1.70$) during the NS-VWM condition. Furthermore, a trend towards significance ($p = .09$) during the NS-VWM condition indicated a reduction in expressed initial deviation for close proximity, newly presented distractors ($M = -7.09$, $SE = 1.70$) in comparison to after the presentation of far proximity, newly presented distractors. No other significant planned comparisons were found. In the non-active rehearsal VWM condition, a comparable degree of initial deviation was found after the presentation of far proximity distractors (previously presented distractor: $M = -10.64$, $SE = 2.03$, newly presented distractor: $M = -10.67$, $SE = 1.59$). In contrast, a non-significant reduction in initial deviation was found after the presentation of close proximity, previously presented distractors ($M = -7.68$, $SE = 2.11$) in comparison to close proximity, newly presented distractors ($M = -10.16$, $SE = 1.62$); see *fig. 7.2*.

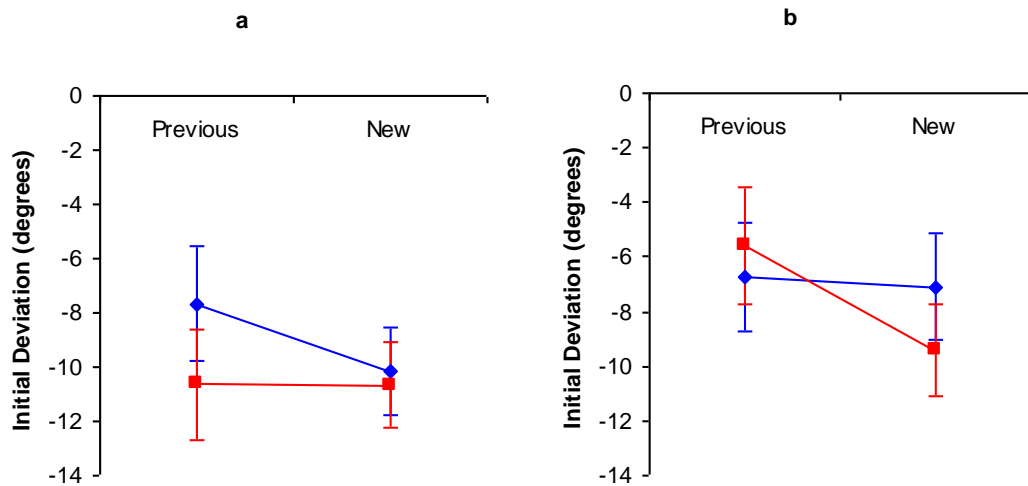


Fig. 7.2. Three-way interaction for initial deviation. a. shows initial deviation during the non-active rehearsal VWM condition. b. shows initial deviation during the NS-VWM condition. Red lines denote far proximity distractors. Blue lines denote close proximity distractors. Error bars represent ± 1 SE.

Saccade Deviation

No significant results were found for the saccade deviation measure for the non-active rehearsal VWM condition (prior presentation of a distractor: $F(1, 23) = 0.11$, $p = .75$, $\eta p^2 = .01$, distractor proximity to a target: $F(1, 23) = 0.22$, $p = .65$, $\eta p^2 = .01$), the NS-VWM condition (prior presentation of a distractor: $F(1, 23) = 0.07$, $p = .80$, $\eta p^2 = .00$, distractor proximity to a target: $F(1, 23) = 0.54$, $p = .47$, $\eta p^2 = .02$), or indeed across the two conditions (prior presentation of a distractor: $F(1, 23) = 0.01$, $p = .93$, $\eta p^2 = .00$, distractor proximity to a target: $F(1, 23) = 0.52$, $p = .48$, $\eta p^2 = .02$, condition: $F(1, 23) = 0.81$, $p = .38$, $\eta p^2 = .03$). No significant interactions were found.

Saccade Accuracy

No significant results were found during the non-active rehearsal VWM condition for saccade accuracy (prior presentation of a distractor: $F(1, 23) = 0.16$, $p = .70$, $\eta p^2 = .01$,

distractor proximity to a target: $F(1, 23) = 1.11, p = .30, \eta p^2 = .05$). Furthermore, distractor proximity to a target was not found to make a significant difference to saccade accuracy during the NS-VWM condition; $F(1, 23) = 0.03, p = .86, \eta p^2 = .00$. In contrast, during the NS-VWM condition, a significant main effect was found for the prior presentation of a distractor; $F(1, 23) = 9.66, p < .01, \eta p^2 = .30$. These results indicated that saccades made after the display of a previously presented distractor landed closer to the target ($M = 1.20, SE = 0.03$) than saccades made after newly presented distractors were displayed ($M = 1.27, SE = 0.02$); see *fig. 7.3*.

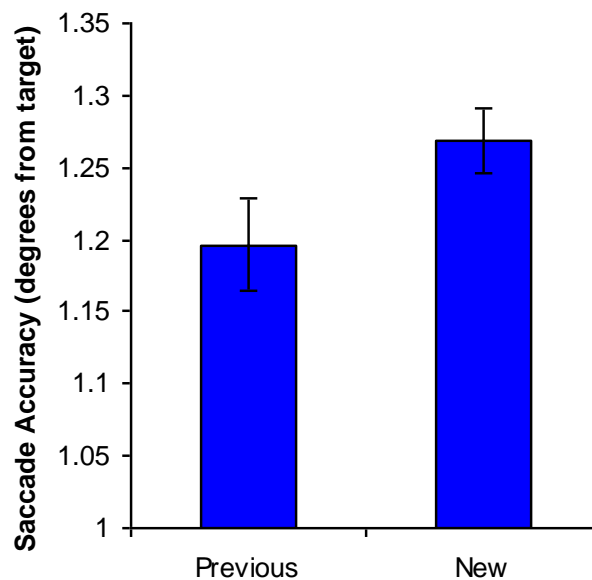


Fig. 7.3. Saccade accuracy for prior distractor presentation during NS-VWM. Error bars represent ± 1 SE.

A further $2 \times 2 \times 2$ repeated measures ANOVA across the conditions revealed no significant main effects for distractor proximity to a target [$F(1, 23) = .30, p = .59, \eta p^2 = .01$] or condition [$F(1, 23) = 0.12, p = .91, \eta p^2 = .00$], however a trend towards a significant main effect was found for the prior presentation of a distractor; $F(1, 23) =$

3.65, $p = .07$, $\eta p^2 = .14$. Previously presented distractor spatial locations resulted in saccades that landed closer to a target ($M = 1.21$, $SE = 0.03$) than saccades made after the presentation of distractors at newly presented spatial locations ($M = 1.25$, $SE = 0.01$); see *fig. 7.4*. No significant interactions were found.

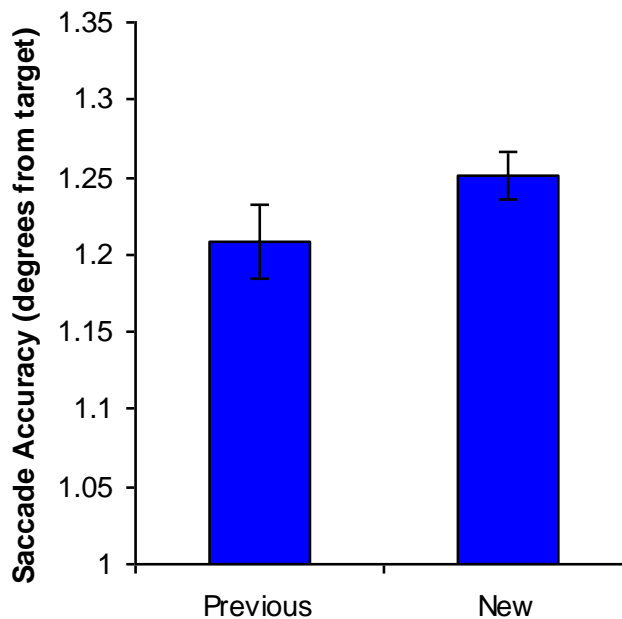


Fig 7.4. Saccade accuracy for the prior presentation of distractors across conditions. Error bars represent ± 1 SE.

Saccade Latency

Saccade latency results demonstrated a significant main effect for the prior distractor presentation during the non-active rehearsal VWM condition; $F(1, 23) = 10.61$, $p < .005$, $\eta p^2 = .32$. This result indicated that newly presented distractors elicited longer saccade latencies ($M = 305.62$, $SE = 4.58$) in comparison to previously presented distractors ($M = 290.23$, $SE = 4.47$); see *fig.7.5*. These findings were not replicated during the NS-VWM condition [$F(1, 23) = 1.31$, $p = .27$, $\eta p^2 = .05$]. No significant main effect was found for distractor proximity to a target across either condition (non-active

rehearsal VWM: $F(1, 23) = 0.51, p = .49, \eta p^2 = .02$, NS-VWM: $F(1, 23) = 0.17, p = .69, \eta p^2 = .01$). No significant interactions were found.

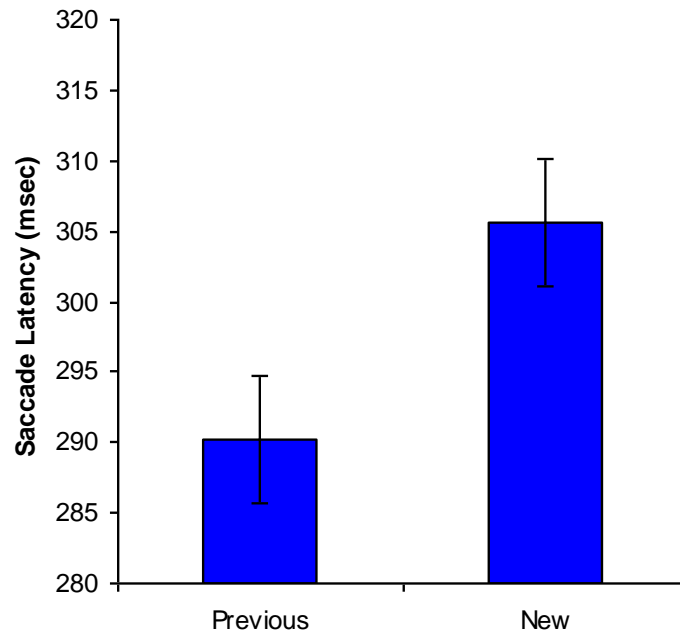


Fig. 7.5. Saccade latencies for the prior presentation of a distractor during the non-active rehearsal VWM condition. Error bars represent ± 1 SE.

A further $2 \times 2 \times 2$ repeated measures ANOVA across the conditions revealed no significant differences for distractor proximity [$F(1, 23) = 0.48, p = .50, \eta p^2 = .02$], or condition [$F(1, 23) = 0.04, p = .85, \eta p^2 = .00$] for the saccade latency measure; however a trend towards significance was found for the prior presentation of a distractor; $F(1, 23) = .2.91, p = .10, \eta p^2 = .11$. Newly presented distractor spatial locations elicited longer saccade latencies ($M = 299.84, SE = 2.97$) in comparison to newly presented distractor spatial locations ($M = 294.11, SE = 3.34$); see *fig 7.6*. Furthermore, a significant interaction was found for the prior presentation of a distractor and condition; $F(1, 23) = 16.05, p < .005, \eta p^2 = .41$. Planned comparisons confirmed that during the non-active rehearsal VWM condition significantly ($p < .005$) shorter saccade

latencies were expressed after previously presented distractors were displayed in comparison to after the display of newly presented distractors; this result was not observed in the NS-VWM condition. In this condition, a non-significant reduction in the latencies of saccades was observed for newly presented distractors ($M = 294.06$, $SE = 3.67$) in comparison to previously presented distractors ($M = 297.99$, $SE = 4.93$); see *fig. 7.7*.

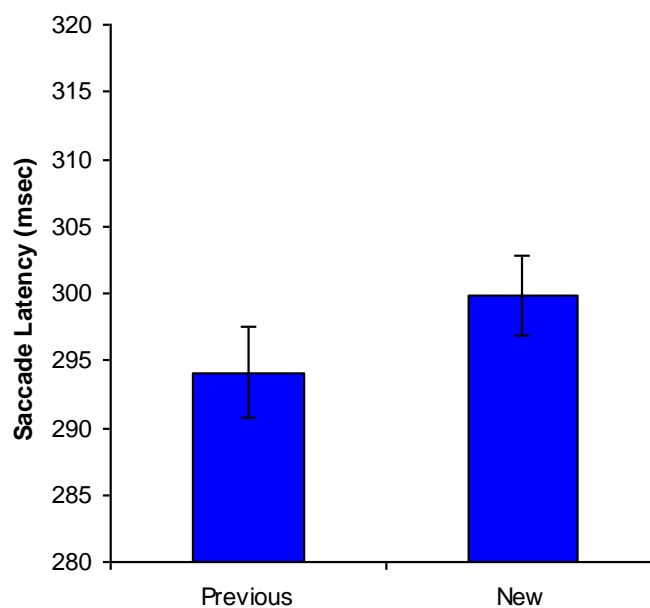


Fig 7.6. Saccade latencies for the prior presentation of a distractor across conditions. Error bars represent ± 1 SE.

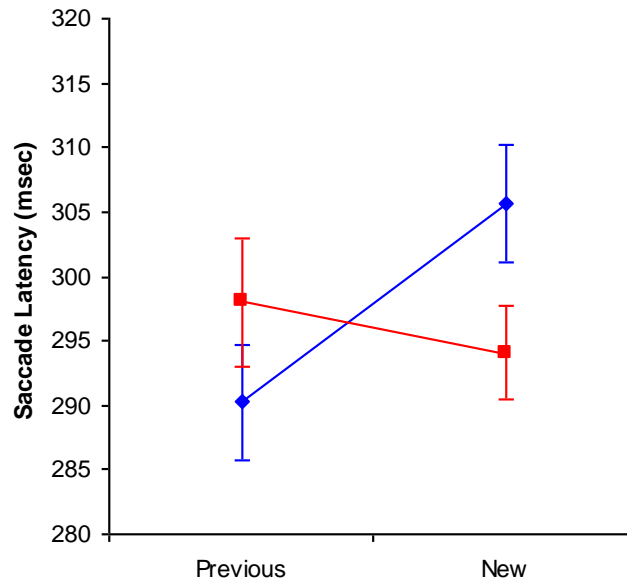


Fig 7.7. Prior presentation of a distractor \times condition interaction for saccade latency. Red line denotes NS-VWM. Blue line denotes non-active rehearsal VWM. Error bars represent ± 1 SE.

Mean Direction

No significant results were found for the mean direction measure during the non-active rehearsal VWM condition (prior presentation of a distractor: $F(1, 23) = 0.70$, $p = .42$, $\eta p^2 = .03$, distractor VF: $F(1, 23) = 0.01$, $p = .93$, $\eta p^2 = .00$), the NS-VWM condition (prior presentation of a distractor: $F(1, 23) = 0.49$, $p = .50$, $\eta p^2 = .02$, distractor VF: $F(1, 23) = 1.49$, $p = .23$, $\eta p^2 = .06$), or across the conditions (prior presentation of a distractor: $F(1, 23) = 0.72$, $p = .40$, $\eta p^2 = .03$, distractor VF: $F(1, 23) = 0.63$, $p = .43$, $\eta p^2 = .03$, condition: $F(1, 23) = 1.49$, $p = .24$, $\eta p^2 = .06$). No significant interactions were found.

Discussion

In this experiment the theoretical implications of VWM-oculomotor interactions were explored. Four main conclusions are drawn from this study: 1. The effects of

attentional IOR can be observed in the deviations of saccades in NS-VWM conditions but not in non-active rehearsal VWM conditions; 2. Reduced oculomotor inhibition due to saccadic IOR facilitates saccade latencies by reducing attentional IOR responses during the non-active rehearsal VWM condition; 3. Attentional IOR during NS-VWM conditions increases saccade accuracy to a target; 4. The mean direction of a saccade is not influenced by distractors presented at previously presented spatial locations. These results are discussed in relation to the integration of VWM on saccade deviation models.

Attentional IOR and saccadic IOR on the characteristics of saccades

This thesis has described attentional IOR as the tendency to prioritise attention towards new information and inhibit attention towards previously attended information. In contrast saccadic IOR has been defined as IOR at the level of the neuronal oculomotor saccade map. Godijn and Theeuwes (2004) have presented evidence distinguishing attentional IOR and saccade trajectory deviations. In this study the trajectories of saccades were minimally influenced by the previous presentation of distractor as no significant results were found (though trends towards significance were indicated). These results suggest a temporal limit to the prolonged nature of VWM facilitated oculomotor inhibition and in turn to the occurrence of saccadic IOR. Though this thesis will not explore the variability of this limit, future research may be able to provide insight on the temporal limitations of VWM facilitated saccades.

A trend towards a significant three-way interaction indicated a tendency during the NS-VWM condition for a reduced degree of initial deviation after far proximity, newly presented distractors were displayed in comparison to after the display of far

proximity, previously presented distractors and close proximity, newly presented distractors. These results can be seen as secondary to attentional IOR of task-relevant stimuli. Far proximity distractors in this study were presented in the opposite hemifield to a saccade target stimulus. Spatial attention for far proximity distractors would be required to be directed across two VFs; divided attention to multiple spatial locations has been found impact the accuracy of saccades (Hoffman and Subramaniam, 1995). The results from this study suggest that the first exposure of a spatial location results in initial saccade deviation as a consequence of divided spatial attention. The second exposure of the same spatial location results in reduced deviation due to attentional IOR suppressing attention at the point of the distractor location. For close proximity, newly presented distractors, the degree of initial deviation is consequent of inhibition in the oculomotor saccade map. This reduced initial deviation after far proximity, newly presented distractors supports previous findings of saccades deviating away from distractor stimuli presented in the same hemifield as target stimuli (e.g. Doyle & Walker, 2001). These results were not replicated in the non-active rehearsal VWM condition suggesting that attentional IOR does not influence saccade trajectories to the same extent after the presentation of task-irrelevant briefly presented distractor stimuli.

Further support for an attentional IOR influence on NS-VWM conditions is garnered by the saccade accuracy results. Saccades were found to be more accurate during the NS-VWM condition after the presentation of previously presented distractors in comparison to after the presentation of newly presented distractors. It has been previously surmised that attentional IOR would reduce the influence of divided spatial attention. Reduced saccade accuracy has been attributed to divided spatial attention

(Hoffman and Subramaniam, 1995). Thus, in conditions triggering attentional IOR, saccades would be more accurate after the presentation of a distractor than saccades made in conditions not triggering attentional IOR.

In contrast, saccade latency results support a saccadic IOR influence on saccade characteristics during the non-active rehearsal VWM condition. During this condition previously presented distractor locations elicited shorter saccade latencies in comparison to newly presented distractor locations; a result not replicated in the NS-VWM condition. Based on the framework presented by Godijn and Theeuwes (2004), this is suggested to illustrate the effect of saccadic IOR. Reduced oculomotor inhibition due to saccadic IOR results in reduced ‘tag for inhibition’ to the PFC; this in turn sends a reduced level of input to the pre-oculomotor attentional map in the LIP. Reduced input to the LIP would result in reduced LIP input to the saccade map and a reduced degree of attentional IOR. Thus, saccadic IOR would result in shorter saccade latencies for previously presented distractors.

Mean Saccade Direction

The mean direction of a saccade was not found to be influenced by the prior presentation of distractors at previously presented or newly presented spatial locations. These results suggest that the direction of a saccade is not largely influenced by attentional or saccadic IOR. Saccade deviation away from distractor locations has been related to top-down processing. It has been suggested that top-down inhibition of neurons at the site in the SC coding for the distractor (McSorley, Haggard, & Walker, 2006), or the top-down excitation of neurons in the contralateral site of the SC coding for the distractor (White, Theeuwes, & Munoz, 2012) results in saccade deviation away

from presented distractors. It may be that attentional IOR after previously presented distractor does result in reduced deviation away. However, comparatively, reduced oculomotor inhibition due to saccadic IOR, after previously presented distractors, does not result in deviation towards a distractor. The behavioural consequences of this IOR stalemate can be seen in the non-significant mean direction results.

EXPERIMENT 5 – SUMMARY

This study has demonstrated the separable influence of top-down and bottom-up interaction with the oculomotor system. It also supports previous assertions of distinguishable dorsal pathway parallel processing and ventral pathway top-down mediation of VWM-oculomotor interaction.

Godijn and Theeuwes (2004) presented a framework of saccade deviation (previously presented in chapter 2 and seen in *fig. 7.8.*). In this framework oculomotor inhibition is facilitated by an inhibitory control system located in the PFC. Attentional inhibition is facilitated by input from the LIP to the SC. The results of this study suggest that ventral pathway processing may interact in this framework at the point of the LIP. This conclusion is based on previous assertions of ventral pathway interaction with frontoparietal cortices in order to promote efficient visual processing (Corbetta et al., 1998). In contrast, dorsal pathway processing could occur at various regions along this framework but can be seen particularly during non-active rehearsal VWM conditions to occur in the initial SC saccade map resulting in bottom-up prolonged neuronal inhibition (as inferred from findings in chapter 4, 5, and 6 of spatially driven distractor proximity to a target vs. target VF interactions). For the top-down dorsal pathway,

VWM interactions, the DLPFC has been implicated in the suppression of task-irrelevant information, and has been found to be preferentially active during VSWM tasks. This site could be a possible source of VSWM interaction with the oculomotor system. Chapter 8 will explore whether VWM could, and should, be integrated into saccade deviation models.

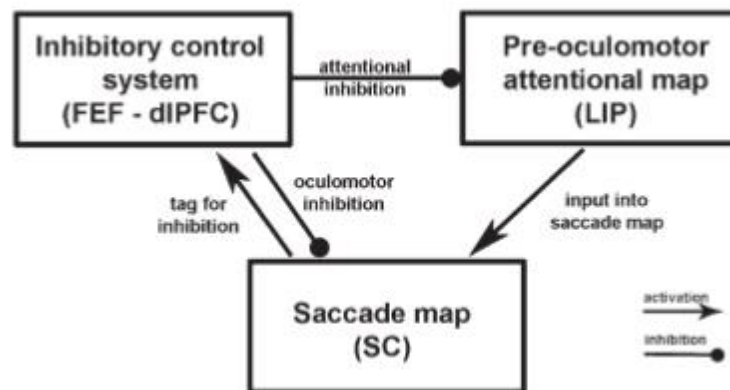


Fig 7.8. Saccade deviation framework. Image from Godijn and Theeuwes (2004).

Experiment 5 has been concerned with the theoretical implications of VWM-oculomotor inhibition; experiment 6 explores the clinical implications.

Experiment 6

Method

The database used in experiment 5 was also utilised in this experiment. Both non-active rehearsal VWM and NS-VWM conditions were used.

Design

Data was filtered in the same way as previous chapters using MATLAB (R2010a, Mathworks, Natick, MA) and previously defined exclusion criteria. Saccade measures

used were: mean saccade deviation, initial deviation, saccade accuracy, saccade latency, and mean direction of a saccade.

Participant percentage number of correct memory trials was calculated for the NS-VWM condition. Participants were then ranked on their percentage score. Top scoring participants formed the 'high' performance VWM group; other participants formed the 'low' performance VWM group. Twelve participants were placed in each group. An independent samples t-test analysed memory performance between groups.

A $2 \times 2 \times 2$ mixed measures design was implemented on saccade data from the conditions. The independent within-subjects variables were distractor proximity to a target (close proximity vs. far proximity), and target VF (upper VF vs. lower VF). The between subjects variable was VWM performance group (high vs. low). A further $2 \times 2 \times 2 \times 2$ mixed measures design was used to ascertain whether there was a difference between conditions with distractor proximity to a target, target VF and condition being the within-subjects independent variable. The between subjects variable was VWM performance group.

For the mean direction of a saccade, target VF was replaced by distractor VF (left vs. right VF). $2 \times 2 \times 2$ mixed measures ANOVA's were run across the three previously stated conditions. A $2 \times 2 \times 2 \times 2$ mixed measures ANOVA explored differences within these conditions.

Planned comparisons will examine any significant interactions found across the independent variables.

Results

Memory Data

An independent samples t-test found a significant difference in VWM performance for the high and low VWM performance groups; $t(14.64) = 5.22, p < .001$. Degrees of freedom were corrected for unequal variances across the groups. The high performance group performed significantly better ($M = 90.76, SE = 1.54$) than participants in the low performance group ($M = 69.73, SE = 3.72$); see *fig. 7.9*.

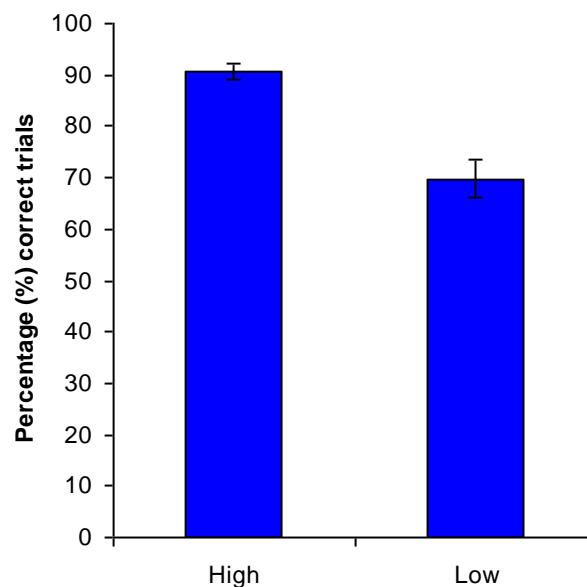


Fig. 7.9. Mean percentage memory across VWM performance groups. Error bars represent ± 1 SE.

Initial Deviation

$2 \times 2 \times 2$ mixed measures ANOVA's found no significant between-subjects main effects for VWM performance group in the non-active rehearsal VWM condition [$F(1, 22) = 0.51, p = .48, \eta p^2 = .02$] or the NS-VWM condition [$F(1, 22) = 0.64, p = .43, \eta p^2 = .03$]

on the initial deviation of a saccade. Furthermore, no significant within-subjects effects were found for the non-active rehearsal VWM condition (distractor proximity to a target: $F(1, 22) = 0.86, p = .36, \eta p^2 = .04$, target VF: $F(1, 22) = 0.80, p = .38, \eta p^2 = .04$) or the NS-VWM condition (distractor proximity to a target: $F(1, 22) = 0.35, p = .56, \eta p^2 = .02$, target VF: $F(1, 22) = 0.05, p = .83, \eta p^2 = .00$). A trend towards significance was found for the interaction between the two variables during the non-active rehearsal VWM condition; $F(1, 22) = 3.36, p = .08, \eta p^2 = .13$. Planned comparisons revealed a trend towards significance ($p = .06$) suggesting that saccades made to the upper VF after the presentation of close proximity distractors expressed a reduced degree of initial deviation ($M = -10.90, SE = 3.00$) in comparison to saccades made after the presentation of far proximity distractors ($M = -13.71, SE = 2.90$). This result was not replicated in the lower VF. In this VF a non-significant reduction in initial deviation was found after the presentation of far proximity distractors ($M = -7.71, SE = 3.20$) in comparison to after the presentation of close proximity distractors ($M = -8.49, SE = 2.77$); see *fig. 7.10*.

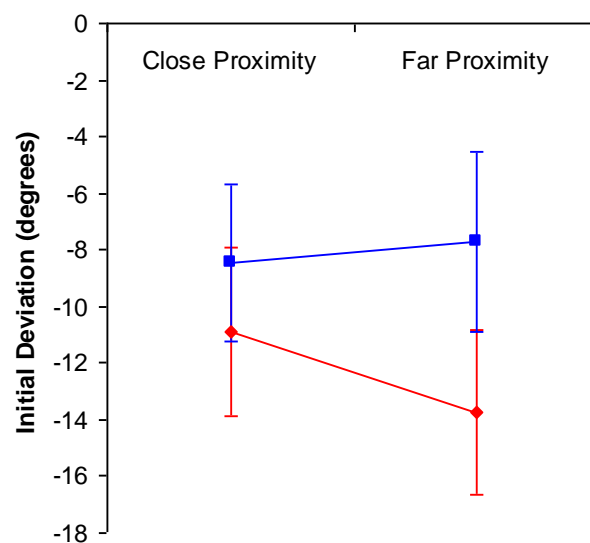


Fig. 7.10. Distractor proximity to a target \times target VF interaction for the non-active rehearsal VWM condition. Blue line shows lower VF. Red line shows upper VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 2 \times 2$ mixed measures ANOVA found no significant within-subjects main effects for distractor proximity [$F(1, 22) = 0.77, p = .39, \eta p^2 = .03$], target VF [$F(1, 22) = 0.01, p = .92, \eta p^2 = .00$], or condition [$F(1, 22) = 0.75, p = .40, \eta p^2 = .03$] across conditions. No between-subjects main effects were found for VWM performance group; $F(1, 22) = 0.01, p = .95, \eta p^2 = .00$ and no significant interactions were revealed.

Saccade Deviation

No significant between-subjects main effect was found for VWM performance group during the non-active rehearsal VWM [$F(1, 22) = 0.66, p = .42, \eta p^2 = .03$] or the NS-VWM [$F(1, 22) = 0.05, p = .83, \eta p^2 = .00$] conditions; nor were any significant within-subjects main effects found for the non-active rehearsal VWM (distractor proximity: to a target $F(1, 22) = 0.77, p = .39, \eta p^2 = .03$, target VF: $F(1, 22) = 0.00, p = .95, \eta p^2 = .00$] or NS-VWM conditions (distractor proximity to a target: $F(1, 22) = 0.17, p = .68, \eta p^2 = .01$, target VF: $F(1, 22) = 0.66, p = .43, \eta p^2 = .03$). A trend towards significance was revealed for a 3-way interaction between distractor proximity to a target, target VF and VWM performance group in the non-active rehearsal VWM condition [$F(1, 22) = 3.64, p = .07, \eta p^2 = .14$]. Saccade directional differences seem apparent for high and low VWM performers in relation to target VF as shown by opposing positive and negative values. Low VWM performers expressed upper and lower VF saccades which deviated rightward whilst high VWM performers expressed saccades which deviated leftward for upper and lower VF targets. A reduced degree of saccade deviation was expressed

after the presentation of close proximity distractors in both altitudinal VF's, for both the low (lower VF: $M = -2.44$, $SE = 1.91$, upper VF: $M = 0.76$, $SE = 2.44$) and the high (lower VF: $M = 1.39$, $SE = 1.65$, upper VF: $M = -1.70$, $SE = 1.43$) VWM performance groups, in comparison to far proximity distractors (low VWM performance group, lower VF: $M = -2.79$, $SE = 2.04$, low VWM performance group, upper VF: $M = 1.33$, $SE = 2.31$, high VWM performance group, lower VF: $M = 2.80$, $SE = 1.89$, high VWM performance group, upper VF: $M = -2.15$, $SE = 1.55$); see *fig 7.11*. However, planned comparisons did not reveal any significant differences between the variables.

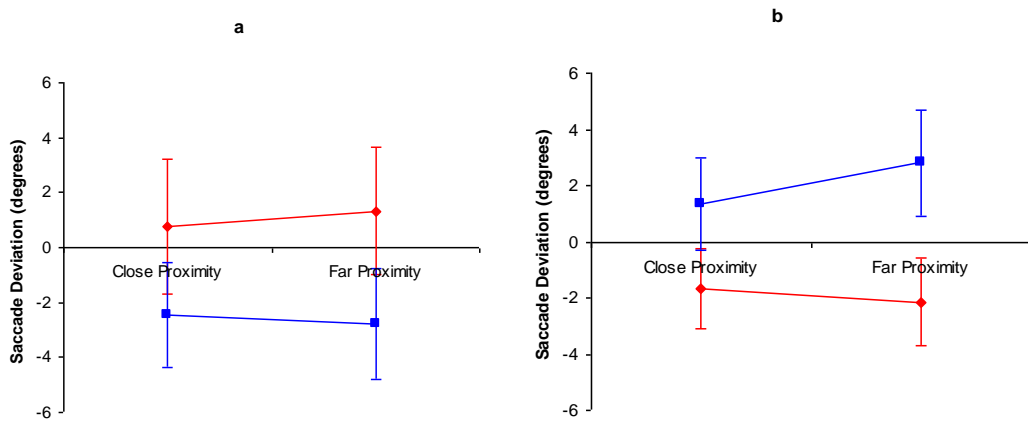


Fig. 7.11. Three-way interaction during the non-active VWM condition for saccade deviation. a. shows low VWM performers. b shows high VWM performers. Blue line shows lower VF. Red line shows upper VF. Error bars represent ± 1 SE.

During the NS-VWM condition, a trend towards significance was found for the interaction between distractor proximity and target VF; $F(1, 22) = 4.32$, $p = .05$, $\eta p^2 = .16$. Planned comparisons indicated a trend towards significance ($p = .07$) suggesting that saccades made to the upper VF expressed a reduced degree of saccade deviation after the presentation of close proximity distractors ($M = 0.77$, $SE = 1.41$) in comparison to after the presentation of far proximity distractors ($M = 1.62$, $SE = 1.34$);

a result not replicated in the lower VF. In this VF a non-significant reduction in saccade deviation was observed after the presentation of close proximity distractors ($M = -0.68$, $SE = 1.40$) in comparison to far proximity distractors ($M = -1.27$, $SE = 1.44$); see *fig. 7.12*.

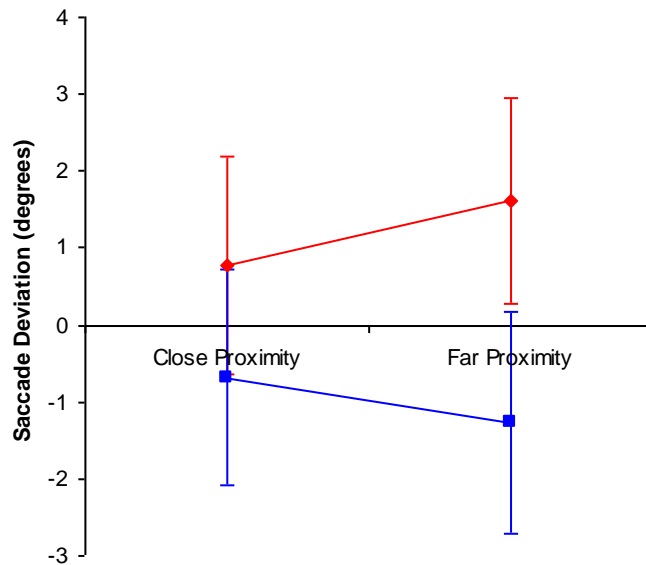


Fig. 7.12. Distractor proximity \times target VF interaction during the NS-VWM condition for saccade deviation. Error bars represent ± 1 SE.

A $2 \times 2 \times 2 \times 2$ mixed measures ANOVA analysis across the non-active rehearsal VWM and NS-VWM conditions found no significant between-subjects main effect for VWM performance group [$F(1, 22) = 0.05$, $p = .83$, $\eta p^2 = .00$], or within-subjects main effect for distractor proximity to a target [$F(1, 22) = 0.58$, $p = .46$, $\eta p^2 = .03$], target VF [$F(1, 22) = 0.18$, $p = .68$, $\eta p^2 = .01$], or condition [$F(1, 22) = 0.65$, $p = .43$, $\eta p^2 = .03$]. However, a significant interaction was found for the interaction between distractor proximity to a target, target VF, and condition; $F(1, 22) = 10.07$, $p < .005$, $\eta p^2 = .31$. The aforementioned distractor proximity to a target and target VF interaction was observed during the NS-VWM condition. In the non-active rehearsal VWM condition,

saccades made to the upper VF expressed comparable deviations were observed after the presentation of close ($M = -0.46$, $SE = 1.40$) and far proximity distractors ($M = -0.40$, $SE = 1.41$). In the lower VF reduced deviation was apparent after the presentation of far proximity distractors ($M = 0.01$, $SE = 1.47$) in comparison to close proximity distractors ($M = -0.55$, $SE = 1.11$). Planned comparisons, however, did not reveal any significant difference across these variables.

A four-way significant interaction was also found; $F(1, 22) = 7.39$, $p < .05$, $\eta p^2 = .25$. Low VWM performance participants, during the non-active VWM condition were found to exhibit reduced saccade deviations for close proximity distractors (upper VF: $M = 0.76$, $SE = 2.44$, lower VF: $M = -2.44$, $SE = 1.92$) in comparison to far proximity distractors (upper VF: $M = 1.33$, $SE = 2.31$, lower VF: $M = -2.78$, $SE = 2.04$) across both altitudinal VF's; see *fig. 7.13a*. During the NS-VWM condition, for saccades directed to the lower VF, low VWM performance participants expressed a reduced degree of saccade deviation after close proximity distractors ($M = -1.83$, $SE = 2.15$) in comparison to after far proximity distractors ($M = -2.51$, $SE = 2.02$). In contrast, a reduced degree of saccade deviation for far proximity distractors ($M = 1.33$, $SE = 1.82$) was observed in comparison to far proximity distractors ($M = 2.67$, $SE = 1.74$) for saccades directed to the upper VF; see *fig 7.13b*. High VMM performance participants expressed a reduced degree of saccade deviation for close proximity distractors (upper VF: $M = -1.68$, $SE = 1.43$, lower VF: $M = 1.35$, $SE = 1.65$) in the non-active rehearsal VWM condition across both altitudinal VF's in comparison to deviation expressed after far proximity distractors (upper VF: $M = -2.15$, $SE = 1.55$, lower VF: $M = -2.81$, $SE = 1.89$); see *fig 7.13c*. During the NS-VWM condition, the opposite pattern was observed for high VWM performance participants; a reduced degree of deviation for far proximity

distractors (upper VF: $M = 0.05$, $SE = 1.91$, lower VF: $M = -0.03$, $SE = 2.08$) across both altitudinal VF's in comparison to close proximity distractor deviation (upper VF: $M = -1.12$, $SE = 2.12$, lower VF: $M = 0.47$, $SE = 1.86$); see *fig 7.13d*. However, planned comparisons again did not find any significant differences across any of the variables.

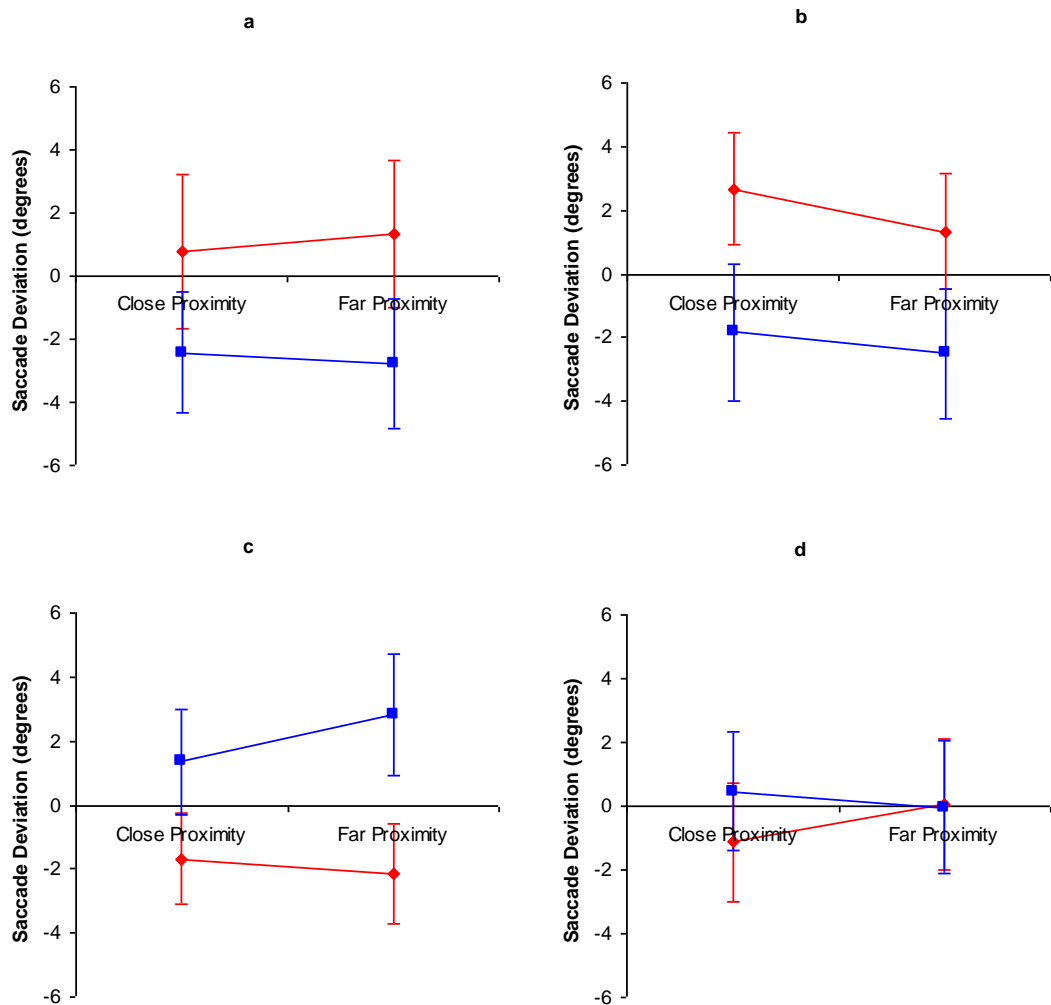


Fig. 7.13. Four-way interaction for saccade deviation. a. shows non-active VWM for low VWM performers. b. shows NS-VWM for low VWM performers. Blue lines show lower VF. Red lines show upper VF. Error bars represent ± 1 SE.

Saccade Accuracy

No significant results were found for saccade accuracy during either the non-active rehearsal VWM condition (VWM performance group: $F(1, 22) = 0.12, p = .73, \eta p^2 = .01$, distractor proximity to a target: $F(1, 22) = 2.73, p = .11, \eta p^2 = .11$, target VF: $F(1, 22) = 1.45, p = .24, \eta p^2 = .06$), or the NS-VWM condition (VWM performance group: $F(1, 22) = 1.03, p = .32, \eta p^2 = .05$, distractor proximity to a target $F(1, 22) = 0.48, p = .50, \eta p^2 = .02$, target VF: $F(1, 22) = 2.16, p = .16, \eta p^2 = .09$). Furthermore no significant results were found across the two conditions (condition: $F(1, 22) = 0.35, p = .56, \eta p^2 = .02$, distractor proximity to a target: $F(1, 22) = 2.19, p = .15, \eta p^2 = .09$, target VF: $F(1, 22) = 2.27, p = .15, \eta p^2 = .09$). No significant interactions were indicated.

Saccade Latency

Neither condition found a significant between-subjects main effect for VWM performance group (non-active rehearsal VWM: $F(1, 22) = 1.74, p = .20, \eta p^2 = .07$, NS-VWM: $F(1, 22) = 2.41, p = .14, \eta p^2 = .10$), or a significant within-subjects main effect for distractor proximity to a target (non-active rehearsal VWM: $F(1, 22) = 0.36, p = .56, \eta p^2 = .02$, NS-VWM: $F(1, 22) = 0.00, p = .96, \eta p^2 = .00$). A significant within-subjects main effect was found for target VF in both the non-active rehearsal VWM [$F(1, 22) = 9.14, p < .01, \eta p^2 = .29$], and the NS-VWM [$F(1, 22) = 17.64, p < .001, \eta p^2 = .46$] conditions. Both conditions found that the latencies of saccades to upper VF targets (non-active rehearsal VWM: $M = 289.94, SE = 5.43$, NS-VWM: $M = 280.55, SE = 4.60$) were shorter than saccade latencies to lower VF targets (non-active rehearsal VWM: $M = 313.33, SE = 4.63$, NS-VWM: $M = 310.11, SE = 5.59$); see *fig. 7.14.* for non-active rehearsal VWM condition and *fig. 7.15.* for NS-VWM condition.

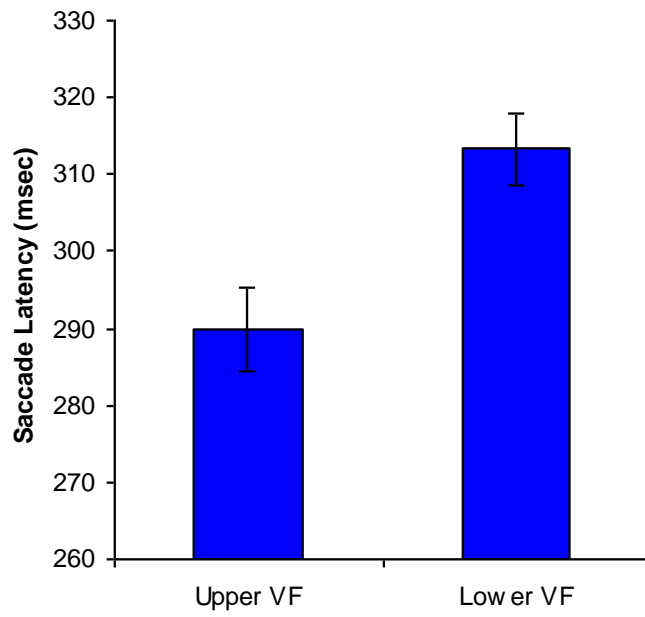


Fig. 7.14. Saccade latencies during the non-active rehearsal VWM condition for target VF. Error bars represent ± 1 SE.

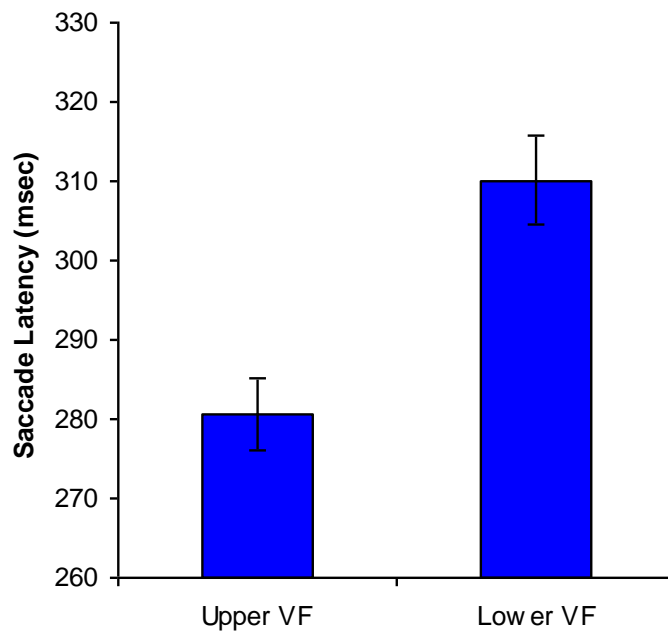


Fig. 7.15. Saccade latencies during the NS-VWM condition for target VF. Error bars represent ± 1 SE.

In a $2 \times 2 \times 2$ mixed measures ANOVA across the conditions this pattern was repeated. No significant main effects were found for VWM performance group [$F(1, 22) = 2.45, p = .14, \eta p^2 = .10$] or distractor proximity to a target [$F(1, 22) = 0.10, p = .76, \eta p^2 = .00$], and a significant main effect was found for target VF [$F(1, 22) = 16.03, p < .005, \eta p^2 = .42$]. Saccade latencies to upper VF targets ($M = 285.24, SE = 3.57$) were shorter than saccade latencies to lower VF targets ($M = 311.72, SE = 311.72$). Furthermore, no significant main effect was found for condition; $F(1, 22) = 0.37, p = .55, \eta p^2 = .02$.

A trend towards significance was revealed for the interaction between target VF, condition, and VWM performance group [$F(1, 22) = 3.15, p = .08, \eta p^2 = .13$]. Planned comparisons revealed shorter saccade latencies to upper VF targets (non-active rehearsal VWM: $M = 301.21, SE = 9.12$, NS-VWM: $M = 303.17, SE = 7.25$) in comparison to lower VF targets (non-active rehearsal VWM: $M = 336.91, SE = 7.29$; NS-VWM: $M = 335.70, SE = 9.64$) in the low VWM performance group across both conditions (non-active rehearsal VWM: $p < .005$, NS-VWM: $p < .05$); see *fig. 7.16a*. For the high VWM performance group, planned comparisons revealed significantly shorter saccade latencies to upper VF targets ($M = 257.92, SE = 5.73$) in comparison to lower VF targets ($M = 288.39, SE = 6.05$) in the NS-VWM ($p < .01$) condition but not in the non-active rehearsal VWM condition (upper VF: $M = 278.66, SE = 5.67$, lower VF: $M = 291.04, SE = 5.83$) where more consistent saccade latencies were observed; see *fig. 7.16b*.

Planned comparisons also revealed that saccades made, by the high VWM performance group, to the upper VF during the NS-VWM condition were significantly shorter ($p < .05$) than saccades made to the upper VF during the non-active rehearsal

VWM condition; this result was not replicated in the low VWM performance group. It was also found that saccades made by the high VWM performance group, during the NS-VWM condition, to the upper VF had shorter latencies than saccades made to the upper VF by the low VWM performance group ($p < .05$). This pattern of results was replicated for saccades made to the lower VF during the NS-VWM condition ($p < .05$). In the non-active rehearsal VWM condition, planned comparisons revealed a trend towards significance indicating that saccades made to the lower VF by the high VWM performance group were shorter than saccades made to the lower VF by the low VWM performance group ($p = .08$); no significant difference was found for saccades directed to the upper VF.

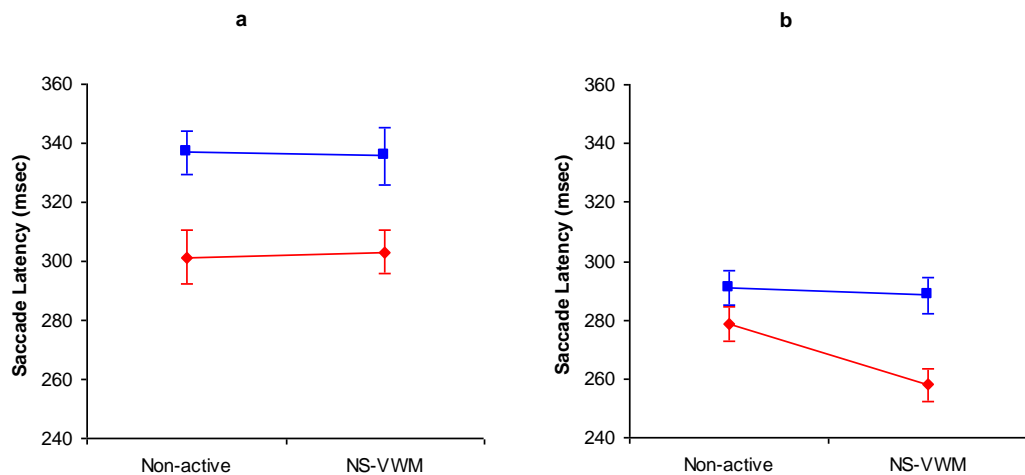


Fig.7.16. Target VF \times condition \times VWM performance group for saccade latency. a. shows the low VWM performance group. b. shows the high VWM performance group. Blue lines show lower VF. Red lines show upper VF. Error bars represent ± 1 SE.

Mean Direction

No significant between-subjects main effects were found for VWM performance group in either the non-active rehearsal VWM condition [$F(1, 22) = 1.74, p = .20, \eta p^2 = .07$],

or the NS-VWM condition [$F(1, 22) = 1.79, p = .20, \eta p^2 = .08$]. Furthermore, no significant within-subjects main effect for distractor proximity to a target was found during the non-active rehearsal VWM [$F(1, 22) = 0.05, p = .83, \eta p^2 = .00$], though a significant main effect was found for this variable during the NS-VWM condition [$F(1, 22) = 6.82, p < .05, \eta p^2 = .24$]. Saccades made after the presentation of close proximity distractors expressed a reduced degree of rightwards direction ($M = 0.07, SE = 0.02$) in comparison to saccades made after the presentation of far proximity distractors ($M = 0.10, SE = 0.02$); see *fig. 7.17*.

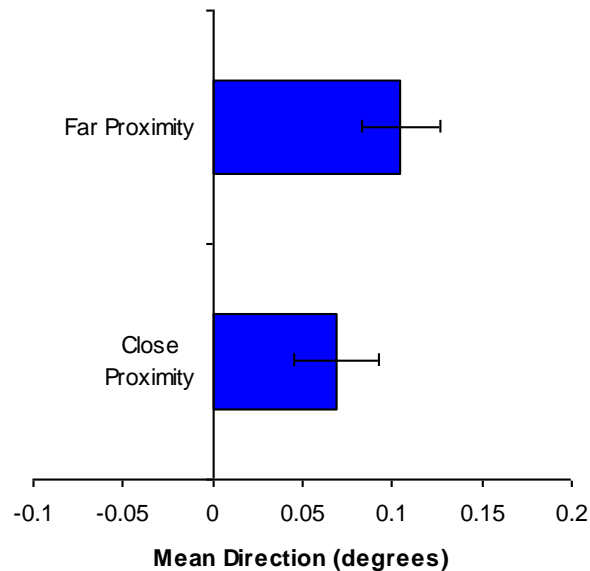


Fig. 7.17. Mean direction of saccades during the NS-VWM condition for distractor proximity to a target. Error bars represent ± 1 SE.

In both the non-active rehearsal VWM condition and the NS-VWM condition a significant main effect was found for distractor VF (non-active rehearsal VWM: $F(1, 22) = 15.56, p < .005, \eta p^2 = .41$, NS-VWM: $F(1, 22) = 6.85, p < .05, \eta p^2 = .24$). These conditions found that saccades made after the presentation of a left VF distractor (non-active rehearsal VWM: $M = 0.06, SE = 0.02$, NS-VWM: $M = 0.11, SE = 0.02$) were

directed rightwards to a greater extent than saccades made after a right VF distractor (non-active rehearsal VWM: $M = 0.00$, $SE = 0.02$, NS-VWM: $M = 0.07$, $SE = 0.02$); see *fig. 7.18.* for non-active rehearsal VWM condition, and *fig. 7.19.* for NS-VWM condition. No significant interactions were found in either condition.

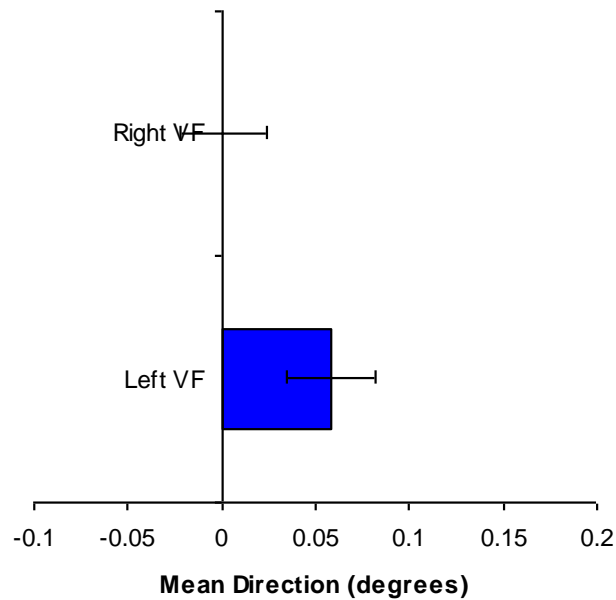


Fig. 7.18. Mean direction during the non-active VWM condition for distractor VF. Error bars represent ± 1 SE.

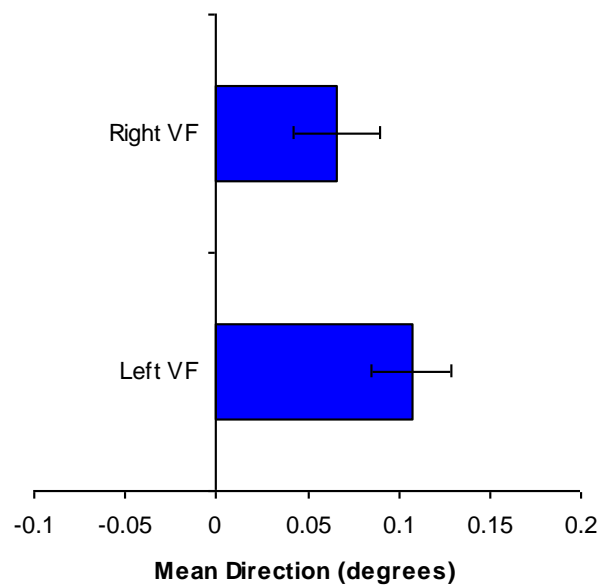


Fig 7.19. Mean direction of saccades during the NS-VWM condition for distractor VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 2 \times 2$ mixed measures ANOVA found no significant between-subjects main effects for VWM performance group; $F(1, 22) = 0.96, p = .34, \eta p^2 = .04$. Moreover, no significant within-subjects main effects for distractor proximity [$F(1, 22) = 1.86, p = .19, \eta p^2 = .08$], or condition [$F(1, 22) = 0.89, p = .36, \eta p^2 = .04$] were found across the conditions. A significant within-subjects main effect for distractor VF was found; $F(1, 22) = 15.11, p < .005, \eta p^2 = .40$. Saccades made after the presentation of left VF distractors ($M = 0.08, SE = 0.02$) were directed rightwards more so than saccades made after the presentation of right VF distractors ($M = 0.03, SE = 0.02$). A trend towards significance was revealed for the interaction between distractor proximity to a target, condition and VWM performance group [$F(1, 22) = 3.41, p = .08, \eta p^2 = .13$]; see *fig. 7.20*. Planned comparisons found a trend towards significance ($p = .08$) suggesting that high VWM performance participants, after the presentation of far proximity distractors, expressed leftwards directed saccades during the non-active rehearsal VWM condition ($M = -0.06, SE = 0.04$) in comparison to rightwards directed saccades during the NS-VWM condition ($M = 0.06, SE = 0.03$). The same pattern was found for high VWM performance participants after the presentation of close proximity distractors (non-active rehearsal VWM: $M = -0.03, SE = 0.04$, NS-VWM: $M = -0.06, SE = 0.04$); however planned comparisons did not find that this was significant. For the low VWM performance group, the mean direction of saccade was directed to the right VF. A reduced degree of rightwards deviation was indicated during the non-active rehearsal VWM condition in comparison to the NS-VWM after the presentation of both close proximity (non-active rehearsal VWM: $M = 0.08, SE = 0.03$; NS-VWM: $M = 0.11, SE = 0.03$) and far proximity distractors (non-active rehearsal VWM: $M = 0.12, SE$

= 0.03; NS-VWM: $M = 0.14$, $SE = 0.03$); though no significant planned comparisons were found in these variables.

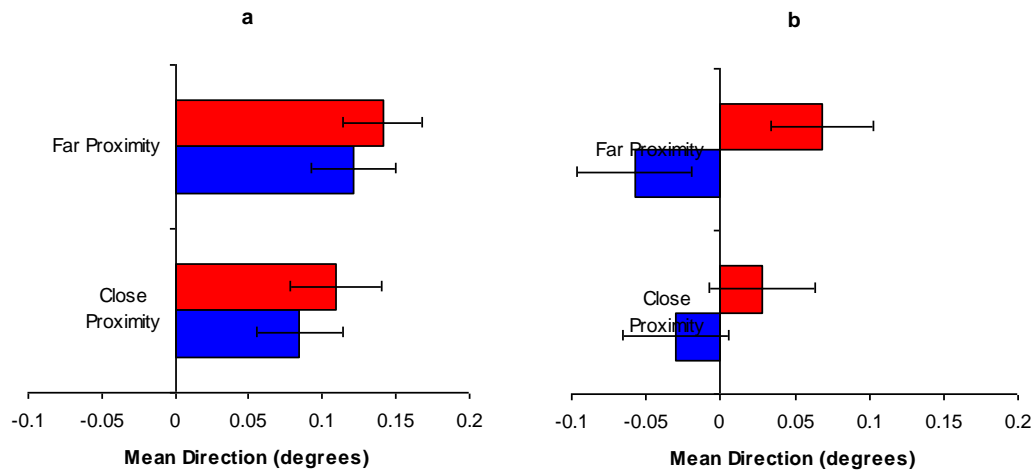


Fig. 7.20. Distractor proximity \times condition \times VWM performance group interaction for mean direction of a saccade. a. shows low VWM performance group. b. shows high VWM performance group. Blue bars show non-active VWM condition. Red bars show NS-VWM condition. Error bars represent ± 1 SE.

Discussion

This experiment was concerned with the clinical implications of VWM-oculomotor interaction. It was hypothesised that differential saccade characteristics may be discerned across participants due to VWM performance abilities. Two main findings were found in this experiment: 1. saccade trajectories appeared to differ directionally across VWM performance groups, and 2. saccade latency VF specialism differed across VWM performance groups and condition.

VWM performance level on saccade characteristics

Participants in this experiment were ranked and placed into a high VWM performance group and a low VWM performance group in order to assess at a basic level whether

VWM ability influences saccade characteristics. As participants were placed in VWM performance groups based on performance in the NS-VWM task also presented in this experiment, it should be noted that this experiment does not in itself examine VWM ability or capacity. This experiment does highlight the possibility of general association between how a person performs on a VWM task and the generation of saccades. Future experiments should explore more specifically how VWM capacity influences the characteristics of saccades.

No significant main effects were found throughout this experiment for VWM performance group. It can therefore be concluded that saccade characteristics did not significantly differ in individuals who performed at different levels in the NS-VWM task. If any significant difference was found across these groups then this would have highlighted the possibility that visual perception in individuals less able to utilise VWM could differ in comparison to individuals more able to utilise VWM. The VWM performance group variable was found to interact with other variables in this study; these interactions will now be discussed.

Saccade deviation results highlight the possibility of directional differences across VWM performance groups during the non-active VWM condition. Participants in the low VWM group expressed rightward deviation whilst the high VWM performance group expressed leftward deviation. The right VF (left hemisphere) has been associated with non-spatial visual processing whilst the left VF (right hemisphere) has been associated with visuo-spatial processing (D'Esposito et al., 1998; Köhler et al. 1995). Furthermore, this thesis has provided some evidence suggesting that non-active VWM conditions are associated with the dorsal processing stream (chapter 6). Saccade

deviation results indicate the possibility that, during the non-active VWM condition, the high VWM performance group produce saccades which are directed to the VF theorised to be specialised for the to-be-completed visual processing task. It should be noted that planned comparisons however, did not find evidence of differences between these variables. Furthermore, this result was not replicated in the NS-VWM condition.

Support for a theory suggesting that the high VWM performance group may preferentially utilise specialised visual processing streams to interact with the oculomotor system can be seen in the mean direction results. It was found that the low VWM performance group consistently produced saccades directed rightwards. In contrast, the high VWM performance group produced saccades which differed directionally dependent on condition. During non-active VWM conditions, the high VWM performance group produced leftward directed saccades; rightwards saccades were expressed during the NS-VWM condition. These results continue to suggest that high VWM performance participants may preferentially utilise specialised visual pathways during the generation of saccades in a way not seen in low VWM participants.

A trend towards significance also found that VWM performance group interacted with condition and target VF for the saccade latency measure. Low VWM performance participants showed a consistent upper VF advantage for shorter saccade latencies, in comparison to the lower VF, across both conditions. In contrast, the high VWM performance participants expressed shorter latency saccades to the upper VF saccades during the NS-VWM conditions but not in the non-active VWM condition. The high

VWM performance group also showed consistently shorter latencies, in comparison to the low VWM performance group, during the NS-VWM condition across the altitudinal VF's. In the non-active rehearsal VWM condition, a trend towards significance demonstrated a tendency towards shorter saccade latencies, for the high VWM performance group, to the lower VF, in comparison to the low VWM performance group. No such difference was found for saccades directed to the upper VF. These results suggest that, for the high VWM performance group, NS-VWM conditions facilitate rapid saccades in specialised visual pathways; the upper VF being specialised for ventral pathway processing facilitating these rapid saccades. In contrast no such facilitation can be seen for low performance VWM participants, or for saccades directed to the lower VF by the high VWM performance group.

It has been suggested that top-down, ventral pathway communication with frontoparietal areas facilitate rapid saccades to enhance visual processing (Corbetta et al., 1998) and that evidence of this can be observed in shorter saccade latencies to upper VF targets (Zhou & King, 2002). Results suggesting shorter saccade latencies in the high VWM performance group, in comparison to the low VWM performance group, and results of consistent saccade latencies across altitudinal VF's during the non-active rehearsal VWM condition, highlights the possibility that this top-down, ventral pathway communication is prevalent in high VWM performance individuals.

EXPERIMENT 6 – SUMMARY

This experiment explored how high performing, and low performing, VWM participants were influenced by VWM facilitated saccades during two conditions: a

non-active rehearsal VWM, and a NS-VWM condition. Differential saccade deviations and latencies were found for participants who were in the high VWM performance group in comparison to their low VWM performance group counterparts. Results indicated the possibility that the high VWM performance group preferentially utilised specialised visual pathways. Top-down communication in these performers is theorised to result in reduced saccade deviations and shorter saccade latencies. Future research should endeavour to qualify the appropriateness of this conclusion. VWM capacity has been associated with neuronal activation (Vogel & Machizawa, 2004). It is therefore possible that increased neuronal activation along the ventral pathway is causally related to VWM-oculomotor interactions and consequent behavioural consequences. This experiment, however, did not measure neuronal activation along the ventral pathway and conclusions are based on behavioural observations (saccade trajectories) and theoretical inferences.

It has been stated that this experiment did not measure VWM capacity or total ability, instead noting performance levels across participants. VWM performance may fluctuate across participants due to other factors apart from VWM capacity and ability. For instance, participant motivation could influence VWM performance levels. Thus, these findings cannot be immediately generalised across all clinical populations with noted VWM deficits. However, there is evidence presented in this experiment suggesting that groups of participants who perform poorly across VWM tasks may process their visual environment differently, being less able to utilise appropriate visual pathways for efficient processing and top-down suppression of visual distracting stimuli. Future experiments should clarify how VWM capacity and ability influence

saccade trajectories. Brain imaging studies could provide evidence of preferential visual stream processing across VWM performance groups.

GENERAL DISCUSSION

This chapter has been concerned with the theoretical and clinical implications of VWM facilitated oculomotor inhibition. It has been concluded that VWM interacts with the oculomotor system in both bottom-up and top-down manner. Belopolsky and Theeuwes (2011) have suggested that any saccade deviation frameworks incorporating VWM must account the parallel aspect of VWM-oculomotor interactions. The final experimental chapter of this thesis is concerned with whether VWM could, and should, be incorporated into models of saccade deviation. If VWM solely aids oculomotor action in this way, it is argued that research would be benefitted by VWM incorporation into saccade deviation models. However, this benefit is arguably questionable if other cognitive systems can be utilised to aid oculomotor action. This chapter has also been concerned with how VWM performance may influence oculomotor action. Though the clinical implications of VWM-oculomotor interaction need to be further assessed, this chapter has provided evidence of differential saccade characteristics across two groups of VWM performers. This suggests that clinical groups with VWM deficits may be less able to suppress task-relevant behaviour appropriately.

Chapter 8

Manual responses influence saccade
trajectories

The current thesis has been concerned with how the VWM system influences the trajectories of saccades and interacts with the oculomotor system. It has been argued that VWM-oculomotor interaction should be considered in models of saccade trajectory deviation (Belopolsky & Theeuwes, 2011). However, if VWM does not uniquely interact with the oculomotor system to facilitate saccade deviation after the brief presentation of distractor stimuli, the usefulness of adding a VWM cognitive component to saccade models is questionable. Previous research has related reaching trajectories and saccade trajectories (Tipper, Howard, & Paul, 2001). Common neural mechanisms underpin saccade and motor inhibition (Leung & Cai, 2007) and motor-facilitated oculomotor inhibition may be apparent after the brief presentation of visual stimuli. In this chapter three conditions were presented to participants: 1. a non-active rehearsal VWM condition, 2. a saccade task and manual 'tapping' response condition, and 3. a saccade task and manual spatial 'tapping' response conditions. In this way, motor mechanism interaction with the oculomotor system can be explored. Results found differential saccade characteristics across conditions. Findings are discussed in relation to how the oculomotor system is able to draw on a network of cognitive systems to facilitate vision processing.

MANUAL MECHANISMS AND OCULOMOTOR INHIBITION

Evidence of VWM facilitation of oculomotor inhibition has been presented throughout this thesis. Moreover, the possibility of VWM performance influencing oculomotor action has been highlighted (chapter 7). It has been proposed that VWM facilitates the oculomotor system by maintaining visual representations for the enhancement of visual processing (Belopolsky & Theeuwes, 2011) and that the addition of VWM in

models of saccade trajectory deviation may assist research. Though it is not disputed that VWM facilitates oculomotor inhibition, this chapter explores the usefulness of adding specific cognitive components to models of oculomotor inhibition.

The premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994), and the population coding theory (Tipper, Howard, & Houghton, 2000), suggest that saccade deviation is the result of inhibition at sites in the topographical oculomotor saccade map in the SC. The suppression of task-irrelevant saccade stimuli, in favour of task-relevant saccade targets, has been found to lead to deviation away from distracting stimuli (e.g., McSorley, Haggard, & Walker, 2006). The inhibition of neurons relating to a distractor stimuli leads to a shift in activation in the population of neurons coding for the saccade target. Shifts in neuronal activation can also be seen during reaching and grasping experiments (Tipper, Howard, & Houghton, 2000); communication between systems responsible for oculomotor and manual actions resulting in reaching influencing the trajectories of saccades (Tipper, Howard, & Paul, 2001).

Cortical regions associated with trajectory deviations (both manual and saccade) include the LIP, the ventral intraparietal area (VIP), the DLPFC and the VLPFC. As aforementioned, activation in the LIP has been linked to both the presentation of visual distractors, and to visual attention (Powell & Goldberg, 2000). Within the saccade trajectory deviation framework, the pre-oculomotor attentional map is localised to the LIP and afferents are sent from this map to the SC. In contrast, the VIP, which sends afferents to the ventral premotor area and can be seen to receive tactile inputs, is thought to control manual reaches (Tipper, Howard, & Paul, 2001).

The DLPFC and VLPFC have both been associated in the inhibition of eye movements and manual responses. Activation in the DLPFC has been found during the suppression of task-irrelevant information (Johnston & Everling, 2006) and the completion of anti-saccade tasks (Matsuda et al., 2004). Johnston, Koval, Lomber & Everling (2013) suggest that an excitatory drive from the DLPFC to the SC may suppress or disinhibit saccade-related neurons in the SC. In an fMRI study, Leung and Cai (2007) highlight a VLPFC network involved in the inhibition of both manual and saccade responses. The dorsal processing pathway has also been implicated in reaching and grasping experiments (Dankert & Goodale, 2001).

There has been evidence of DLPFC and VLPFC involvement in VWM and that functional separation exist between these two regions; the DLPFC being responsible for VSWM and the VLPFC being responsible for the maintenance of visual object features (Wilson, Ó Scalaidhe, & Goldman-Rakic, 1993). Moreover, predominant DLPFC activation has been observed during the completion of a matrix rotation task whilst predominant VLPFC activation has been observed during the completion of a matrix comparison task (Suchan, 2002). Thus evidence suggests that common cortices sub-serve both manual mechanisms and VWM and that both cognitive systems may interact with the oculomotor system during visual processing.

This chapter investigates how manual mechanisms (tapping responses), thought to align along the dorsal pathway (Dankert & Goodale, 2001), influence the trajectories of saccades after the brief presentation of peripheral distractor stimuli. If VWM preferentially maintains saccade programmes across temporal delay periods to facilitate oculomotor inhibition, manual response facilitation of oculomotor inhibition

should not be observed. However, if oculomotor inhibition can still be found to occur in conditions not requiring VWM, this would suggest that saccade deviations are a product of a network of cortical (and sub-cortical) activations interacting with the oculomotor system in order to facilitate visual processing. Three conditions were presented to participants: a non-active rehearsal VWM condition, a manual tapping condition, and a spatial manual tapping condition. The manual tapping condition acted as a baseline condition indicating how saccade trajectories were influenced by motor tapping. In turn, the spatial manual tapping condition required participants to manually tap at the spatial location of a distractor stimulus, thus maintaining a 'motor' representation of the visual stimuli. It was hypothesised that the facilitation of prolonged oculomotor inhibition would be evident during the spatial manual tapping condition indicating that manual responses could be used to maintain saccade programmes across temporal delay periods.

Experiment 7

Method

Participants

Twelve participants were recruited for this study; two male and ten female ($M_{\text{age}} = 21.83$, $SD_{\text{age}} = 2.41$). All participants self-reported as right-handed. All participants had normal or corrected colour vision. All participants gave informed consent; the study conformed to all applicable ethical guidelines.

Apparatus

Apparatus used were consistent with previous chapters. A hand-held stylus (pointer) and a Trust TB-6300 touch tablet (20 × 15 cm) were used for manual tapping responses. No data was collected from the touch tablet. The touch tablet was positioned to the right of participants. Participants made manual responses with their right, dominant, hand.

Stimuli

Stimuli were identical to that presented in the previous chapter.

Procedure

Participants took part in three conditions; a non-active rehearsal VWM condition, a manual tapping condition and a spatial manual tapping condition. The saccade portion of conditions was identical to conditions described in previous chapters. All conditions required participants to make a saccade to target stimuli positioned in the upper or lower VF after the brief presentation of a peripheral distractor stimulus. The manual tapping condition further required participants to tap at the region of the touch tablet corresponding with the central fixation stimulus throughout the entirety of the saccade portion of the task. Thus, participants were required to manually tap in the centre of the touch tablet throughout the manual tapping condition.

During the spatial manual tapping condition, participants were required to initially tap at the position of the central fixation cross. When participants perceived the peripheral stimulus they were then required to tap at the region on the touch tablet corresponding to the perceived location of the presented distractor. Thus, after the

perception of an upper left VF distractor participants were required to produce a continuous manual tapping response in the upper left region of the touch tablet. Participants were required to maintain spatial tapping until the trial had ended.

Design

Data was filtered in the same way as previous chapters using MATLAB (R2010a, Mathworks, Natick, MA) and previously defined exclusion criteria were used (see chapter 3). Saccade measures used were saccade deviation, initial deviation, saccade accuracy, saccade latency, and mean direction. No motor response data was collected or analysed.

A 2×2 repeated measures design was implemented on saccade data from the conditions with the independent variables being distractor proximity to a target (close proximity vs. far proximity), and target VF (upper VF vs. lower VF). A further $2 \times 2 \times 3$ repeated measures design was used to ascertain whether there was a difference between conditions with distractor proximity to a target, target VF and condition being the independent variables. For the mean direction measure, the target VF measure was replaced by distractor VF in order to ascertain the mean direction of saccade trajectories towards or away from distractors.

Planned comparisons will examine any significant interactions found between the independent variables.

Results

Initial Deviation

2 × 2 repeated measures ANOVA's found no significant main effects across the non-active rehearsal VWM condition (distractor proximity to a target: $F(1, 11) = 0.01$, $p = .93$, $\eta p^2 = .00$, target VF: $F(1, 11) = 0.62$, $p = .45$, $\eta p^2 = .05$), the manual tapping condition (distractor proximity to a target: $F(1, 11) = 1.84$, $p = .20$, $\eta p^2 = .14$, target VF: $F(1, 11) = 0.53$, $p = .48$, $\eta p^2 = .05$), or the spatial manual tapping condition (distractor proximity to a target: $F(1, 11) = 0.19$, $p = .67$, $\eta p^2 = .02$, target VF: $F(1, 11) = 0.10$, $p = .77$, $\eta p^2 = .01$) for the initial deviation measure. A significant interaction was revealed in the spatial manual tapping condition across the two variables; $F(1, 11) = 5.96$, $p < .05$, $\eta p^2 = .35$. Planned comparisons indicated a trend towards significance ($p = .10$) suggesting that the initial deviation of saccades directed to the lower VF was reduced after the presentation of far proximity distractors ($M = -0.23$, $SE = 3.11$) in comparison to close proximity distractors ($M = 3.26$, $SE = 3.01$). This result was not replicated in saccades directed to the upper VF where distractor proximity to a target appeared to result in a more consistent, though directionally different, degree of initial deviation (close proximity distractors: $M = -0.84$, $SE = 3.14$, far proximity distractors: $M = 1.27$, $SE = 3.96$); see *fig. 8.1*.

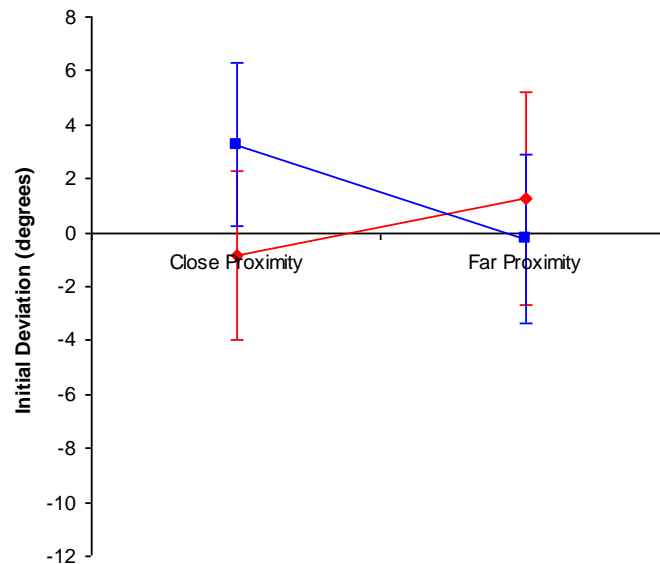


Fig. 8.1. Distractor proximity to a target \times target VF interaction during spatial manual tapping condition for initial deviation. Red line shows upper VF. Blue line shows lower VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effects for distractor proximity to a target [$F(1, 11) = 0.66, p = .44, \eta p^2 = .06$], or target VF [$F(1, 11) = 0.55, p = .48, \eta p^2 = .05$]. A trend towards significance was found for condition; $F(2, 22) = 2.99, p = .07, \eta p^2 = .21$. Post hoc tests using the Bonferroni correction indicated a trend towards significance ($p = .08$) suggesting a reduced degree of initial deviation during the spatial manual tapping condition ($M = 0.86, SE = 1.63$) in comparison to the non-active rehearsal VWM condition ($M = -9.36, SE = 1.85$). No significant difference was found between the manual tapping condition ($M = -1.27, SE = 1.67$) and the other two conditions; see *fig. 8.2*.

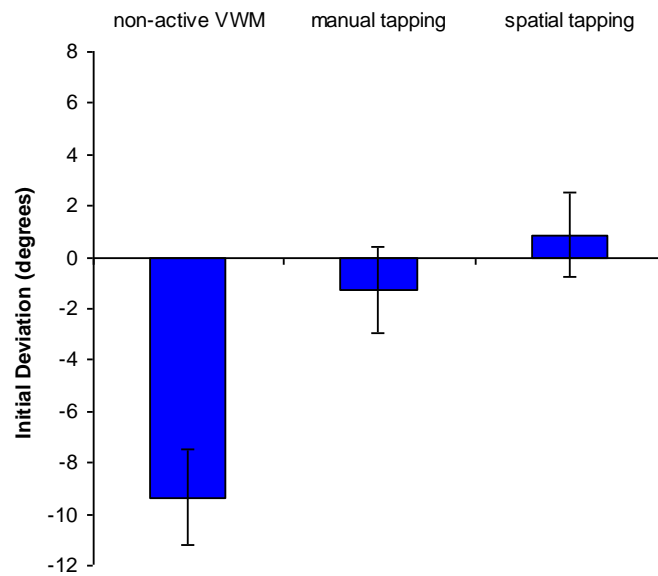


Fig. 8.2. Main effect for condition for initial deviation. Error bars represent ± 1 SE.

A significant interaction was also found between distractor proximity to a target and target VF; $F(1, 11) = 6.42$, $p < .05$, $\eta p^2 = .37$. Planned comparisons found that saccades directed to the lower VF were subject to a significantly ($p < .05$) reduced degree of initial deviation after the presentation of close proximity distractors ($M = -0.58$, $SE = 1.84$) in comparison to far proximity distractors ($M = -3.86$, $SE = 2.16$). For saccades directed to the upper VF, this pattern was reversed (close proximity distractors: $M = -5.21$, $SE = 2.06$, far proximity distractors: $M = -3.38$, $SE = 2.34$); though planned comparison found only a trend towards significance for this VF ($p = .10$). Furthermore, saccades made after the presentation of close proximity distractors expressed a significantly ($p < .05$) reduced degree of deviation when directed to the lower VF than when directed to the upper VF; see *fig. 8.3*.

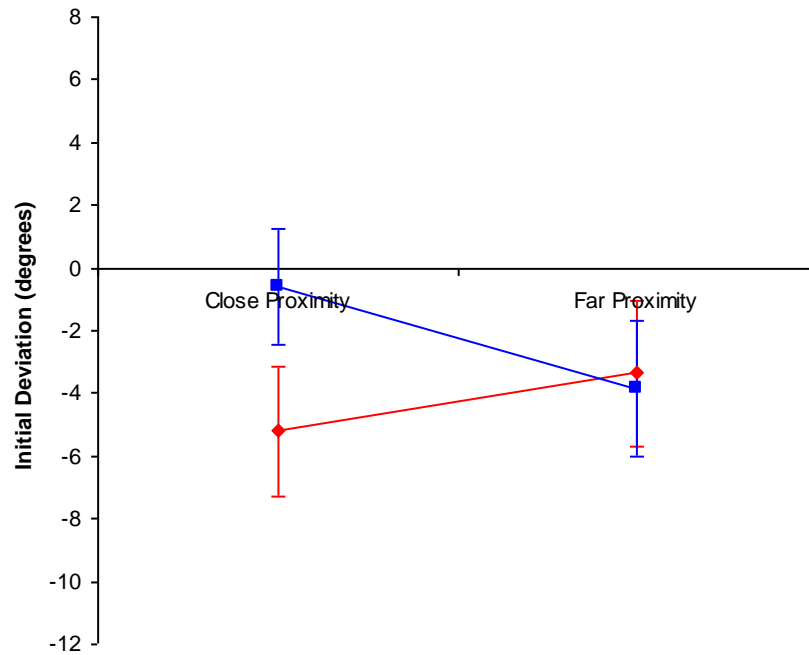


Fig. 8.3. Distractor proximity to a target \times target VF interaction across the conditions for initial deviation. Red line shows upper VF. Blue line shows lower VF. Error bars represent ± 1 SE.

Saccade Deviation

No significant main effects were found in any condition for distractor proximity to a target (non-active rehearsal VWM: $F(1, 11) = 3.08$, $p = .11$, $\eta p^2 = .22$, manual tapping: $F(1, 11) = 2.00$, $p = .19$, $\eta p^2 = .15$, spatial manual tapping: $F(1, 11) = 1.66$, $p = .23$, $\eta p^2 = .13$) or target VF (non-active rehearsal VWM: $F(1, 11) = 0.72$, $p = .42$, $\eta p^2 = .06$, manual tapping: $F(1, 11) = 0.04$, $p = .85$, $\eta p^2 = .00$, spatial manual tapping: $F(1, 11) = 2.08$, $p = .18$, $\eta p^2 = .16$) for saccade deviation.

A significant interaction was found during the manual tapping condition; $F(1, 11) = 8.08$, $p < .05$, $\eta p^2 = .42$. Planned comparisons indicated that saccades directed to the lower VF after the presentation of far proximity distractors ($M = 3.22$, $SE = 1.31$) expressed a significantly ($p < .05$) reduced degree of saccade deviation in comparison to close proximity distractors ($M = 1.10$, $SE = 1.37$). The opposite pattern was found for

saccades directed to the upper VF; reduced saccade deviations were expressed after close proximity distractors ($M = 1.24$, $SE = 1.40$) in comparison to after far proximity distractors ($M = 2.24$, $SE = 1.31$) though a trend towards significance ($p = .10$) indicated this difference (see *fig. 8.4.*).

A significant interaction was also found between distractor proximity to a target and target VF during the spatial manual tapping condition; $F(1, 11) = 6.36$, $p < .05$, $\eta p^2 = .37$. In contrast to the results found in the manual tapping condition, planned comparisons in the spatial manual tapping condition found a significantly ($p < .05$) reduced degree of saccade deviation in saccades directed to the lower VF after the presentation of close proximity distractors ($M = -0.02$, $SE = 1.47$) in comparison to far proximity distractors ($M = -1.91$, $SE = 1.26$). In the upper VF more a more consistent degree of saccade deviation was expressed for close ($M = 3.13$, $SE = 0.88$) and far ($M = 3.56$, $SE = 0.75$) proximity distractors; see *fig. 8.5.*

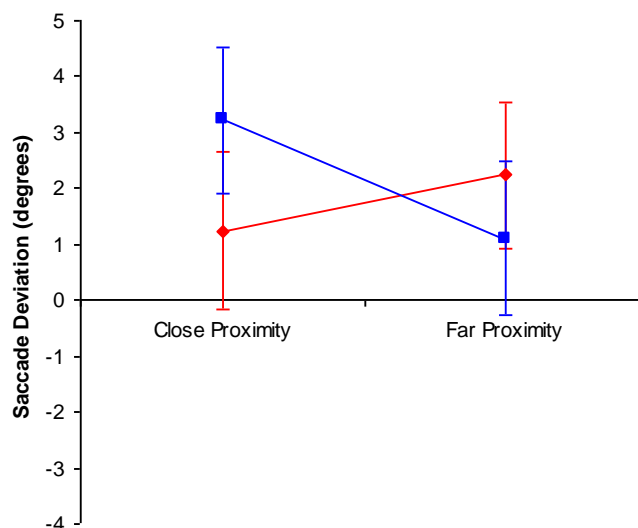


Fig. 8.4. Distractor proximity to a target \times target VF interaction during manual tapping condition for saccade deviation. Red line shows saccades made to the upper VF. Blue line shows saccades made to the lower VF. Error bars represent ± 1 SE.

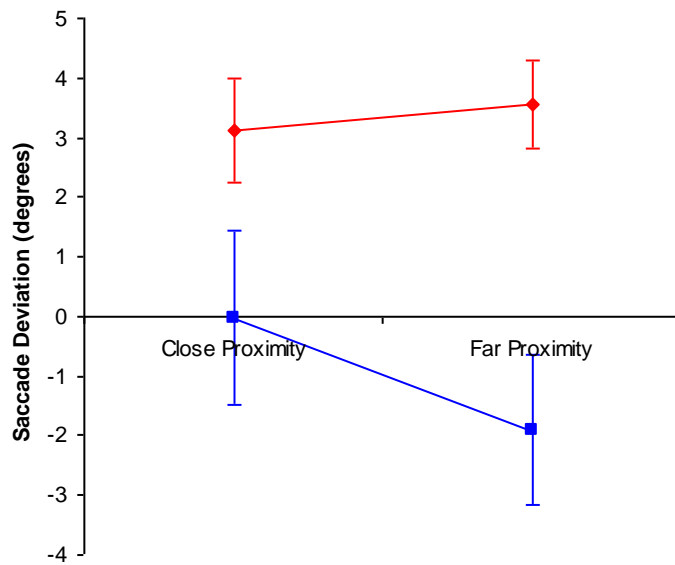


Fig. 8.5. Distractor proximity to a target \times target VF interaction during the spatial manual tapping condition for saccade deviation. Red line shows saccade deviations to the upper VF. Blue line shows saccade deviations to the lower VF. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant main effects for target VF [$F(1, 11) = 1.08, p = .32, \eta p^2 = .09$] or condition [$F(1, 11) = 1.33, p = .29, \eta p^2 = .11$] across the conditions. A trend towards significance was found for distractor proximity to a target; $F(1, 11) = 3.79, p = .08, \eta p^2 = .26$. Reduced saccade deviation was found after the presentation of far proximity distractors ($M = 0.75, SE = 0.66$) in comparison to close proximity distractors ($M = 1.45, SE = 0.60$); see *fig. 8.6*.

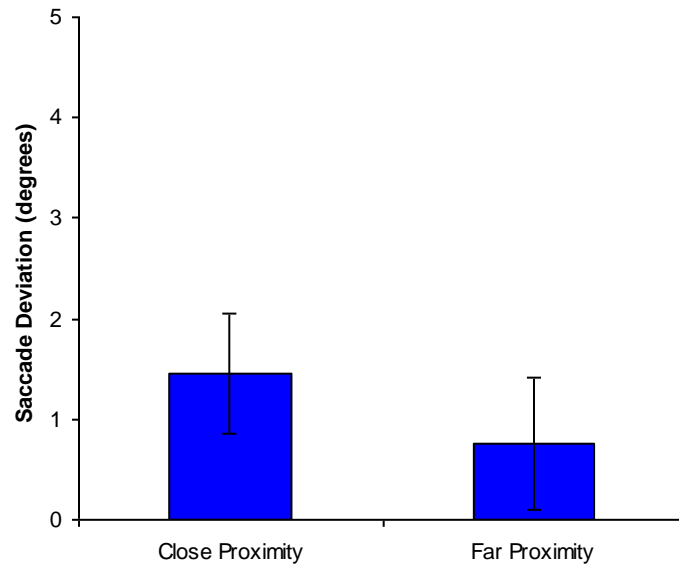


Fig. 8.6. Main effect for distractor proximity across conditions for saccade deviation. Error bars represent ± 1 SE.

A significant interaction was found for distractor proximity to a target and target VF; $F(1, 11) = 11.60, p < .01, \eta p^2 = .51$. Consistent saccade deviation was found for saccades directed to the upper VF after the presentation of close ($M = 1.92, SE = 0.85$) and far ($M = 2.35, SE = 0.92$) proximity distractors. In contrast, saccades to the lower VF expressed significantly ($p < .001$) directionally different saccade deviations (close proximity distractors: $M = 0.98, SE = 0.84$, far proximity distractors: $M = -0.85, SE = 0.88$); see *fig. 8.7*.

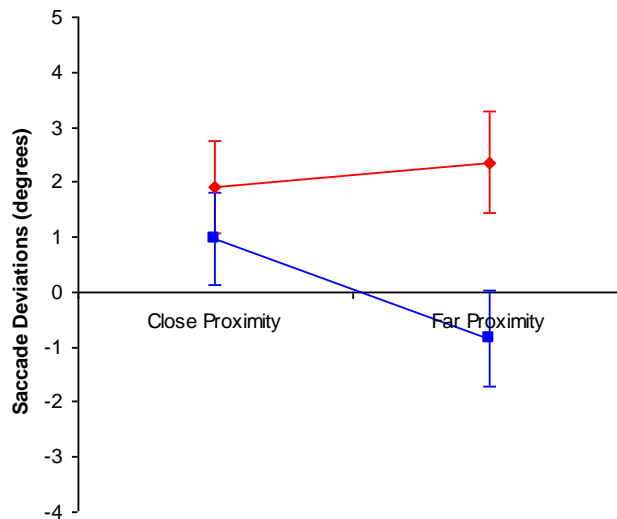


Fig. 8.7. Distractor proximity to a target \times target VF interaction across conditions for saccade deviation. Red line shows saccade deviations to the upper VF. Blue line shows saccade deviations to the lower VF. Error bars represent ± 1 SE.

Saccade Accuracy

No significant main effects were found in the non-active rehearsal VWM (distractor proximity to a target: $F(1, 11) = 0.43$, $p = .52$, $\eta p^2 = .04$, target VF: $F(1, 11) = 1.73$, $p = .22$, $\eta p^2 = .14$) or the manual tapping conditions (distractor proximity to a target: $F(1, 11) = 2.03$, $p = .18$, $\eta p^2 = .16$, target VF: $F(1, 11) = 0.62$, $p = .45$, $\eta p^2 = .05$) for the saccade accuracy measure. Furthermore, no significant main effect was found for target VF [$F(1, 11) = 2.83$, $p = .12$, $\eta p^2 = .21$] during the spatial manual tapping condition. A trend towards significance was found for distractor proximity to a target; $F(1, 11) = 3.37$, $p = .09$, $\eta p^2 = .24$. Saccades, after the presentation of close proximity distractors ($M = 1.16$, $SE = 0.06$), tended to be more accurate than after the presentation of far proximity distractors ($M = 1.26$, $SE = 0.07$); see fig. 8.8.

A significant interaction was also found during the spatial manual tapping condition for distractor proximity to a target and target VF; $F(1, 11) = 7.50$, $p < .05$, $\eta p^2 = .41$.

Planned comparisons revealed that saccades made to the upper VF were significantly ($p < .05$) more accurate after the presentation of close proximity distractors ($M = 1.21$, $SE = 0.07$) in comparison to after the presentation of far proximity distractors ($M = 1.41$, $SE = 0.10$). Consistent levels of accuracy were produced for saccades made to the lower VF after the presentation of close ($M = 1.10$, $SE = 0.09$) and far ($M = 1.10$, $SE = 0.07$) proximity distractors. Saccades made to the lower VF, after the presentation of far proximity distractors, were also found to be significantly ($p < .05$) more accurate than saccades made to the upper VF; see *fig. 8.9*.

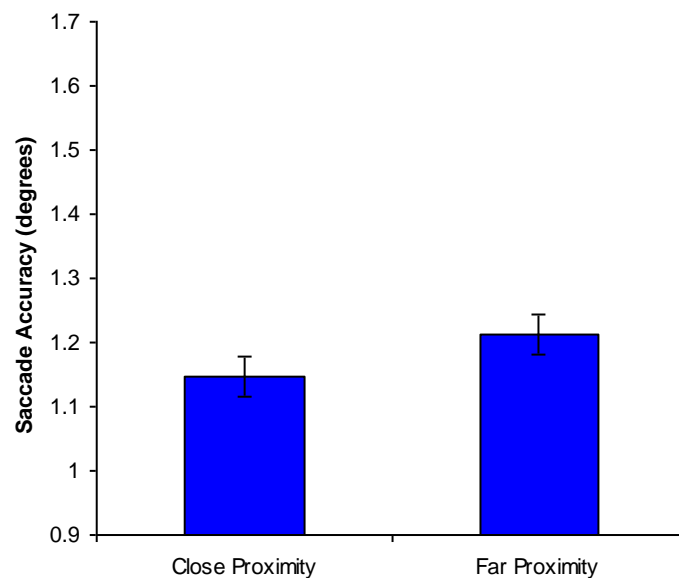


Fig. 8.8. Main effect for distractor proximity to a target during the spatial manual tapping condition for saccade accuracy. Error bars represent ± 1 SE.

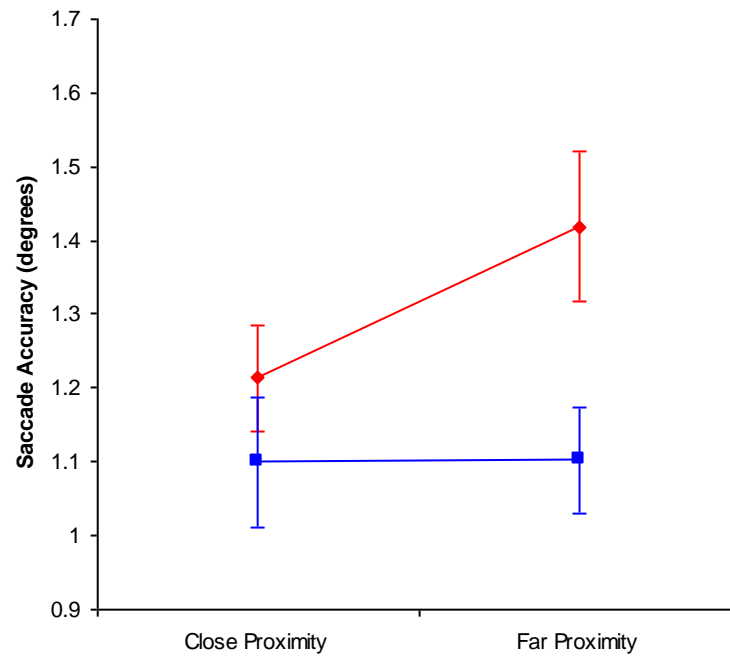


Fig 8.9. Distractor proximity to a target \times target VF interaction during the spatial manual tapping condition for saccade accuracy. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant differences across conditions for target VF [$F(1, 11) = 2.36, p < .15, \eta p^2 = .18$], or condition [$F(2, 22) = 1.68, p = .21, \eta p^2 = .13$]. A significant main effect was found for distractor proximity to a target; $F(1, 11) = 5.90, p < .05, \eta p^2 = .41$. Saccades made after the presentation of close proximity distractors ($M = 1.15, SE = 0.03$) were more accurate than saccades made after the presentation of far proximity distractors ($M = 1.21, SE = 0.03$).

Saccade Latency

Significant main effects were found for target VF in the three conditions (non-active rehearsal VWM: $F(1, 11) = 24.84, p < .001, \eta p^2 = .69$, manual tapping: $F(1, 11) = 10.41, p < .01, \eta p^2 = .49$, spatial manual tapping; $F(1, 11) = 22.93, p < .005, \eta p^2 = .68$). In all three conditions saccade latencies to upper VF targets (non-active rehearsal VWM: M

= 290.67, $SE = 6.52$, manual tapping: $M = 300.10$, $SE = 5.16$, spatial manual tapping: $M = 322.78$, $SE = 8.02$) were shorter than saccade latencies to lower VF targets (non-active rehearsal VWM: $M = 317.35$, $SE = 6.30$, manual tapping: $M = 329.39$, $SE = 5.73$, spatial manual tapping: $M = 357.64$, $SE = 8.49$); see *fig. 8.10*.

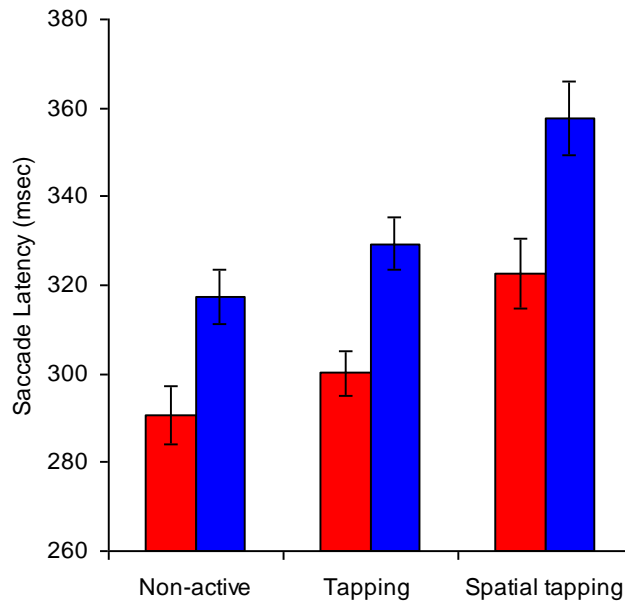


Fig 8.10. Main effect for target VF for saccade latency in the three conditions. Red bars show saccade latencies to upper VF targets. Blue bars show saccade latencies to lower VF targets. Error bars represent $\pm 1 SE$.

A significant difference was also found for distractor proximity to a target during the non-active rehearsal VWM condition [$F(1, 11) = 6.27$, $p < .05$, $\eta p^2 = .36$] whilst a trend towards significance was found for this variable during the spatial manual tapping condition [$F(1, 11) = 4.30$, $p = .06$, $\eta p^2 = .28$]. Shorter latency saccades were produced after the presentation of far proximity distractors (non-active rehearsal VWM: $M = 297.23$, $SE = 5.67$, spatial manual tapping: $M = 334.02$, $SE = 8.35$) than latencies produced after the presentation of close proximity saccades (non-active rehearsal VWM: $M = 310.79$, $SE = 7.77$, spatial manual tapping: $M = 346.41$, $SE = 9.36$) in both

conditions; see *fig. 8.11.* for the non-active rehearsal VWM condition, and *fig. 8.12.* for the spatial manual tapping condition. In contrast, no significant main effect was found for distractor proximity to a target during the manual tapping condition; $F(1, 11) = 0.58, p = .46, \eta p^2 = .05$.

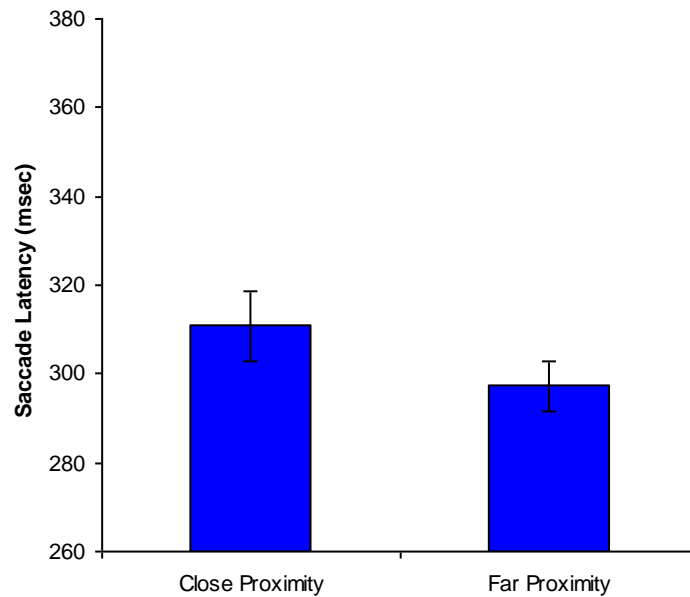


Fig 8.11. Main effect for distractor proximity for saccade latency during the non-active VWM condition. Error bars represent ± 1 SE.

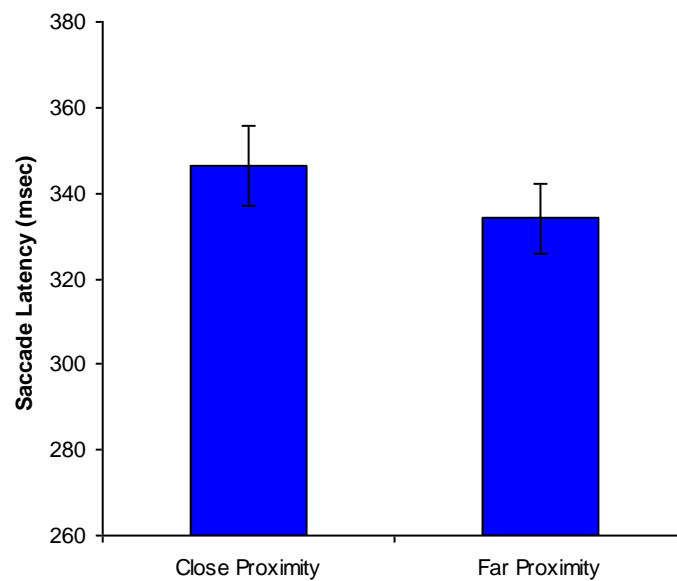


Fig. 8.12. Main effect for distractor proximity for saccade latency during the spatial manual tapping condition. Error bars represent ± 1 SE.

A trend towards significance was found for the interaction between the two independent variables during the non-active rehearsal VWM condition; $F(1, 11) = 4.54$, $p = .06$, $\eta p^2 = .29$. Planned comparisons indicated that saccade latencies to lower VF targets were significantly ($p < .05$) shorter after the presentation of far proximity distractors ($M = 306.06$, $SE = 7.75$) in comparison to close proximity distractors ($M = 328.65$, $SE = 9.09$). More consistent saccade latencies were observed in the upper VF after close ($M = 292.92$, $SE = 10.59$) and far ($M = 288.41$, $SE = 8.04$) proximity distractors; see *fig. 8.13*. Saccades made after the presentation of close proximity distractors were observed to have significantly ($p < .001$) shorter latencies when directed to the upper VF than when directed to the lower VF. Furthermore, saccades made after the presentation of far proximity distractors also expressed significantly ($p < .05$) shorter latencies when directed to the upper VF as opposed to the lower VF.

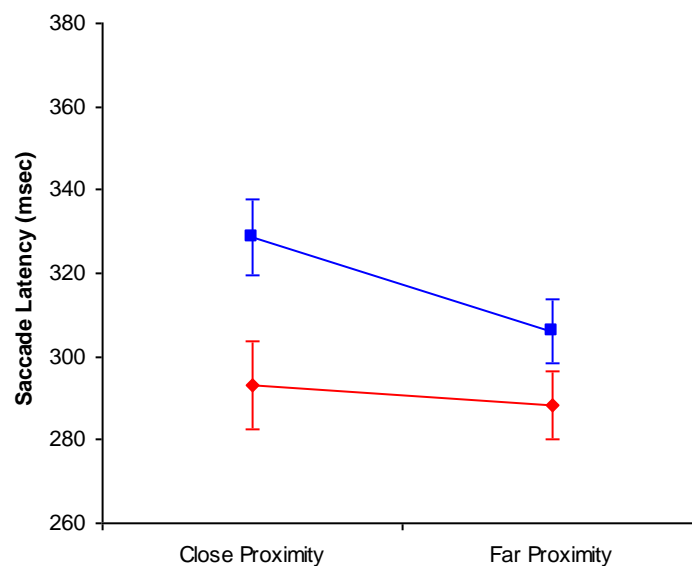


Fig. 8.13. Distractor proximity to a target \times target VF interaction during the non-active VWM condition for saccade latency. Red line shows saccades made to the upper VF. Blue line shows saccades made to the lower VF. Error bars represent ± 1 SE.

A significant interaction was also found during the manual tapping condition; $F(1, 11) = 6.97, p < .05, \eta p^2 = .39$. Planned comparisons revealed that in the upper VF, the brief presentation of close proximity distractors ($M = 290.64, SE = 8.02$) induced significantly ($p < .05$) shorter saccade latencies than the brief presentation of far proximity distractors ($M = 309.57, SE = 5.53$). In the lower VF the opposite pattern was observed (close proximity distractors: $M = 335.41, SE = 9.19$, far proximity distractors: $M = 323.37, SE = 6.80$); though this was not found to be significant. Planned comparisons also found that, after the presentation of close proximity distractors, saccades directed to the upper VF had significantly shorter latencies than saccades directed to the lower VF; this was not replicated after the presentation of far proximity distractors; see *fig. 8.14*. No significant interaction was observed in the spatial manual tapping condition.

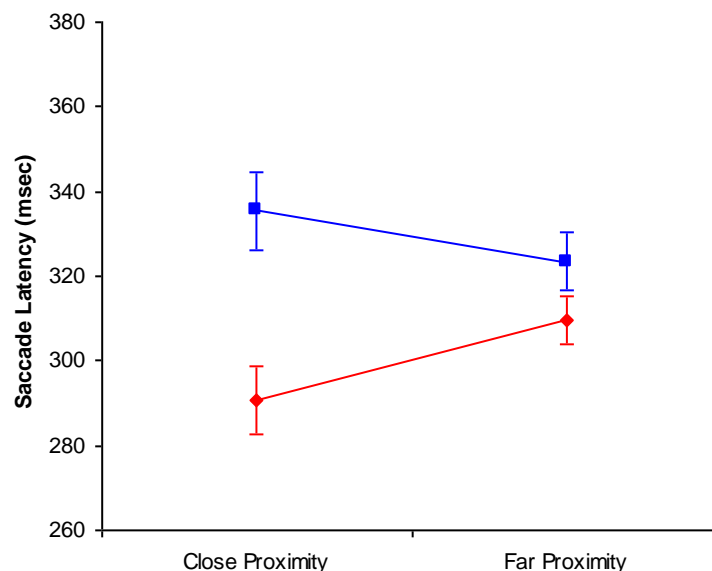


Fig. 8.14. Distractor proximity \times target VF interaction for saccade latency for the manual tapping condition. Red line shows upper VF saccade latencies. Blue line shows lower VF saccade latencies. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA found a trend towards significance for distractor proximity [$F(1, 11) = 3.82, p = .07, \eta p^2 = .26$] across the conditions. Saccade latencies made after the presentation of far proximity distractors ($M = 315.91, SE = 4.06$) were shorter than latencies made after the presentation of close proximity distractors ($M = 323.41, SE = 5.09$). A significant main effect was also found for target VF; $F(1, 11) = 20.72, p < .005, \eta p^2 = .65$. Consistent with previous findings, saccades made to the upper VF ($M = 304.52, SE = 4.09$) expressed shorter latencies than saccades made to the lower VF ($M = 334.80, SE = 4.43$). A significant main effect for condition was found; $F(2, 22) = 3.78, p < .05, \eta p^2 = .26$. Saccade latencies were shortest during the non-active VWM condition ($M = 304.01, SE = 4.89$), followed by the manual tapping condition ($M = 314.75, SE = 4.37$) and the spatial tapping condition ($M = 340.21, SE = 6.27$); however post hoc tests using the Bonferroni correction did not find any significant difference between any two conditions (see *fig 8.15*).

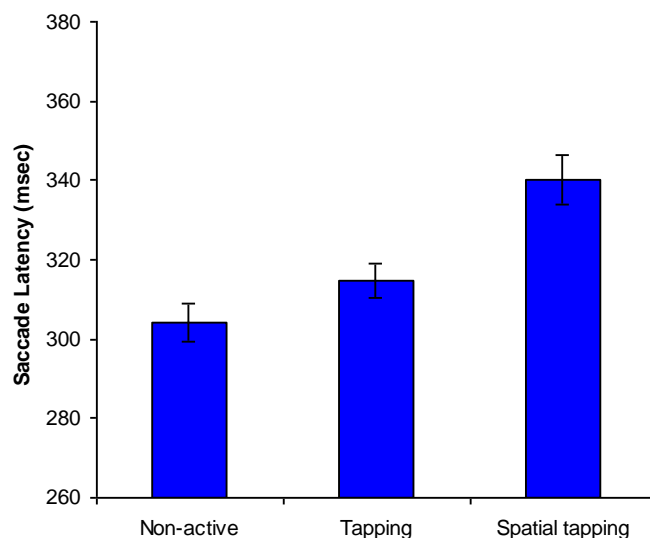


Fig. 8.15. Main effect for condition for saccade latency. Error bars represent ± 1 SE.

A significant interaction was found between distractor proximity to a target and target VF; $F(1, 11) = 6.49, p < .05, \eta p^2 = .37$. Planned comparisons found consistent latencies

for saccades made to the upper VF after the presentation of close proximity ($M = 302.92$, $SE = 6.19$) and far proximity distractors ($M = 306.11$, $SE = 5.42$). However, significantly ($p < .001$) shorter latencies were observed after the presentation of far proximity distractors ($M = 325.70$, $SE = 5.67$), in comparison to close proximity distractors ($M = 343.89$, $SE = 6.54$), when saccades were directed to the upper VF. Furthermore, saccades had significantly ($p < .001$) shorter latencies when directed to the upper VF, after the presentation of far proximity distractors, than when directed to the lower VF. Shorter saccade latencies for upper VF directed saccades, in comparison to lower VF directed saccades, was also found after the presentation of close proximity distractors ($p < .001$); see *fig.8.16*.

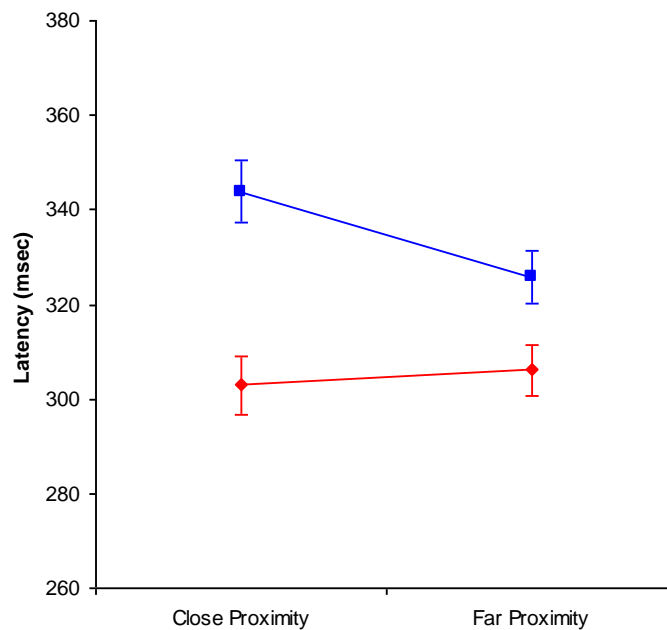


Fig. 8.16. Distractor proximity to a target \times target VF interaction for saccade latency. Blue line shows saccade latencies for non-active VWM condition. Red line shows upper VF saccade latencies. Blue line shows lower VF saccade latencies. Error bars represent ± 1 SE. Error bars represent ± 1 SE.

A significant interaction was also found between distractor proximity to a target and condition; $F(2, 22) = 4.35$, $p < .05$, $\eta p^2 = .28$. Planned comparisons found that after the

presentation of close proximity distractors, the non-active rehearsal VWM condition ($M = 310.79$, $SE = 7.77$), and the manual tapping condition ($M = 316.47$, $SE = 4.52$), had latencies that were significantly (non-active rehearsal VWM: $p < .05$, manual tapping: $p < .005$) shorter than the spatial manual tapping condition ($M = 334.02$, $SE = 8.35$). No significant difference was found between the non-active rehearsal VWM and manual tapping condition. In contrast the non-active rehearsal VWM condition ($M = 297.23$, $SE = 5.76$) had significantly shorter saccade latencies, after the presentation of far proximity distractors, than the manual tapping ($M = 316.47$, $SE = 4.52$) and the spatial manual tapping ($M = 334.02$, $SE = 8.35$) conditions (manual tapping: $p < .005$, spatial manual tapping: $p < .005$). A trend towards significance was found between the manual tapping condition and the spatial manual tapping condition ($p = .09$); see *fig. 8.17*.

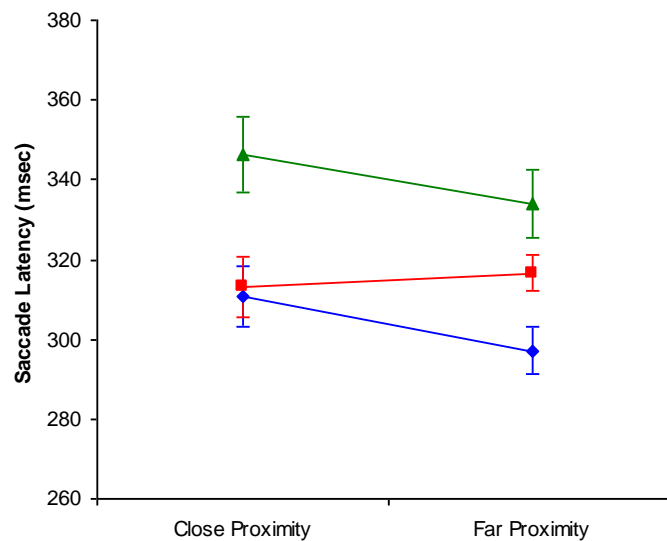


Fig. 8.17. Distractor proximity \times condition interaction for saccade latency. Blue line shows saccade latencies for non-active VWM condition. Red line shows saccade latencies for manual tapping condition. Green line shows saccade latencies for spatial manual tapping condition. Error bars represent ± 1 SE.

Mean Direction

No significant results were found during the non-active rehearsal VWM condition (distractor proximity to a target: $F(1, 11) = 3.21, p = .10, \eta p^2 = .23$, distractor VF: $F(1, 11) = 3.21, p = .10, \eta p^2 = .23$). Furthermore, no significant main effect was found for distractor VF to a target during the manual tapping condition; $F(1, 11) = 0.09, p = .77, \eta p^2 = .01$. In contrast a significant main effect was found for distractor VF during the spatial manual tapping condition; $F(1, 11) = 5.14, p < .05, \eta p^2 = .32$. Saccades made after the presentation of left VF distractors ($M = 0.15, SE = 0.03$) were directed rightwards to a greater degree than distractors made after the presentation of right VF distractors ($M = 0.07, SE = 0.03$); see *fig. 8.18*.

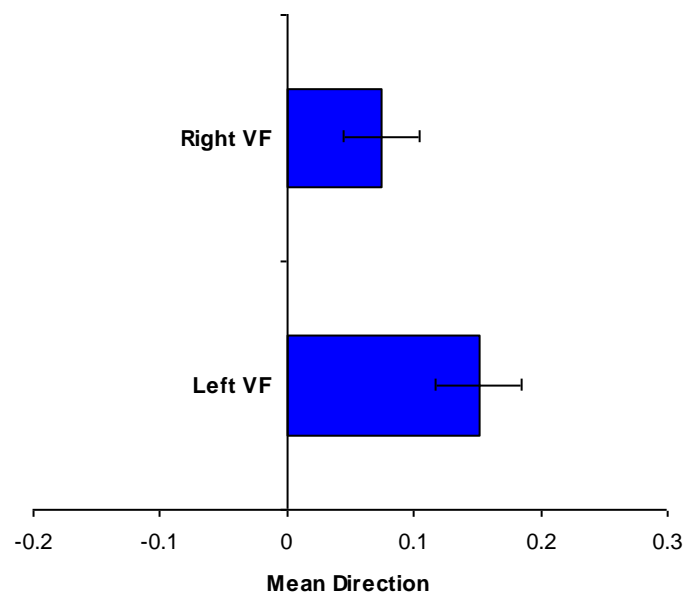


Fig. 8.18. Main effect for distractor VF during spatial manual tapping condition for mean direction. Error bars represent ± 1 SE.

Significant main effects were found for the distractor proximity to a target variable for both the manual tapping [$F(1, 11) = 7.73, p < .05, \eta p^2 = .41$] and the spatial manual

tapping [$F(1, 11) = 8.61, p < .05, \eta p^2 = .44$] conditions. During the manual tapping condition, far proximity distractors ($M = -0.04, SE = 0.04$) elicited saccades that were directed leftward to a lesser extent than saccades made after close proximity distractors ($M = -0.11, SE = 0.04$); see *fig. 8.19*. The spatial manual tapping condition found that saccades made after the presentation of close proximity distractors ($M = 0.08, SE = 0.04$) were directed to the right to a lesser extent than saccades made after far proximity distractors ($M = 0.14, SE = 0.03$); see *fig. 8.20*.

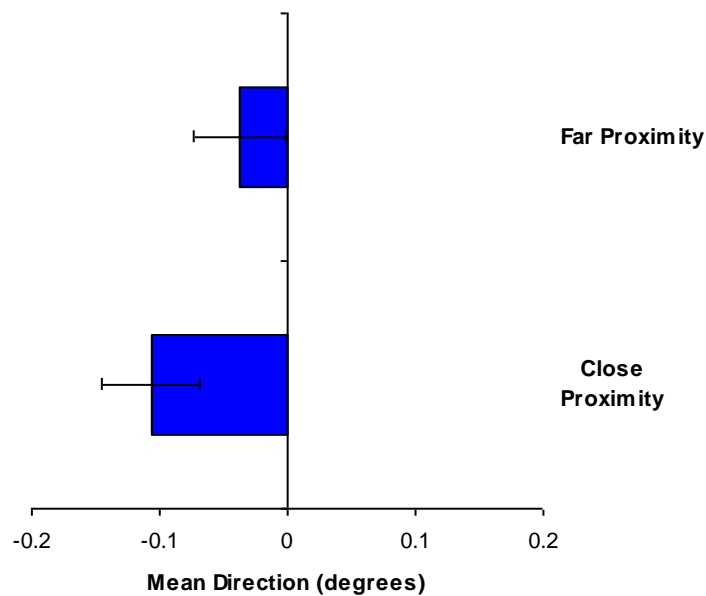


Fig. 8.19. Main effect for distractor proximity to a target during the manual tapping condition for mean direction. Error bars represent ± 1 SE.

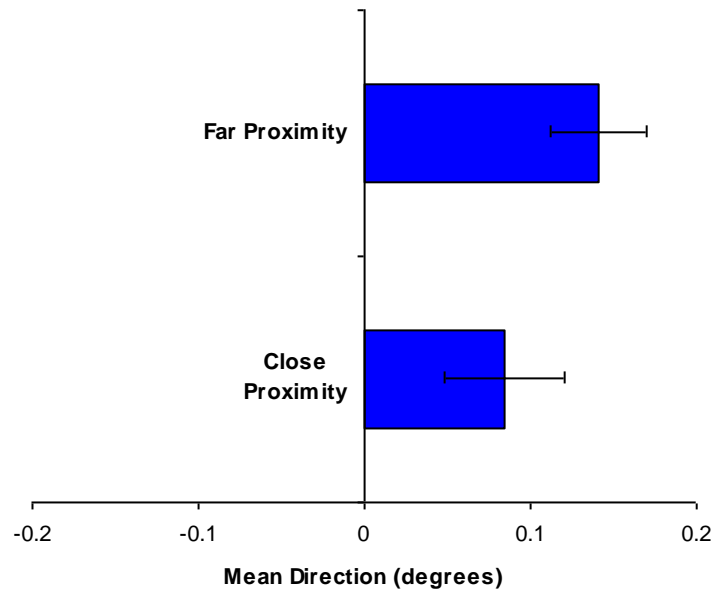


Fig 8.20. Main effect for distractor proximity to target during the spatial manual tapping condition for mean direction. Error bars represent ± 1 SE.

Analysis for the manual tapping condition revealed a trend towards significance for the interaction between the two independent variables [$F(1, 11) = 4.79, p = .05, \eta p^2 = .30$]; this interaction was found to be significant during the spatial manual tapping condition [$F(1, 11) = 9.67, p < .05, \eta p^2 = .47$]. Planned comparisons revealed that, during manual tapping condition, saccades made after right VF, far proximity distractors ($M = 0.00, SE = 0.05$) were directed leftward to a significantly ($p < .005$) lesser extent than after the presentation of right VF, close proximity distractors ($M = -0.14, SE = 0.04$). Saccades expressed a more consistent degree of leftward trajectory direction after the presentation of left VF distractors (close proximity distractors: $M = -0.08, SE = 0.07$, far proximity distractors: $M = -0.08, SE = 0.06$); see fig 8.21. During the spatial manual tapping condition, consistent rightward directed saccades were found after the presentation of both left VF close ($M = 0.16, SE = 0.05$), and left VF far ($M = 0.14, SE = 0.04$), proximity distractors. In contrast, planned comparisons found that saccades

expressed significantly ($p < .005$) less rightward direction after the presentation of right VF, close proximity distractors ($M = 0.00$, $SE = 0.04$) than after right VF, far proximity distractors ($M = 0.14$, $SE = 0.04$); see *fig. 8.22*. Furthermore, saccades made after the presentation of right VF, close proximity distractors expressed a significantly ($p < .05$) lesser degree of rightward direction than after the presentation of left VF, close proximity distractors.

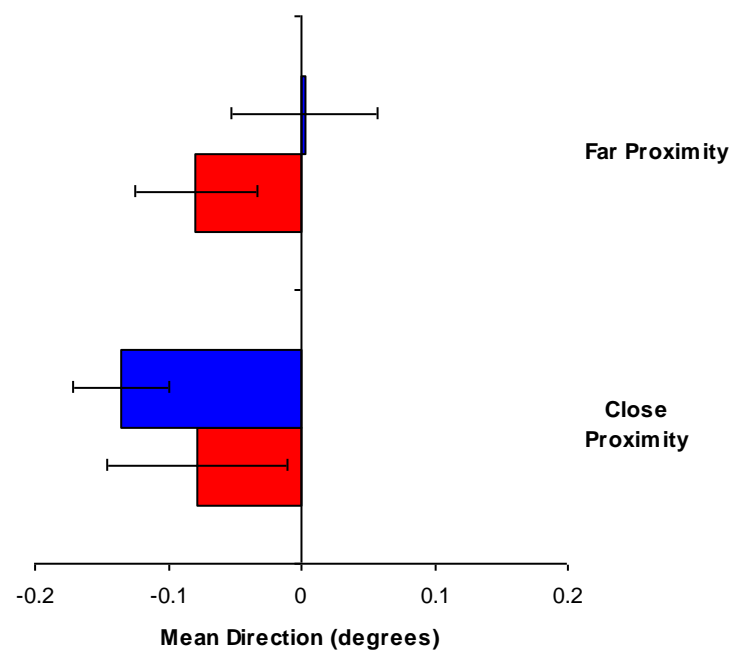


Fig. 8.22. Distractor proximity to a target \times target VF interaction during the manual tapping condition for mean direction. Red bars show left VF distractors. Blue bars show right VF distractors. Error bars represent ± 1 SE.

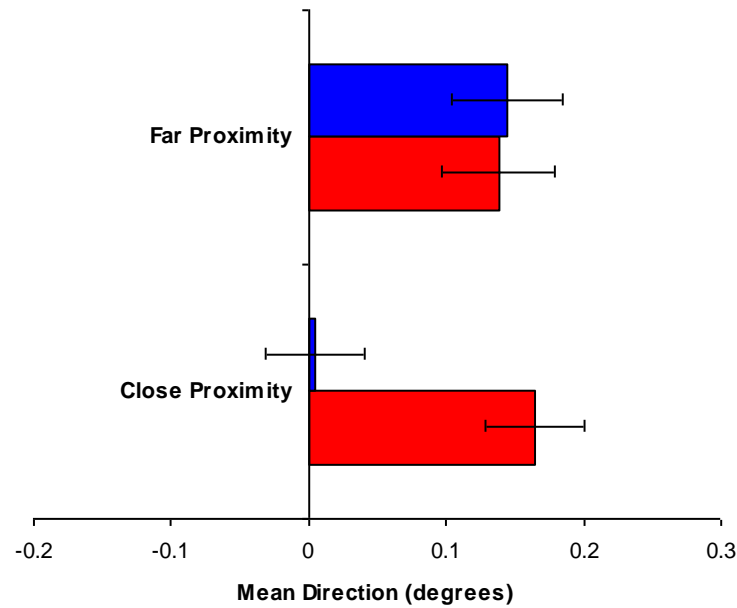


Fig. 8.22. Distractor proximity to a target \times distractor VF interaction for mean direction during spatial manual tapping condition. Red bars show left VF distractors. Blue bars show right VF distractors. Error bars represent ± 1 SE.

A further $2 \times 2 \times 3$ repeated measures ANOVA revealed no significant difference for distractor VF; $F(1, 11) = 0.25$, $p = .25$, $\eta p^2 = .12$. However, a significant main effect for distractor proximity to a target was found; $F(1, 11) = 15.82$, $p < .005$, $\eta p^2 = .59$. Greater rightward direction was found in saccades after the presentation of far proximity ($M = 0.07$, $SE = 0.02$) distractors in comparison to close proximity distractors ($M = 0.01$, $SE = 0.02$). A trend towards significance was also found for condition; $F(1, 11) = 2.90$, $p = .08$, $\eta p^2 = .47$. Saccades made during the manual tapping condition were directed leftwards ($M = -0.07$, $SE = 0.03$) in comparison to the other two conditions. Post hoc tests (Bonferroni corrected) found that the mean direction of these saccades during the manual tapping condition differed significantly ($p < .05$) in comparison to saccades made during the spatial manual tapping condition ($M = 0.11$, $SE = 0.02$). However the manual tapping condition was not found to be significantly different to the non-active

rehearsal VWM condition ($M = 0.08$, $SE = 0.03$) which in turn was not found to be significantly different to the spatial manual tapping condition; see *fig 8.23*.

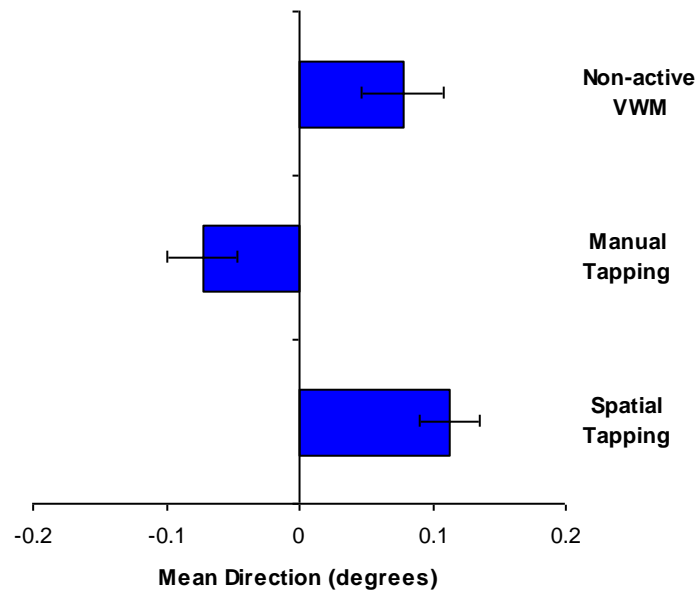


Fig. 8.23. Main effect for condition for mean direction across the conditions. Error bars represent ± 1 SE.

A significant interaction was found for distractor proximity to a target and distractor VF; $F(1, 11) = 8.56$, $p < .05$, $\eta p^2 = .44$. Saccades made after right VF, close proximity distractors ($M = -0.03$, $SE = 0.03$) were directed leftwards and planned comparisons found that the mean direction of these saccades were significantly ($p < .05$) different to right VF, far proximity distractors ($M = 0.08$, $SE = 0.03$) which were found to be directed rightwards. No significant differences were found for the mean direction of saccades after the presentation of left VF, close ($M = 0.06$, $SE = 0.04$) or far proximity distractors ($M = 0.06$, $SE = 0.03$); see *fig. 8.24*. Furthermore, it was found that the mean direction of saccades made after the presentation of right VF, close proximity distractors were significantly different ($p < .05$) to the mean direction of saccades made after the presentation of left VF, close proximity distractors; see *fig 8.24*.

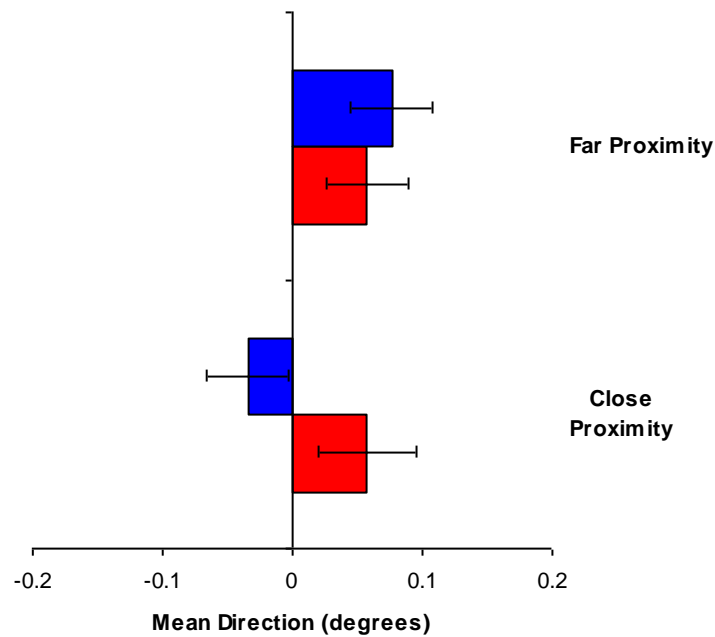


Fig. 8.24. Distractor proximity to a target \times distractor VF interaction for mean direction across conditions. Red bars show left VF distractors. Blue bars show right VF distractors. Error bars represent ± 1 SE.

A significant interaction was found for distractor VF and condition; $F(1, 11) = 4.72$, $p < .05$, $\eta p^2 = .30$. Planned comparisons revealed that saccades made during the manual tapping condition ($M = -0.08$, $SE = 0.04$), after the presentation of left VF distractors, had a mean direction that was significantly (non-active rehearsal VWM: $p < .05$, spatial manual tapping: $p < .001$) different to the mean direction of saccades during the non-active rehearsal VWM condition ($M = 0.10$, $SE = 0.04$) and the spatial manual tapping condition ($M = 0.15$, $SE = 0.03$). After the presentation of right VF distractors, the mean direction of saccades was found to be significantly different ($p < .01$) during the manual tapping condition ($M = -0.07$, $SE = 0.04$) in comparison to the mean direction of saccades during the spatial manual tapping condition ($M = 0.07$, $SE = 0.03$). A trend towards significance ($p = .09$) indicated a difference between the manual tapping

condition and the non-active rehearsal VWM condition ($M = 0.05$, $SE = 0.05$); see *fig. 8.25*.

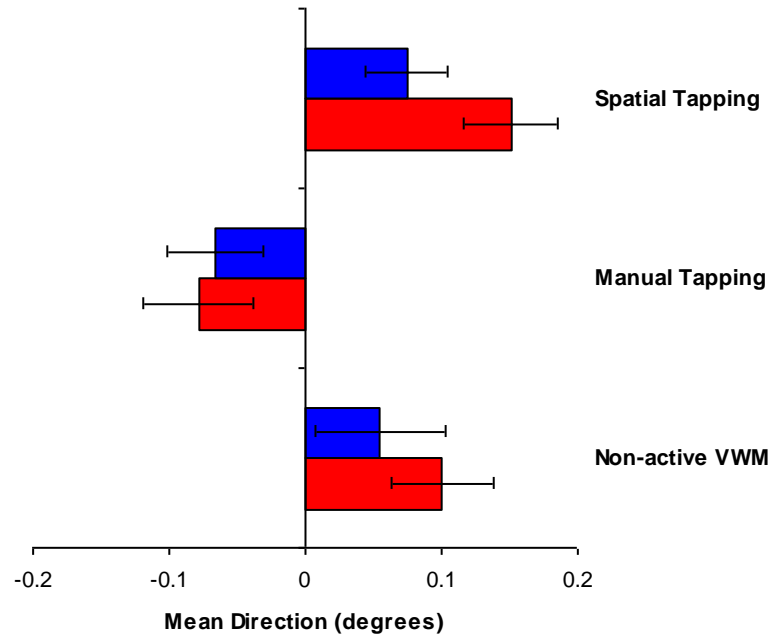


Fig. 8.25. Distractor proximity to a target \times condition interaction for mean direction. Red bars show left VF distractors. Blue bars show right VF distractors. Error bars represent ± 1 SE.

Discussion

This chapter examined whether motor representations of visual stimuli can be used by the oculomotor system to inform oculomotor action. Three conditions were used: a non-active rehearsal VWM condition, a manual tapping condition, and a spatial manual tapping condition. Four main findings will be discussed: 1. distractor proximity to a target and target VF interactions influenced the deviation of saccades during the manual tapping and the spatial manual tapping conditions, 2. increased accuracy was related to distractor proximity during the spatial manual tapping condition, 3. saccade latencies were found to be differential across conditions, and 4. the mean direction of saccades were found to be different across the three conditions.

Facilitation of oculomotor inhibition by manual responses

Two conditions were designed to test how manual responses interact with the oculomotor system during the generation of saccades: the manual tapping condition and the spatial manual tapping condition. The non-active rehearsal VWM condition acted as a baseline indicating how the brief presentation of a distractor affected the trajectories of saccades without the influence of an additional manual task. In contrast, the manual tapping condition provided data on how basic manual responses influenced saccade characteristics after the brief presentation of a task-irrelevant distractor.

The interaction between distractor proximity to a target and target VF was found to influence the trajectories of saccades during the manual tapping and the spatial manual tapping conditions. In previous chapters of this thesis, saccade trajectory deviations associated with the spatial relationship between a distractors proximity to a target and a targets VF have been theorised to be indicative of neuronal, bottom-up, activation in the saccade oculomotor map. Thus, findings that this spatial relationship influences the trajectories of saccades during the manual tapping and the spatial manual tapping conditions supports a hypothesis of manual responses maintaining saccade programmes across temporal delays.

Further support for manual response maintenance of saccade programmes across temporal delays can be seen in the saccade accuracy results. The accuracy of saccades was not found to be influenced by distractor proximity during the non-active rehearsal VWM condition or the manual tapping condition. However, a trend towards

significance found that saccades made after the presentation of close proximity distractors were more accurate than saccades made after the presentation of far proximity distractors during the spatial manual tapping condition. Increased attention at the locus of a target stimulus has been said to increase the accuracy of saccades to targets (Kowler, Anderson, Doshier & Blaser, 1995). It is therefore possible that during the spatial manual tapping condition, a visual representation of a briefly presented distractor was maintained, and that maintenance of this visual representation influenced saccade accuracy.

An interaction during the spatial manual tapping condition also found that saccades made to upper VF targets were more accurate after the presentation of close proximity distractors in comparison to far proximity distractors. Consistent saccade accuracy was found for saccades directed to the lower VF after the presentation of both close proximity and far proximity distractors. The upper VF advantage for processing visual object information has been documented (Zhou & King, 2002) and short saccade latencies for upper VF targets, in support of this advantage, have again been observed in this experiment. In this chapter, increased accuracy to visual objects in the upper VF appears to be mediated by distractor proximity to a target during the spatial manual tapping condition. It is possible that the task-relevant nature of presented distractor stimuli in the spatial manual tapping task facilitates saccade latencies to upper VF targets. This further evidence of an interaction between distractor proximity to a target and target VF continues to support a conclusion of the maintenance of motor representations in the facilitation of saccades.

Distractor proximity to a target and target VF interactions were also observed during the non-active rehearsal VWM condition and the manual tapping conditions. Previous chapters have also observed interactions between these two variables during the non-active rehearsal VWM condition (chapter 4, 5, & 6). It is likely that a degree of non-active rehearsal VWM occurs across all three conditions. Differences in saccade characteristics between the three conditions may highlight the influence of manual response maintenance of visual representations, and non-active rehearsal VWM maintenance of visual representations, on the characteristics of saccades.

Saccade latency results, and mean direction results, highlight differences across the conditions on the characteristics of saccades. Saccade latency, after the presentation of close proximity distractors, was significantly longer during the spatial manual tapping condition in comparison to the non-active rehearsal VWM, and the manual tapping conditions. Far proximity distractors elicited shorter latency saccades during the non-active rehearsal VWM condition in comparison to the other two conditions. Thus, the impact of manual response interaction with the oculomotor system, after the presentation of task-irrelevant and task-relevant distractors, is demonstrated in the saccade latency results.

McSorley, Haggard and Walker (2005) have suggested that increased saccade latency for close proximity distractors is due to a remote distractor effect mediated by distractor proximity to a target. Thus it is proposed that competitive interaction between saccade programmes coding for distractor spatial locations, and target spatial locations, results in longer saccade latencies for close proximity distractors. Shorter saccade latencies during the non-active rehearsal VWM condition, and the manual

tapping condition, after the presentation of close proximity distractors, in comparison to during the spatial manual tapping condition, suggests an increase in strength for the competitive interaction between the saccade programmes in the spatial manual tapping condition. Thus, it may be that manually maintained visual representations of distractor stimuli enhance interactions observed during non-active rehearsal VWM conditions.

This experiment noted a leftward mean direction of saccades during the manual tapping condition in comparison to the non-active rehearsal VWM condition and the spatial manual tapping condition. Rightward directed saccades have been observed throughout this thesis and it may be that a leftward deviation is consequent of the tapping aspect during the manual tapping condition. The left VF has been associated with dorsal processing (D'Esposito et al., 1998; Köhler et al. 1995) and it is possible that increased activation along this pathway induces saccades to be directed leftward to a greater extent. Increased dorsal pathway activation would also be theorised to occur during the spatial manual tapping condition. However, in this condition there is no evidence of a leftward mean direction. It is likely that by tapping at the spatial location of a given distractor, directional attributes are mediated by the distractor VF as opposed to dorsal pathway activation. This conclusion is supported by findings of increased rightward deviation after the presentation of left VF distractors, during the spatial manual tapping condition, in comparison to right VF distractors. This finding suggests that during the spatial manual tapping condition, saccades deviated away from presented distractors. Saccade deviation away from the spatial location of a distractor has, again, been associated with top-down inhibition (McSorley, Haggard, & Walker, 2006).

SUMMARY

This chapter explored saccade characteristics modulation by the brief presentation of distractors during conditions not requiring the active rehearsal of information stored in VWM. VWM facilitation of oculomotor inhibition has been identified throughout this thesis; however, the usefulness of a VWM specific component in models of saccade trajectory deviations was questioned. The experiment in this chapter was designed to explore whether manually maintained visual representations could also be seen to facilitate the deviations of saccades. Motor-oculomotor interaction suggests that it would be more useful for research to incorporate a system of cognitive processes which facilitate visual processing.

The extent of saccade trajectory deviation was found to be influenced by distractor proximity to a target and target VF suggesting that prolonged inhibition facilitated by the motor representation of distractor stimuli did result in differential saccade trajectory deviations. Moreover, saccades were found to deviate away from distractor stimuli during the spatial manual tapping condition. This result supports the hypothesis that other cognitive systems may result in saccade deviation away from distractor stimuli. In turn the usefulness of a specific VWM component in models of saccade deviations is questionable.

It has been suggested that VWM acts in order to facilitate saccade deviations by maintaining saccade programmes across temporal delays. Results from this chapter suggest that motor representations of distractor stimuli can also maintain saccade

programmes across temporal delays. It is suggested that the oculomotor system interacts with a network of sensory information in order to inform oculomotor action. By incorporating VWM into models of saccade deviation there is a potential to overstate the importance of a singular cognitive system limiting research designs.

The next chapter will conclude this thesis. The main findings of this thesis will be summarised and details of questions these findings have raised will be discussed. The theoretical and clinical implications of this research will be highlighted as well as a proposal of how sensory information may be integrated into the oculomotor system in order to inform oculomotor action.

Chapter 9

Conclusions

This thesis has explored VWM interactions with the oculomotor system. Previous evidence had noted that saccades deviate away from information stored in VWM (Theeuwes and colleagues, 2005, 2006). However, it was also found that the active rehearsal of information was not necessary to produce saccades that deviate away from briefly presented distractors (König, 2010). Researchers have suggested that visual representations maintained in VWM facilitate oculomotor inhibition by preserving saccade programmes (Belopolsky & Theeuwes, 2011). In this way VWM has been found to mediate the deviation of saccades away from distractor stimuli presented briefly in peripheral vision.

This thesis aimed to further explore the way in which, and the extent to which, VWM influences the trajectories of saccades. In the first experimental chapter of this thesis (chapter 4) it was found that VWM is utilised to facilitate prolonged inhibition during conditions not requiring the active rehearsal of visual information. Chapter 5, in turn, explored how saccade deviations differed in conditions requiring active rehearsal of visual information, and in conditions not requiring active rehearsal. Separable influences from the dorsal and ventral pathways were highlighted. Moreover, parallel processing (both top-down and bottom-up) was theorised as being apparent in non-active rehearsal VWM conditions, contrary to primarily top-down influences during the active VWM condition. Dorsal and ventral pathway influences on saccade deviation was investigated in chapter 6. Chapter 7 explored the theoretical and clinical implications of findings of VWM-oculomotor interaction. The final experimental chapter of this thesis (chapter 8) was concerned with whether other cognitive systems could be found to interact with the oculomotor system in order to maintain saccade programmes across temporal delays. It was thought that if such a comparable pattern

was found then models of saccade deviations would not be necessarily benefitted by the addition of a specific VWM component. The main results from this thesis will now be discussed.

Non-active rehearsal VWM influences saccade deviation

The active rehearsal of information has been found to be unnecessary for VWM facilitated prolonged oculomotor inhibition throughout this thesis supporting findings by König (2010). Separable cortical areas have been implicated in the temporary storage (posterior parietal region; Todd & Marois, 2004), and maintenance (prefrontal region; D'Esposito, 2007) of information in VWM. Furthermore, an 'unconscious' pathway has been theorised to exist from the SC to the dorsal pathway (Ro, 2008) and findings from this thesis suggest that it may be this pathway which leads to saccade deviation away from briefly presented task-irrelevant distractors. During non-active VWM conditions, task-irrelevant distractor stimuli are presented and participants are not instructed as to the presence of the presented distractor. However, during these conditions distractor information is stored in VWM (as evidenced in chapter 4) and is utilised to preserve saccade programmes across a temporal delay.

Dorsal and ventral processing pathways

The dorsal and the ventral pathways were found to differentially interact with the oculomotor system throughout this thesis. For example, distractor proximity to a target and target VF interactions were found to mediate saccade trajectory deviations in dorsal pathway related conditions but not in ventral pathway related conditions. This difference in oculomotor interaction for these pathways may stem from the cortical pathways thought to be involved in the deviation of saccades, many of which

are aligned along the dorsal pathway. For example, the DLPFC and the LIP have been associated with the dorsal pathway as well as being implicated in the suppression of task irrelevant saccades (DLPFC; Johnston & Everling, 2006) and visual attention (LIP; Powell & Goldberg, 2000). In turn, that dorsal and ventral associated conditions differentially influence the characteristics of saccades is probable and is supported by the evidence presented in this thesis. It is notable however, that though the ventral pathway was not specifically highlighted in the saccade deviation framework presented by Godijn and Theeuwes (2004), the experiments described in this thesis raise the possibility that the ventral pathway may interact with the oculomotor system. Research may benefit from an extension to this framework so that it incorporates the ventral pathway.

Top-down and bottom-up processing

It has been proposed that bottom-up processes and top-down processes leads to deviation towards and deviation away from a distractor respectively (McSorley, Haggard, & Walker, 2006). In this thesis it was suggested that the dorsal pathway interaction with the oculomotor system may reflect both bottom-up and top-down influences in a parallel form. Distractor proximity to a target and target VF interactions were found to modulate the extent of saccade trajectory deviations during conditions aligned along the dorsal pathway (non-active rehearsal VWM conditions and VSWM conditions). In contrast this effect was not found for conditions aligned along the ventral pathway (the NS-VWM condition). Thus, it was proposed that deviation dependent of distractor proximity to a target and target VF was suggestive of bottom-up influences. However, dorsal pathway associated conditions also found evidence of

deviation away from the location of a presented distractor. This result is indicative of top-down influence.

It is proposed that the dorsal pathway may interact with the SC saccade map via two separate routes: one route responsible for bottom-up SC inhibition and initiated from the SC through to the DLPFC/FEF and other regions associated with visually guided attention, and the other route responsible for top-down induced SC inhibition initiated from the LIP to the SC. This proposed parallel route is consistent with the framework proposed by Godijn and Theeuwes (2004). Ventral pathway interaction with the oculomotor system has been primarily found to be influenced by top-down processes. It is thought that ventral pathway communication with regions associated with visual attention (such as the LIP) could be responsible for ventral pathway-oculomotor interaction.

The conclusions regarding cortical pathways and top-down and bottom-up processing during this thesis are based on behavioural evidence of saccade characteristics. Future neuroimaging research should attempt to establish whether the indirectly implicated cortical regions do indeed mediate saccade trajectory deviations as claimed in this thesis.

Sensory representations influence oculomotor action

In chapter 8, motor representations of distractor stimuli were found to maintain saccade programmes across temporal delays. This in turn facilitated saccade deviation away from briefly presented distractors. It had been proposed that VWM should be incorporated into models of saccade deviations (Theeuwes & Belopolsky, 2009);

however results presented in chapter 8 suggest VWM does not work uniquely to facilitate oculomotor actions. Attentional mechanisms have been found to influence the trajectories of saccades whilst distractors are present on screen at the time of saccade initiation. In turn, that motor representations are able to facilitate saccade deviation suggests that oculomotor inhibition may be facilitated by a variety of sensory systems.

Future research in this topic could further explore how manual responses maintain saccade programmes for the facilitation of oculomotor inhibition. Moreover, there is scope for the understanding of how other sensory systems interact with the oculomotor system. For example, evidence suggests that common coordinates for auditory signals and visual signals are located in the SC. It is possible that auditory sensory information may be investigated in order to inform oculomotor behaviour.

SUMMARY

VWM interactions with the oculomotor system have been explored in this thesis. Saccades have been found to deviate away from briefly presented distractor stimuli in peripheral vision. It is proposed that this deviation is the result of both top-down and bottom-up processing. Moreover, separable effects for tasks thought to be processed by the dorsal and ventral pathways can be observed. Chapter 7 (experiment 6) found that VWM performance levels influence the trajectories of saccades; a result that may lend itself to important clinical implications. If VWM ability is able to influence visual processing and mediate oculomotor actions, clinical populations who have documented VWM deficits may process their visual environments differently to people

in the 'normal' population. Evidence was also presented which suggests that VWM does not act uniquely to facilitate oculomotor inhibition. It was suggested that research may not be helped by the implementation of specific cognitive systems into models of saccade deviation; instead future research should attempt to clarify how a network of cortical pathways interact to facilitate accurate and efficient visual processing.

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