DOCTOR OF PHILOSOPHY

The effect of inter-stimulus competition on visual short-term memory capacity.

Miller, Claire

Award date:
2016

Awarding institution:
Bangor University

The effect of inter-stimulus competition on visual short-term memory capacity.

Claire Elizabeth Miller

Thesis submitted for the degree of Doctor of Philosophy

Bangor University, School of Psychology

Final submission: May 2016

Acknowledgements

I would like to say a huge thank you to my academic supervisor, Kimron Shapiro, for his support, advice and understanding throughout the Ph.D. process. Even when incredibly busy, he always manages to make time to be there for his students, and I am incredibly glad to have had the pleasure of working with him throughout my M.Sc. and Ph.D. studies.

I am extremely grateful to my collaborators. Firstly, many thanks to Steven Luck, who allowed me to visit his lab at UC Davis for 4 months, to learn ERP methodology, conduct experiments, and attend his fantastic ERP Bootcamp. I am grateful to Kia Nobre, for her support and advice with several of the experiments in this thesis, and many thanks to Niklas Ihssen, whose help and advice was invaluable in the early stages of this research.

I would like to thank the individuals who were in the Luck Lab during my time there; in particular Emily Kappenman and Risa Sawaki for their help with learning the necessary skills to conduct good ERP research, and their generous advice which helped to ensure that the EEG lab at Bangor University was set up to a similar specification.

Many thanks to the previous Shapiro/Raymond lab at Bangor University, particularly Paul Thomas, whose enthusiasm and support were appreciated during my transition between Bangor University and the University of Birmingham. I would also like to thank Jane Raymond, and members Visual Experience Lab at Birmingham, who have been generous and welcoming in allowing me to join their lab. Jess Kerlin and Jumana Ahmad's advice and supportiveness have been particularly appreciated.

Last but not least, I would like to thank my close friends and family. Thanks to my parents, for being patient and supportive, and to Alan, whose advice and encouragement has been consistently appreciated throughout my M.Sc. and Ph.D. studies. I would also not be where I am in this process without the motivation and encouragement of Chris and Xiaoxi. Finally, Hannah, Matt and Nathan have been particularly supportive during the final stages of completing this thesis.

Publications and papers submitted

Miller, C. E., Shapiro, K. L., & Luck, S. J. (2015). Electrophysiological measurement of the effect of inter-stimulus competition on early cortical stages of human vision. *NeuroImage, 105*, 229-237.

Miller, C. E., & Shapiro, K. L. (under review). The influence of top-down control over the contents of visual short-term memory. Under review for *Journal of Experimental Psychology: Human Perception and Performance.*

Ihssen, N., Linden, D. E. J., Miller, C. E., & Shapiro, K. L. (2015). Neural mechanisms underlying visual short-term memory gain for temporally distinct objects. *Cerebral Cortex, 25*(8), 2149-2159.Shapiro, K. L. & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

Shapiro, K. L. & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

Ph.D. Summary

A study by Ihssen, Linden and Shapiro (2010) increased visual short-term memory (VSTM) performance by either repeating an 8-item array, or presenting it across two 4-item sequential displays. These increases were suggested to occur due to decreases in overall inter-stimulus competition, enabled in a top-down and bottom-up manner respectively (Ihssen, Linden, Miller & Shapiro, 2015). These studies add to growing evidence that reducing competition in visual cortex may improve VSTM performance (see Shapiro & Miller, 2011).

This thesis sought to further investigate the effects of competition on VSTM, through manipulation of both bottom-up and top-down elements of inter-stimulus competition. Bottom-up competition was manipulated by varying properties of to-be-remembered sequential stimulus displays; more specifically by presenting either a similar number of items in each display or several more items in one display than the other. Reducing overall inter-stimulus competition using this manipulation elicited increased VSTM performance. Further experiments considered the ability of participants to use top-down cues to manipulate VSTM contents. The novel cueing paradigm used in Chapter 5 revealed specific impairments in inhibiting the encoding of new stimuli at short notice, whilst holding items in VSTM. In contrast, VSTM could be easily updated when participants were required to remove old items and encode new ones in their place. The effect of ageing on the top-down and bottom-up aspects of Ihssen et al.'s findings was also investigated, to determine whether the multiple stimulus display presentation may help to compensate for VSTM decreases seen in older adults (e.g., Jost, Bryck, Vogel & Mayr, 2011).

In addition, the ERP experiments reported in Chapter 3 manipulated low-level competition by varying inter-stimulus proximity. Significantly, evidence of competition was found in the initial feedforward V1 response, using a novel method developed to assess competition throughout visual cortex by measuring early visual ERP components. This method has future potential for assessing competition present in visual cortex, and the contribution of feedforward and feedback processes at different time points to perceptual and cognitive processes.

Contents

List of Figures

List of Tables

1 Introduction

1.1 What is visual short-term memory? A brief history of theories of memory

Short-term memory is of extreme importance for successfully navigating the world and performing many everyday tasks. In particular, visual short-term memory (VSTM), the holding in mind of visual information for use in current tasks (Luck & Vogel, 2013), has been a widely researched area in recent years (see Brady, Konkle & Alvarez, 2011, for a review). Despite this, aspects such as the nature of its limited capacity and how objects are represented are yet to be fully understood. This chapter reviews previous research into VSTM, outlining different approaches to its subdivision and conceptualisation, and its interaction with other memory components. It also provides an overview of recent research into VSTM, reviewing evidence supporting the complex network of brain areas and mechanisms suggested to underlie it. One such mechanism which will be discussed in detail is inter-stimulus competition, which we suggest to influence the limited capacity of VSTM (Shapiro & Miller, 2011).

1.1.1 Early models of memory: compartmentalising memory systems

1.1.1.1 Visual and verbal working memory

An influential model by Baddeley and Hitch (1974) conceptualised working memory (WM) as comprising a visual component (visuospatial sketchpad), a verbal/auditory component (phonological loop) and a central executive (akin to attention) controlling encoding and retrieval of information into WM. Their model suggests that participants can perform well on two tasks if one is visual and one verbal, but performance on two simultaneous tasks relying on the same system is significantly impaired (Cocchini, Logie, Della Sala, MacPherson & Baddeley, 2002).

However, it is clear that visual memory and auditory memory are closely related, with many tasks involving the use of both of these systems. For example, when participants are asked to recall words that sound similar phonologically, they perform better when the words are visually dissimilar than when similar (Logie, Della Sala, Wynn & Baddeley, 2000). In light of such evidence, Baddeley's three-component model was adapted to include an episodic buffer, in which binding of visual and auditory information could occur, as well as connections with episodic LTM.

Nevertheless, VSTM and verbal STM differ in some characteristics, such as their capacity. Early estimates of STM capacity suggested 7 +/- 2 'chunks' of information could be stored. This was later found to be an overestimate, with Cowan (2001) suggesting that a limit of 7 items may only be achievable when items can be grouped or rehearsed, but that VSTM is limited to approximately 4 items. Furthermore, the capacity of verbal STM appears to be linked to the amount of time it takes to rehearse the verbal information, with decreases in capacity for words as time to articulate each word increases (Schweickert & Boruff, 1986).

1.1.1.2 Sensory, long-term and short-term memory

Another model, proposed by Atkinson and Shiffrin (1968; Shiffrin & Atkinson, 1969), divided memory broadly into sensory memory (e.g., iconic memory; Sperling, 1960), short-term memory (STM) and long-term memory (LTM). According to this model, items can be copied between the memory stores in a hierarchical manner; items present in sensory memory have a chance of being copied into STM, and those in STM have a chance of LTM storage. The model assumes that LTM stores items relatively permanently, and these may be transferred into STM as required, to be used in ongoing tasks. Items represented only in STM were proposed to have a lifespan of less than 30 seconds, if not rehearsed. In support of these ideas, STM impairments can lead to difficulties in storing items in LTM, for example during language learning (Baddeley, Gathercole & Papagno, 1998), and further research suggests amnesic patients with LTM deficits can have preserved STM (Baddeley & Warrington, 1970). However, a case study by Shallice and Warrington (1970) describes an individual with impaired verbal STM capacity but preserved LTM storage, suggesting that information may not always pass through STM before storage in LTM.

STM and LTM are also supported by different underlying neural mechanisms. STM is typically thought to involve fluctuations in neural firing rates (e.g., Fuster & Alexander, 1971), and LTM to involve changes in neural connectivity elicited by mechanisms such as long-term potentiation and long-term depression (Rolls & Deco, 2002). However, there is some interaction between memory stores. A model proposed by Phaf and Wolters (1997), suggests WM to involve feedback loops between LTM and perception, highlighting the interplay between the STM and LTM stores. They suggest a critical role of the pre-frontal cortex (PFC) in allowing the loop to feed back into the network. Similarly, Jensen and Lisman (1996) emphasise the importance of LTM in

supporting familiar items in STM, and allowing error correction as items degrade. Knowledge stored in LTM is also implicated in enabling practised individuals to build up larger 'chunks' of meaningful information, thereby aiding STM in learned tasks (Ericsson & Kintsch, 1995). Although the primary focus of this thesis in VSTM, it is important to remember that these interactions make it difficult to view the separate memory stores in isolation. Indeed, the inclusion of the 'episodic buffer' in the recent incarnation of Baddeley's three-component model of WM emphasises the importance of LTM (Baddeley, 2010).

1.1.2 Components of visual memory

1.1.2.1 Iconic memory

The term 'iconic memory' was coined by Sperling (1960), who suggested the existence of a visual sensory memory store, characterised by its high capacity and quick decay following stimulus offset. Early research suggested iconic memory to be due to retinal after-effects (e.g., Sakitt, 1976; Long & Sakitt, 1980). More recent studies suggest additional involvement of V1 and perhaps even later visual areas, such as temporal cortex (Keysers, Xiao, Földiák & Perrett, 2005).

In one of his experiments, Sperling (1960) presented participants with 6 letters, in 2 lines of 3. When asked to recall all letters, they could only recall a small proportion; however, if they were asked to recall only one line, indicated by an auditory cue within .25 seconds of item offset, performance was significantly better. This suggests that all 6 letters were available briefly (iconic memory), allowing participants to choose a limited selection to encode into the more durable visual short-term memory (VSTM). These findings were corroborated by a similar experiment using visual cues (Averbach & Coriel, 1961).

More recent research quantifies iconic memory capacity for complex stimuli as 6.1 items (Sligte, Vandenbroucke, Scholte & Lamme, 2010), which is significantly higher than traditional VSTM capacity, although iconic capacity for simple stimuli may be virtually unlimited (Sligte, Scholte & Lamme, 2008). Sligte et al. (2010) also suggest that a greater proportion of items represented in iconic memory are of high resolution compared with items represented in traditional VSTM.

1.1.2.2 Visual short-term memory

Traditional VSTM, the main system under investigation in this thesis, is typically thought to hold a small number of items (approx. 3-4; Luck & Vogel, 1997) for a short amount of time (approx. 4 seconds; Sligte, Scholte & Lamme, 2008). VSTM was first referred to as 'short-term visual memory' (e.g., Phillips, 1974), and is often used interchangeably with the closely related term 'visual working memory' (see Luck, 2008). For simplicity, the term VSTM will be used throughout this thesis.

VSTM performance is often measured using the change detection paradigm (Phillips, 1974; Luck & Vogel, 1997), in which participants are shown a "memory" display of items followed by a blank "retention" or "delay" interval, before the ("test") display of items reappears, either identical or with 1 item changed. Participants' task is to indicate whether the test display is the same or different. Sometimes the test display contains a single probe item, and participants should indicate whether this item was present in or absent from the memory display.

1.1.2.3 Fragile memory: a new form of memory?

Using a modified change detection task, recent studies have revealed an increase in VSTM performance by 'retro-cueing' (cueing after stimulus offset) to indicate which item will be tested (Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003; Sligte, Scholte & Lamme, 2008; 2009). This so-called 'fragile VSTM' appears to be cleared on presentation of new visual information, such as additional stimuli or test displays (Sligte, Scholte & Lamme, 2008).

Although still controversial (e.g., Matsukura & Hollingworth, 2011; Makovski, 2012), fragile memory has been argued to be a visual memory component distinct from both iconic memory and VSTM (Sligte, Scholte & Lamme, 2008; Sligte, Vandenbroucke, Scholte & Lamme, 2010). Whereas iconic memory can be overwritten using a light mask, suggesting some dependence on retinal after-effects, fragile memory survives this form of masking, but is overwritten by a pattern mask (Sligte, Scholte & Lamme, 2008).
The increased performance for items stored in fragile VSTM compared with traditional VSTM is suggested to be due to the focussing of attention onto one item increasing the durability of the memory trace (Makovski, Sussman & Jiang, 2008); however, a significant benefit has not been found by retro-cuing multiple stimuli simultaneously (Makovski & Jiang, 2007).

1.1.2.4 Temporal visual memory

Although not typically considered alongside traditional spatial aspects of memory, there is increasing evidence for a mechanism by which memory for temporal stimulus order is stored. Temporal limitations of the attentional system have been widely researched, particularly the attentional blink (AB; Raymond, Shapiro & Arnell, 1992), which refers to a brief inability to detect a second target, when it appears approximately 100-400 ms after a first target. This finding implies that the visual system places particular importance on the order of stimuli, which is logical given the clear importance of attention to and memory for the order in which stimuli occur in everyday life.

Bowman and Wyble's (2007) Simultaneous Type Serial Token (STST) model computationally explains how we attend to events through time, and how they may be formed into VSTM representations. The main premise of the model is that the brain contains a 'type' for each kind of item which could be presented, which when activated (stage 1) are bound to a token (stage 2, 'tokenization'), which represents a specific episodic instance of the stimulus being presented. The tokens are smaller and more durable than the types, and allow items to be held in VSTM without continuous activation of the stage 1 ('type') architecture. This frees up the first stage of the process to represent further types, in upcoming temporal 'episodes'. Only one item is typically tokenised at a time (at a given spatial location). Bowman and Wyble suggest that the AB (Raymond, Shapiro & Arnell, 1992) is a mechanism for preventing upcoming items from becoming too active, and potentially affecting the encoding of an item which has been attended and should be remembered.

The first stage of the STST model works in parallel, with items processed simultaneously (perhaps representing iconic memory). At this stage items are extremely vulnerable to decay and or overwriting, and may be activated to different levels if imbued with either top-down or bottom-up salience. The second stage can be thought of as the encoding of stimuli into VSTM. Events occurring at a particular time point are represented as episodes, but with a consolidation bottleneck: items presented very slightly before or after each other may be represented by the same or token. Although often not considered alongside models of working memory it is clear that the STST model describes a temporal aspect of attention and working memory which deserves consideration.

1.1.3 VSTM: Just another term for attention?

There has long been an association between attention and VSTM. The two systems are closely related; attention is required to filter out irrelevant information and allow relevant material to be stored in memory. Inattentional blindness and inattentional amnesia studies emphasise how items which are not sufficiently attended cannot be stored in VSTM (e.g., Neisser & Becklen, 1975; Simons & Chabris, 1999; Moore, 2001). It is therefore unsurprising that attention and VSTM performance tend to be at least interrelated (e.g., Pessoa, Gutierrez, Bandettini & Ungerleider, 2002), but perhaps even interchangeable terms (Rensink, 2002). Additionally, the contents of VSTM can guide attention (Downing, 2000), often in an automatic fashion (Oliver, Maijer & Teeuwes, 2006). This is especially clear in the biased competition model (Desimone & Duncan, 1995), in which an item in visual memory biases attention on the onset of a visual display.

Attention and VSTM have similar characteristics, such as their limited capacity (Cavanagh & Alvarez, 2005). For example, multiple object tracking studies suggest that we can attend approximately four items at once (Pylyshyn & Storm, 1988), consistent with proposed VSTM capacity limits (Luck & Vogel, 1997). There is also a great deal of overlap between the brain areas implicated in VSTM and those involved in attention. Ultimately, this evidence has led several researchers to posit that attention and VSTM may actually be two terms for the same construct (e.g., Rensink, 2002; Oliver, Maijer & Teeuwes, 2006; Chun, 2011; Shimi, Woolrich, Mantini & Astle, 2015).

1.2 Brain areas underlying VSTM

There is still much to be understood about the neural mechanisms underlying VSTM encoding and maintenance, but it is clear that a complex network of brain areas are involved, including prefrontal cortex (PFC; Fuster & Alexander, 1971), fronto-parietal areas (Pessoa, Gutierrez, Bandettini & Ungerleider, 2002) and posterior parietal areas (Todd & Marois, 2004; Sauseng et al., 2009). However, due to the similarities previously described, it is difficult to ascertain whether there are differences in brain areas engaged during VSTM and attentional processes, and if so to pull apart their neural contributions.

1.2.1 Prefrontal Cortex

Historically, the importance of frontal areas in VSTM has been established using a number of techniques, including patient studies observing that individuals with frontal lobe dysfunction also exhibit disrupted VSTM (Baddeley, 1986; 1992). Evidence for increased

PFC activation during retention of items in VSTM comes from primate single unit recording studies (e.g., Fuster & Alexander, 1971). In addition, Hasegawa et al. (1998) provide evidence of PFC aiding inferior temporal cells in successful visual memory retrieval in monkeys with severed corpora callosa, and lesions in bilateral PFC of monkeys have been shown to impair working memory performance (e.g., Jacobsen, 1935). However, problems with lesion studies include potential degeneration of inter-connected areas and the development of compensatory strategies by the animal. Lesion studies can also not be run in fully controlled within-subjects counterbalanced designs, since an animal with a lesion cannot be run in a control condition afterwards (Bauer & Fuster, 1976).

Cortical cooling is an alternative technique used to temporarily deactivate an area of cortex, by extracting heat from the area. Both bilateral and unilateral cooling to the monkey dorsolateral prefrontal cortex (DLPFC) has been shown to influence tasks requiring both spatial and non-spatial VSTM (Fuster & Alexander, 1970; Bauer & Fuster, 1976), with cooling to PFC but not parietal areas leading to faster decay of information than a non-cooling control condition. These findings emphasise the importance of the DLPFC in visual memory retention, and further suggest that either hemisphere can perform this function independently. There is also more recent evidence of a positive correlation between individual subjects' VSTM capacity and activation in prefrontal areas during the delay interval, in addition to an inverse relationship between capacity and frontal eye field activation (Linden et al., 2003). However, on retrieval of memorized stimuli Linden et al. observed an inverse correlation between left DLPFC and VSTM performance.

Despite the overwhelming evidence for the influence of frontal areas on VSTM, their precise role is still debated. More recent research by Curtis and D'Esposito (2003) suggest DLPFC to aid during working memory maintenance, by allowing attention to be directed to internal stimulus representations in posterior areas. Petrides (2000) reviews evidence suggesting that mid-DLPFC reflects executive control needed to monitor stimuli in VSTM. Vogel, McCollough and Machizawa (2005) implicate PFC in contralateral delay activity (CDA), an ERP component thought to index how efficient an individual is at excluding irrelevant items from visual memory. In contrast, Phaf and Wolters (1997) suggest that feedback from LTM to perceptual processes enabled by PFC underlies working memory. Evidence from a visuospatial working memory task (Edin, Klingberg, Johansson, McNab, Tegnér & Compte, 2009) suggests DLPFC 'boosts' parietal storage capacity.

Support for Edin et al.'s suggestion comes from studies which will be described and elaborated on in this thesis (Ihssen, Linden, Miller & Shapiro, 2015; see also Ihssen, Linden & Shapiro, 2010) which found VSTM performance to be increased by either presenting an 8-item array twice (repetition), or presenting the 8 items in two 4-item displays (sequential). The increase observed in the repetition condition was associated with increased BOLD response in DLPFC, which the authors suggest reflects an attentional shift aided by PFC, allowing participants to focus first on one part of the display and then the other. The sequentially presented displays did this intrinsically, requiring less top-down control.

1.2.2 Parietal Cortex

Parietal cortex activation is correlated with VSTM performance, with higher activity observed in fronto-parietal areas during the delay interval of a VSTM task for correct-response trials, than for those responded incorrectly (Pessoa, Gutierrez, Banadettini & Ungerleider, 2002). Posterior parietal cortex, and in particular intra-parietal sulcus (IPS) has been suggested to reflect VSTM capacity (Todd & Marois, 2004). Specifically, Xu and Chun (2009) suggest that inferior and superior IPS work together, with inferior IPS representing items in low resolution, and superior IPS encoding a subset of these into VSTM in increased resolution, with support from higher visual areas. Gamma and theta cycles in posterior parietal areas have also been implicated in VSTM, with Sauseng et al. (2009) suggesting these oscillations to influence VSTM capacity (see 1.3.2 for further description).

1.2.3 Temporal Cortex

Inferior temporal cortex (ITC) delay activity is thought to be important in VSTM, in addition to reflecting top-down attentional modulations, for example in visual search (Chelazzi, Duncan, Miller & Desimone, 1998). The delay activity elicited by these two tasks may reflect one underlying construct, as supported by the previously described research into the attention/VSTM crossover. Miller, Li and Desimone (1991) further suggest ITC to function as a detector of novel stimuli, allowing them to be processed and remembered preferentially. Evidence of medial temporal lobe involvement in VSTM includes Olson, Moore, Stark and Chatterjee (2006), who suggest patients with medial temporal lobe damage to have lower visual working memory performance than age-matched controls.

1.2.4 Occipital Cortex

There is also evidence of occipital involvement in VSTM, and especially in its capacity. For example, Vogel and Machizawa's (2004) study into an electrophysiological correlate of VSTM capacity known as contralateral delay activity (CDA; see section 1.3.1 for further description) detected its presence above lateral occipital cortices, as well as posterior parietal areas. Other research has suggested lateral occipital areas work in conjunction with superior IPS, to maintain a number of visual objects determined by their complexity (Xu & Chun, 2006). Xu and Chun's fMRI study found dorsal occipital cortex was among areas activated more strongly during correctly than incorrectly responded trials during stimulus encoding

In another fMRI experiment, Courtney, Ungerleider, Keil and Haxby (1997) examined event-related BOLD response during a VSTM task, in order to determine which areas were related to the perception and to the memory of stimuli. Although, as would be expected, occipital activation was highly correlated with perception, and prefrontal activation to memory, this was not exclusively the case. Courtney et al. suggest that occipitotemporal areas can be used to support maintenance of items in VSTM, if these areas are not currently in use for perception of new stimuli. Smith and Jonides (1998) also found evidence that a visuospatial working memory task involved occipital areas, predominantly in the right hemisphere, in addition to posterior parietal cortex and frontal areas. The previously described evidence supports the logical notion that visual perceptual processes occurring in occipital areas should play a significant role in visual memory. Links between occipital cortex and VSTM capacity found in previous studies provide some basis for many of the ideas which will be described in this thesis, regarding the importance of striate and extrastriate cortex on VSTM.

1.3 Characterizing VSTM and its capacity limitations

1.3.1 Slots Models and Resource Models

How best to characterise VSTM and the source of its limitations is currently an intensely debated issue. VSTM capacity is often characterised as a limited number of 'slots' which can each be filled with a whole object (e.g. Luck & Vogel, 1997), implying a fixed capacity limit equivalent to the number of slots an individual has. In contrast, others propose a limited amount of unspecified 'resource' which can be flexibly distributed between to-be-remembered stimuli (Bays & Husain, 2008), and still others suggest a

system on the continuum between these extremes such as a 'slots and averaging' model (Zhang & Luck, 2008).

There are good grounds for thinking that the slots model is realistic. Substantial evidence for an object-based element of attention suggests that items are often processed as wholes. One feature of each of two objects has been shown more difficult to attend than two features of the same object (Duncan, 1984; Baylis & Driver, 1993), and a target located on the opposite end of a cued rectangle is more quickly detected than a target located the same distance from the cue, but in a separate object (Egly, Driver & Rafal, 1994). These studies suggest that information about a whole object is readily accessible when only part of the object is attended. Indeed, Marshall and Bays (2013) found evidence for automatic encoding of irrelevant features within an attended item.

In a seminal paper, Luck and Vogel (1997) conducted a series of behavioural experiments indicating that VSTM capacity was limited to four objects. Participants performed well on a change detection task involving 1-3 objects, but performance declined rapidly when 4-12 items were presented. Each object could consist of up to four 'features' including, in the case of colour, multiple instances of the same feature (but see also Wheeler & Treisman, 2002). This suggests that information is stored in VSTM in chunks, in a similar way to verbal WM (e.g., Miller, 1956).

Further support for the notion that storage of items in VSTM is limited by a capacity rather than resource bottleneck comes from Zhang and Luck (2008), who found memory representations became less precise as set size increased between 1 and 3 items, and then remained constant when increased above this level. They suggested a 'slots and averaging' model, whereby individuals have 3 units of resource. They can either allocate these to separate stimuli or use multiple units together to increase the representation of one stimulus. The authors further suggest that items are lost from memory via 'sudden death', rather than by gradual decay of representations (Zhang & Luck, 2009).

In addition, Murray, Nobre, Clark, Cravo and Stokes (2013) found that directing attention to an item in VSTM during the retention interval improved its recognition, but not the precision by which it was represented in VSTM. This suggests that items are represented discretely, rather than with varying precision dependent upon resources.
Xu and Chun (2006) suggest that inferior and superior IPS and lateral occipital complex work together, to encode and maintain items in VSTM. They found inferior IPS to increase in activation until 4 objects were presented, regardless of complexity, whereas fewer objects could be represented in superior IPS and lateral occipital complex. They suggested

that inferior IPS allows attention to be directed to 4 objects, and superior IPS and lateral occipital complex allow some of these attended items to be encoded and maintained in VSTM.

However, there is individual variation in capacity. Vogel and Machizawa (2004) measured ERPs while participants performed a simple change detection task, and found evidence for an electrophysiological correlate of VSTM capacity, known as contralateral delay activity (CDA) and also referred to as sustained posterior contralateral negativity (SPCN; Dell'Acqua, Sessa, Jolicoeur & Robitaille, 2006). This activity increased alongside the number of stimuli participants had to remember, reaching a maximum at 3-4 items. Further analysis of individuals' data suggests that a participant's CDA increases until set size matches their capacity. Participants also had significantly smaller CDA on incorrect trials than on correct trials. These findings demonstrate a direct relationship between electrophysiological activity and visual memory capacity.

Other researchers suggest that rather than a fixed capacity limit of several items, an individual's memory is restricted by a limited pool of resources, which can be distributed flexibly among items (e.g., Bays & Husain, 2008). Bays and Husain's task found a large increase in precision between 1 and 2 to-be-remembered items, and evidence of increased resource allocation to items which attract attention or are the targets of eye movements. They suggested that previous studies have seen little precision increase prior to 3 stimuli due to easy item discriminations, and that Zhang and Luck's (2008) lack of control over eye movements may explain their contrasting findings. Bays and Husain's findings are supported by results from Huang (2010), who tested participants on all 6 items held in memory on each trial, and found results consistent with a simulated 'resource' model.

A more recent study by van den Berg, Sin, Chou, George and Ma (2012) suggests that resources are allocated to stimuli in variable amounts, leading to fluctuating precision across the contents of VSTM. The variations in precision between items accounts for occasional random guessing, which would not be expected in a model in which resources were split evenly between all items. Further, there is evidence that this capacity/precision trade-off is not under top-down control (Zhang & Luck, 2011; Murray, Nobre, Astle & Stokes, 2012).

Although models on the 'slots' to 'resources' continuum are useful for developing testable hypotheses, thereby furthering our knowledge of VSTM, it has been pointed out that it may not be appropriate to place too much emphasis on the specifics of the models,

as it detracts from more useful questions (Suchow, Fougnie, Brady & Alvarez, 2014). Nevertheless, the nature of VSTM in terms of the slots/resources debate is still unclear.

1.3.2 A role of oscillations in VSTM capacity?

Oscillations may play a direct role in storing items in VSTM, potentially as a mechanism underlying the abstract idea of 'slots'. An early theory of oscillations by Lisman and Idiart (1995) suggests that up to seven high frequency oscillations representing items in STM may be nested into a low frequency oscillation. They propose a mechanism by which, due to changing membrane excitability with after-depolarisation states following neuronal firing, items are able to be stored between low frequency oscillations, with each item represented by a simultaneously-firing group of neurons. Due to the slow rise of after-depolarisation states, the earliest firing cells should have the highest levels of excitation. This would lead the earliest firing cells in a particular low frequency oscillation to also be most excitable at the beginning of the next low frequency oscillation.

This theory, and the idea that alpha oscillations enable suppression of irrelevant stimuli, is supported by evidence from Sauseng et al. (2009). In accord with Lisman and Idiart (1995), Sauseng et al. posit that individual items in VSTM are represented in posterior parietal areas as gamma cycles (of frequency greater than 50Hz), nested within theta waves (approx. 5Hz). Sauseng et al. further suggest contralateral theta-locked gamma phase synchronisation to increase as memory capacity increases, with a significant positive correlation between each individual's memory capacity and the difference in their lateralised theta-locked gamma phase synchronisation between loads 4 and 2. They provide evidence that lateralised theta-locked gamma phase synchronisation is associated only with retention of relevant items, irrespective of irrelevant information. Gamma phase relative to theta was also suggested to influence the chance of a stimulus being remembered. Taken together with evidence that alpha oscillations may underlie suppression of irrelevant stimuli (to be discussed shortly), these findings suggest that oscillations play a significant role in VSTM capacity.

1.3.3 Impaired Suppression underlying VSTM capacity limits?

It has been suggested that ability to suppress irrelevant information is central to limitations in VSTM performance. Vogel, McCollough and Machizawa (2005) found participants with a low VSTM capacity to have similar CDA amplitude when presented with 2 to-be-remembered stimuli and 2 distractors as when presented with 4 items which

should all be remembered. In contrast, high capacity participants exhibited similar CDA to 2 relevant and 2 irrelevant stimuli as they did to 2 relevant stimuli alone. This suggests that individuals thought of as having a low capacity have difficulty ignoring irrelevant stimuli, and may therefore have even been holding more in VSTM than their "high capacity" counterparts. However, this difficulty appeared not solely due to a general executive deficit, as these participants could successfully perform other functions requiring executive control, such as appending new stimuli into VSTM without displacing the existing items. The importance of efficient ignoring of irrelevant information was emphasised by Zanto and Gazzaley (2009) who found increased suppression of irrelevant stimulus features to be associated with optimal VSTM performance.

It has also been suggested that impaired suppression of irrelevant information early in visual processing may underlie VSTM capacity declines during the ageing process (Gazzaley, Cooney, Rissman & D'Esposito, 2008). Declines in VSTM performance are well established, with research suggesting younger adults (19-38 years old) to have an average capacity of 2.99 items, and older adults (64-92 years old) only 2.05 items (Jost, Bryck, Vogel & Mayr, 2011). However, in comparing CDA between participants, Jost et al. found that older adults' VSTM was not like that of low capacity younger adults. Rather, older adults appeared impaired in the filtering of irrelevant information early during the retention interval. Later in the interval strong between-subjects differences were found, reflecting differences in capacity between individuals.

Alpha oscillations have been proposed as a mechanism by which irrelevant stimuli may be suppressed (Kimesch, Doppelmayr, Schwaiger, Auinger & Winkler, 1999; Sauseng et al., 2009). In addition to retention of relevant information, Sauseng et al. also revealed oscillatory correlates of suppression of irrelevant information. These two mechanisms were dissociated, with the authors suggesting that lateralised theta-locked gamma phase synchronisation is associated only with retention of relevant items, irrespective of irrelevant information, and ipsilateral alpha activity is strongly associated with suppression of irrelevant items but only minimally associated with retention of relevant stimuli. Additionally, rTMS administered at alpha frequency (10Hz) ipsilaterally to to-be-remembered stimuli was found to improve VSTM capacity, indicating an element of causation. In contrast, alpha rTMS administered contralaterally worsened VSTM capacity. In addition, alpha amplitude was found to significantly increase as memory load increased. A significant positive correlation found between ipsilateral-minus-contralateral alpha activity and capacity suggests that suppression of irrelevant stimuli does play a role

in visual memory capacity. More recently, there is evidence that certain phases of these alpha oscillations allow optimal suppression of distractors, and alpha phase has been shown to be modifiable, in response to predictable irrelevant stimuli (Bonnefond & Jensen, 2012).

1.4 Inter-stimulus competition

Item representations can compete in visual cortex in a bottom-up (stimulus-driven) or top-down (goal-driven) manner. The following section will discuss several related mechanisms by which items compete, including biased competition (Desimone & Duncan, 1995), lateral inhibition (Hartline, Wagner & Ratliff, 1956; Alpern & David, 1959), surround suppression (Hubel & Wiesel, 1968) and visual crowding.

1.4.1 Lateral inhibition and surround suppression

Lateral inhibition (e.g., Hartline, Wagner & Ratliff, 1956; Alpern & David, 1959) involves the suppression of individual neurons by other neurons. In the visual system, this sharpens visual signals, aiding perception of contrast and contours. Lateral inhibition is involved in such phenomena as orientation perception (Carpenter & Blakemore, 1973), with differing orientations in close proximity summating to lead to incorrect perception, as seen in many optical illusions.

There is evidence that lateral inhibition in both inner and outer retina enables surround inhibition (Werblin, 1974; Cook & McReynolds, 1998). The organisation of horizontal cells sharpens spatial tuning by modulating the size of bipolar cell central receptive fields which are responsive to stimuli, and leading the surrounding receptive field area to become inhibitory. If similar stimuli fall upon an inhibitory surround as those in the central receptive field, the cell's firing rate is suppressed, allowing synaptic gain in the visual system to be controlled. Other mechanisms suggested to underlie surround suppression include extrastriate 'pooling' of responses from multiple V1 neurons, and LGN suppression (see Smith, 2006, for a review). Surround suppression has been observed in V1 (Hubel & Wiesel, 1968); For example, Knierem and Van Essen (1992) found textured surrounds to suppress firing to an oriented line within a V1 classical receptive field by an average of 34%. Through surround suppression, stimuli which are very different from the background can be processed preferentially, which may underlie 'pop out' effects (Kastner, Nothdurft & Pigarev, 1997), and facilitate the resolution of competition between stimulus representations.

1.4.2 Crowding

Another mechanism through which items compete is crowding (e.g., Loomis, 1978), a term usually use to describe difficulties in target discrimination and identification. There is some debate over the mechanism underlying crowding, and whether it is low-level (e.g., lateral inhibition) or high level (e.g., attentional). There is also controversy over the term used to refer to this phenomenon; the term 'lateral masking' is often used the vision science community, where more emphasis has been placed on low-level factors (e.g., Pelli, Palomares & Majaj, 2004). Crowding is suggested to be partly due to increased receptive field sizes in peripheral vision, rendering stimuli in the periphery less easily distinguishable than those projected closer to the fovea (Loomis, 1987). Early studies found flankers to reduce the ability of participants to make judgements about stimuli presented in peripheral vision, with less interaction observed as the stimuli were presented at greater spatial separation (Flom, Weymouth & Kahneman, 1963). But this is not the whole story; the extent of crowding appears asymmetrical depending on where and how stimuli are presented. For example, crowding is stronger when stimuli are presented horizontally than vertically (Feng, Jiang & He, 2007) and stimuli interact more strongly when presented radially relatively to fixation than tangentially (Toet & Levi, 1992). A two-stage model proposed by Levi (2008) suggests an influence of both low-level feature detection in V1, and integration of features in later visual areas. However, crowding is thought to be distinct from surround inhibition (Petrov, Popple & McKee, 2007), and Tripathy and Cavanagh's (2002) findings that peripheral crowding does not scale with target size suggest the involvement of attentional receptive fields, rather than lateral inhibition in early vision.

1.4.3 Competition within visual receptive fields

Visual receptive fields (RFs) are areas of neurons in visual cortex responding to specific properties of stimuli (e.g., Hartline, 1938; Hubel & Wiesel, 1959; 1962). Recent studies suggest inter-stimulus competition is strongest at the level of the RF, i.e., between stimuli which are represented in the RF of the same neuron (Kastner, De Weerd, Desimone & Ungerleider, 1998; Kastner, De Weerd, Pinsk, Elizondo, Desimone & Ungerleider, 2001; Reynolds, Chelazzi & Desimone, 1999). FMRI studies in humans (e.g., Smith, Singh, Williams & Greenlee, 2001) suggest RFs to be smallest in primary visual cortex (V1), getting progressively larger through the visual cortex, towards area V4 and temporal

areas. They also increase in size as they represent more peripheral areas of the visual field. These findings are consistent with findings from many early studies into properties of RFs in macaque and cat cortices (e.g., Hubel & Wiesel, 1962).

In addition to feedforward activation through visual cortex (through the 'ventral stream'; i.e., from V1 to V4/ITC), there are also numerous feedback connections (Felleman & Van Essen, 1991), which allow activation in earlier areas with smaller RFs to be modulated by that in later areas, which have access to a more global representation of the visual field. An EEG study by Fahrenfort, Scholte and Lamme (2008) examining the time course of visual cortex activation, found posterior activation at around 160 ms post-stimulus, which they suggested to be due to a combination of feedforward and feedback processes. Feedback of competitive interactions from higher back to lower visual areas has important implications as a mechanism for allowing areas representing different properties of stimuli to support each other. For example, this could explain the integrated competition hypothesis, which describes how items eliciting greatest activation in one system, such as the visual system, will also dominate in other systems, such as motor areas (Duncan, Humphreys & Ward, 1997).

In their fMRI study, Kastner, De Weerd, Desimone and Ungerleider (1998) found decreased BOLD response in V1, V2, V4 and inferior temporal area TEO to stimuli presented simultaneously within a peripheral RF relative to sequentially, suggesting competitive interactions between concurrently presented stimuli. The BOLD difference between the simultaneous and sequential conditions increased as RF sizes got larger, consistent with competition between stimuli represented within the same RF in a given visual area. In later visual areas, more stimuli fall within a single large RF, leading to higher levels of suppression relative to earlier areas. However, despite evidence of inter-stimulus competition as early as V1, Kastner et al., were unable to conclude whether this competition occurred in a feedforward manner, or required feedback from extrastriate areas.

Single cell research conducted on non-human primates (e.g., Reynolds, Chelazzi & Desimone, 1999) has also found competition at the level of the visual receptive field. When a pair of unattended stimuli was presented within a single V4 receptive field, they jointly determined cell firing rate, with stimuli poor at eliciting a response inhibiting those with higher firing rate. Unfortunately, it has proven difficult to use this technique in earlier visual areas, such as V1, due to small receptive field sizes (Luck, Chelazzi, Hillyard & Desimone, 1997). There are also potential issues with generalising single cells in primates

to populations of neurons in humans, although non-human primates are thought to share memory system similarities with humans (Reinhart et al., 2012).

1.4.4 Bottom-up biases to relevant stimuli

Interestingly, biases to novel and previously relevant items are thought to involve a bottom-up element. For example, Wang, Cavanagh & Green (1994) found visual search to be improved when an unfamiliar target was surrounded by familiar non-targets (see also Reicher et al., 1976). In Shiffin and Scheider's (1977) study, participants were given a set of items to remember, and another set of distractors (e.g., letters to remember and numbers as distractors) When the two sets were switched, reaction times were increased. This suggests that previously relevant items can bias attention, even when no longer relevant to task demands.

Novelty detection may be linked to a subset of cells in rhinal and medial cortices and ITC (e.g., Riches, Wilson & Brown, 1991). In a single-unit recording study, Li, Miller and Desimone (1993) found that as stimuli became more familiar, firing was reduced in approximately a third of cells in anterior-ventral ITC. However, responses to the cells were also related to specific object features, suggesting that these cells are not simply dedicated to novelty detection, but are also stimulus selective. Previous work has also found suppressed neural responses to stimuli that were recently presented (Miller, Li & Desimone, 1991; Miller & Desimone 1994). For example, Fahy, Riches and Brown (1993) found evidence of neurons more responsive to unfamiliar than familiar stimuli, and also a different subset of neurons coding for the recency with which they had previously been presented. However, factors such as novelty and familiarity may also draw attention in a top-down manner, leading cell firing of competing items to be reduced through a phenomenon known as biased competition.

1.4.5 Biased competition: a top-down influence

Biased competition is a mechanism by which stimuli compete to control the firing of neurons in the visual system. In addition to the previously described strong competition between stimuli within the same RF, a key defining feature of the biased competition theory is its top-down component (Duncan & Humphreys, 1989; Desimone & Duncan, 1995). Specifically, competition is biased by directing attention to a particular stimulus. This biasing occurs through a reduction in the suppression of the attended by unattended stimuli, and an increase in the suppression the attended exerts upon unattended stimuli (see

Figure 1.1). This allows the attended stimulus to 'win' the competition for representation by the neuron.

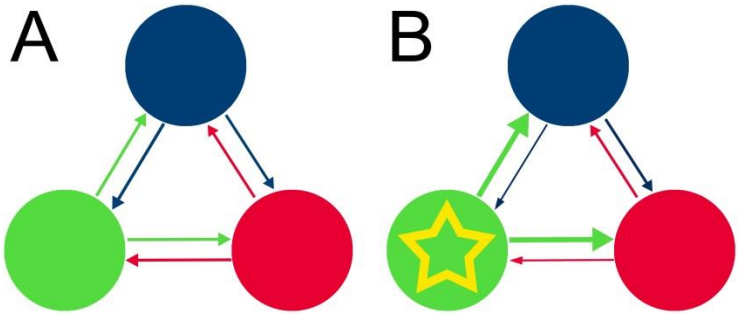


Figure 1.1. Panel A. Arrows representing the competitive interactions between stimuli presented within a visual RF. Panel B. The change in competition when attention is allocated to one stimulus (indicated by the star). The size of the arrows represents the magnitude of the competition.

Duncan and Humphreys found difficulty of a visual search task to increase as non-targets became more similar to targets and less similar to other non-targets. These findings were inconsistent with previous 'feature integration theory' (Treisman & Gelade, 1980), which would predict comparable performance regardless of the similarity of the non-targets. Duncan and Humphrey's results were instead suggested to reflect stimuli with features corresponding to a task-related internal template being weighted more strongly, and similar non-targets being grouped to aid their suppression. Desimone and Duncan (1995) elaborated upon this idea with their model of 'biased competition', in which the previously mentioned template biases attention towards task-relevant items within an array of competing stimuli, through reducing the suppression elicited by the competing stimuli.

Direct evidence for this phenomenon has been found using single-unit recordings in monkey visual cortex. Moran and Desimone (1985) presented one effective and one ineffective stimulus within the same V4/ITC receptive field. They found that the response of the neuron in question approximated the response to just the attended stimulus. Specifically, in the majority of recorded neurons in V4, effective stimuli elicited 50% less firing when they were presented within a RF but not attended, than when they were attended. However, when an effective stimulus was presented inside and the ineffective was outside of the RF, cell firing rate did not change, regardless of which stimulus was attended. A similar but smaller effect was found for neurons in ITC. When both stimuli

were presented within one V1 RF, the monkeys were unable to do the task, but when one was outside and one inside, attention once again had no significant effect upon firing rate.

Kastner, De Weerd, Desimone and Ungerleider (1998) found evidence of biased competition in their human fMRI study. They found that covertly directing attention to one of four items in the peripheral visual field increased the BOLD response elicited by the stimuli. This increase was larger in later visual areas with larger receptive fields, such as V4, and was also larger when stimuli were presented simultaneously than sequentially. Kastner et al. concluded that the increased BOLD was due to reductions in suppressive interactions between stimuli represented within a single RF.

Although placing special emphasis on top-down factors, the theory of biased competition (Desimone & Duncan, 1995) ties together many of the previously described mechanisms of competition, providing a framework within which to view spatial competition in cortical areas. In particular, biased competition centres itself around the following points. First, multiple simultaneously presented stimuli compete for activation of visual cortical neurons, with each item attempting to activate the cell it falls within, and responses ultimately determined by competitive interactions between the stimuli. Second, competition is strongest between items presented within the same receptive field. In addition, competition can be biased towards a particular stimulus using many (previously described) top-down and bottom-up mechanisms, applied in either a location- or feature-based manner. Top-down biasing is primarily driven by prefrontal cortex, which plays an important role in VSTM (as described in Section 1.2.1).

1.5 Towards a Competition Theory of VSTM

Inter-stimulus competition, which has been widely researched with respect to attentional selection, has more recently been suggested to play a significant role in VSTM, and to contribute to its capacity limitations (see Shapiro & Miller, 2011). As previously described, visual stimuli constantly compete for representation in visual cortex, and this competition must be resolved to allow selection of items relevant to current tasks and avoid overstimulation of visual cortex. It is clear that stimuli should compete to be optimally attended, in order that their representation in VSTM is preserved in high resolution.

If previously described bottom-up competitive interactions between stimuli are affecting VSTM performance, one clear prediction is that reducing the competition present between items in a to-be-remembered display should enable better performance on a

VSTM task. Competition may be reduced in a variety of ways. Firstly, one could separate a large display of to-be-remembered items into multiple smaller sequential displays, in a similar way to Kastner, De Weerd, Desimone and Ungerleider (1998), and compare performance to that elicited when all stimuli are presented simultaneously. Alternatively, the space between the to-be-remembered items could be increased (e.g., Kastner, De Weerd, Pinsk, Elizondo, Desimone & Ungerleider, 2001), such that multiple items will not fall within the same receptive fields in the earliest visual areas and thus will begin to compete in later areas of visual cortex with larger RFs.

Biased competition in particular may influence the limited capacity of VSTM by influencing an individual's selection of which stimuli can be encoded, in a top-down manner (Ihssen, Linden & Shapiro, 2010). Additionally, if top-down competition influences VSTM performance, facilitating attention allocation to only part of a display through techniques such as cueing should allow VSTM to be improved. Indeed, this has been shown, in retro-cueing experiments (as described in Section 1.1.2.3). In support of this idea, Murray, Nobre, Clark, Cravo and Stokes (2013) found cueing an item to increase the probability of its recall. Cueing a stimulus enabled significantly higher percentage of correct responses than neutral or no cue conditions. In addition, performance when a stimulus was cued was significantly higher than performance when the probe was presented instead of the cue. This suggests that the cue may actually allow stimuli to transition from an inaccessible to accessible VSTM representation, and further indicates that control over items in VSTM is still possible after the initial encoding of stimuli. The authors suggest that directing attention to a behaviourally relevant stimulus may protect it from inter-item competition. Additionally, this would cause the competing stimuli to be suppressed, potentially contributing to the 'sudden death' of memory items described by Zhang and Luck (2009).

Current evidence suggests that top-down and bottom-up factors work together to influence attention and VSTM capacity. In their VSTM task, Ihssen, Linden and Shapiro (2010) presented encoding displays in three blocked conditions: a condition containing 8-item 'simultaneous' displays, one containing 8-item displays presented twice for the same total duration ('repetition' condition) and a final condition containing two 4-item 'sequential' displays per trial (see Figure 1.2, below). After each encoding display (or pair of displays) participants' memory was tested for four adjacent previously presented stimuli. Performance was better when the stimuli were presented in two sequential displays (minimising the overall amount of competition present across the displays) than when

presented simultaneously, which is consistent with the bottom-up competition account of VSTM. However, participants also showed improved VSTM performance in the repetition condition. It has therefore been hypothesised that the observed benefit may also have a top-down component, with the offset of the 8-item "repetition" display allowing participants to disengage their attention from a subset of items, and re-engage on other stimuli in the display. In the sequential condition, this was enabled automatically through the presentation of the stimuli across two displays with different times of onset.

This presence of a top-down component in this particular task was reinforced in a further study (Ihssen, Linden, Miller & Shapiro, 2015), which used fMRI to investigate the neural correlates of the sequential benefit. The study found increased visual cortical BOLD activity in response to both sequential and repetition conditions in comparison with the simultaneous condition. In addition, the study found frontal networks to be preferentially activated in the repetition condition, suggesting increased top-down control in this condition. Importantly, this demonstrates the varying influence of top-down and bottom-up processes on VSTM, within a single experimental paradigm.

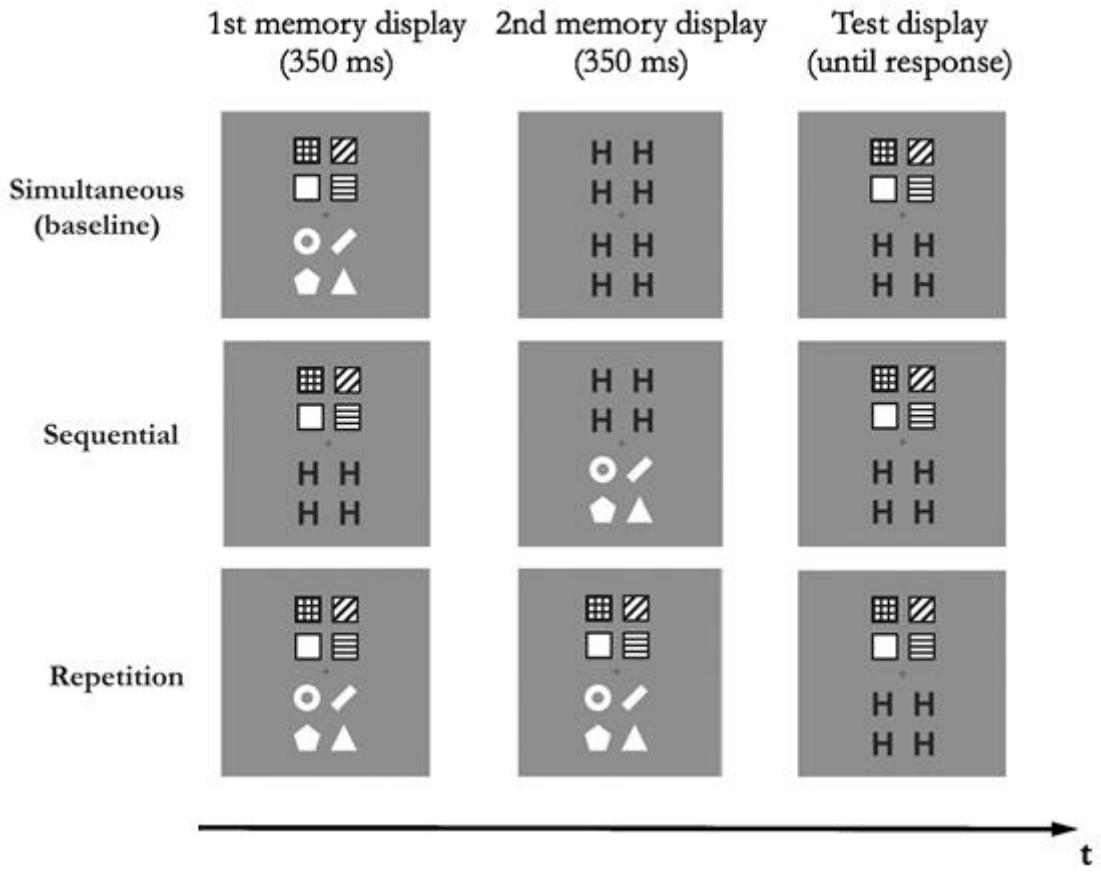


Figure 1.2. The simultaneous (baseline), sequential and repetition conditions used by Ihssen Linden and Shapiro (2010).[1]

Although this idea has only recently regained interest, it was previously suggested that inter-stimulus distance has an effect on VSTM, with more closely spaced items eliciting worse VSTM performance (Eriksen & Rohrbaugh, 1970). Eriksen and Rohrbaugh suggested that this phenomenon may be akin to the interference seen in synchronous pattern masking. Interestingly, in a second experiment, participants seemed unable to exclude distractors in a top-down fashion, when they were dissimilar to the stimuli which they were required to report (i.e. black disks or Xs rather than the target letters A, T, V, and H). However, there is much still to be learned about the way in which stimuli compete, and the effect that this has on VSTM, including at which point during processing inter-stimulus competition exerts its effect. These questions form a key component of this thesis.

[1] Image created by Claire E. Miller, previously published in Shapiro and Miller (2011).

1.6 The Current Studies

The experiments in this thesis sought to further investigate the effects of competition on VSTM. The bottom-up element of competition was manipulated in Chapter 4, through varying the ratio of items between two sequential displays, between presenting similar numbers of items in each display, and presenting several more items in one display than the other. Using this manipulation, we hoped to ascertain whether dividing stimuli across displays in a manner which reduced the overall competition present was also optimal for VSTM performance, thereby lending support to the theory that reducing competition underlies the previously described sequential benefit (Ihssen, Linden & Shapiro, 2010). In the ERP experiments in Chapter 3, bottom-up competition was manipulated by varying the spacing between stimuli, to investigate the effect of low-level visual competition on visual cortex activation, as indexed using early visual ERP components. Through these experiments, we sought to develop a novel method of measuring the competition present in different parts of visual cortex, and the relative contribution of feedforward and feedback processes over time.

In Chapter 5, the ability of participants to use cues to manipulate VSTM contents in a top-down fashion was also investigated. These experiments sought to explore the limits of top-down control, in response to sequentially presented stimuli similar to those used by Ihssen, Linden & Shapiro (2010). Finally, experiments testing older adults (Chapter 6) sought to determine whether presenting stimuli in multiple sequential displays may help to compensate for reduced biased competition thought to be associated with ageing (McCarley, Mounts & Kramer, 2004). We anticipated that the sequential benefit may be even greater in this population, and that older adults may also achieve significantly better performance when presented with sequential than repeated displays, due to frontal control deficits often seen in ageing populations (e.g., West, 1996).

1.7 References

Alpern, M., & David, H. (1959). The additivity of contrast in the human eye. *The Journal of General Physiology*, *43*(1), 109-126.

Atkinson, R.C., & Shiffrin, R.M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence, & J. T. Spence. *The psychology of learning and motivation (Volume 2)*. (pp. 89–195) New York: Academic Press.

Averbach, E., & Coriel, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal, 40*, 309-328.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Neuroscience, 4*(11), 417-423.

Baddeley, A. D., Gathercole, S., & Papagno, C. (1998). The phonological loop as a language learning device. *Psychological Review, 105*(1), 158-173.

Baddeley, A. D., & Hitch, G. J. (1974). Working memory. In G. Bower (Ed.) *Recent Advances in Learning and Motivation, Vol. VIII*. New York: Academic Press.

Baddeley, A. D., & Warrington, E. K. (1970). Amnesia and the distinction between long- and short-term memory. *Journal of Verbal Learning and Verbal Behavior, 9*(2), 176-189.

Baylis, G. C., & Driver, J. (1993). Visual attention and objects: Evidence for hierarchical coding of location. *Journal of Experimental Psychology: Human Perception and Performance, 19*(3), 451-470.

Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science, 321*(5890), 851-854.

Bonnefond, M., & Jenson, O. (2012). Alpha oscillations serve to protect working memory maintenance against anticipated distracters. *Current Biology, 22*(20), 1969-1974.

Bowman, H., & Wyble, B. (2007). The simultaneous type, serial token model of temporal attention and working memory. *Psychological Review, 114*(1), 38-70.

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of Vision, 11*(5), article 4.

Carpenter, R. H. S., & Blakemore, C. (1973). Interactions between orientations in human vision. *Experimental Brain Research, 18*, 287-303.

Cavanagh, P., & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *TRENDS in Cognitive Sciences, 9*(7), 349-354.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory guided visual search. *Journal of Neurophysiology, 80*(6), 2918-2940.

Chun, M. M. (2011). Visual working memory as visual attention sustained internally over time. *Neuropsychologia, 49*(6), 1407-1409.

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

Cook, P. B., & McReynolds, J. S. (1998). Lateral inhibition in the inner retina is important for spatial tuning of ganglion cells. *Nature Neuroscience, 1*(8), 714-719.

Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature, 386*, 608-611.

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

Dell'Acqua, R., Sessa, P., Jolicoeur, P. & Robitaille, N. (2006). Spatial attention freezes during the attention blink. *Psychophysiology, 43*, 394-400.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193-222.

Downing, P. E. (2000). Interactions between visual working memory and selective attention. *Psychological Science, 11*(6), 467- 473.

Duncan, J. (1984). Selective attention and the organization of visual information. *Journal of Experimental Psychology: General, 113*(4), 501-517.

Duncan, J., & Humphreys, G. (1989). Visual search and stimulus similarity. *Psychological Review, 96*(3), 433-458.

Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. Current Opinion in Neurobiology, 7(2), 255-261.

Edin, F., Klingberg, T., Johansson, P., McNab, F., Tegnér, J., and Compte, A. (2009). Mechanism for top-down control of working memory capacity. *PNAS, 106*(16), 6802-6807.

Egly, R., Driver, J., & Rafal, R. (1994). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects. Journal of *Experimental Psychology: General, 123*(2), 161-177.

Ericsson, K. A., & Kintsch, W. (1995). Long-term working memory. *Psychological Review, 102*, 211-245.

Eriksen, C. W., & Rohrbaugh, J. W. (1970). Some factors determining efficiency of selective attention. *The American Journal of Psychology, 83*(3), 330-342.

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2008). The spatiotemporal profile of cortical processing leading up to visual perception. *Journal of Vision, 8*(1):12, 1-12.

Fahy, F. L., Riches, I. P., & Brown, M. W. (1993). Neuronal activity related to visual recognition memory: Long-term memory and the encoding of recency and familiarity information in the primate anterior and medial inferior temporal and rhinal cortex. *Experimental Brain Research, 96,* 457-472.

Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex, 1,* 1-47.

Feng, C., Jiang, Y., & He, S. (2007). Horizontal and vertical asymmetry in visual spatial crowding effects. *Journal of Vision, 7*(2):13, 1-10.

Flom, M. C., Weymouth, F. W., & Kahneman, D. (1963). Visual resolution and contour interaction. *Journal of the Optical Society of America, 53*(9), 1026-1032.

Fuster, J. M., & Alexander, G. E. (1970). Delayed response deficit by cryogenic depression of frontal cortex. *Brain Research, 20*(1), 85-90.

Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science, 173,* 652-654.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8*(10), 1298-1300.

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*(8), 1176-94.

Hartline, H. K., Wagner, H. G., & Ratliff, F. (1956). Inhibition in the eye of limulus. *The Journal of General Physiology, 39*(5), 651-673.

Hartline, H. K. (1938). The response of single optic nerve fibers of the vertebrate eye to illumination of the retina. *American Journal of Physiology, 121,* 400-415.

Hasegawa, I., Fukushima, T., Ihara, T., & Miyashita, Y. (1998). Callosal window between prefrontal cortices: Cognitive interaction to retrieve long-term memory. *Science, 281,* 814-818.

Huang, L. (2010). Visual working memory is better characterized as a distributed resource rather than discrete slots. *Journal of Vision, 10*(14).

Hubel, D. H., & Wiesel, T. N. (1959). Receptive fields of single neurones in the cat's striate cortex. *Journal of Physiology, 148,* 574-591.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal of Physiology, 160,* 106-154.

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195*, 215-243.

Ihssen, N., Linden, D. E. J., Miller, C. E., & Shapiro, K. L. (2015). Neural mechanisms underlying visual short-term memory gain for temporally distinct objects. *Cerebral Cortex, 25*(8), 2149-2159.Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17*(5), 680-686.

Jacobsen, C. F. (1935). Functions of frontal association area in primates. *Archives of Neurology & Psychiatry, 33*, 558-569.

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex, 21,* 1147-1154.

Jensen, O. & Lisman, J. E. (1996). Novel lits of 7 +/- 2 known items can be reliably stored in an oscillatory short-term memory network: Interaction with long-term memory. *Learning & Memory, 3*, 257-263.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282,* 108-111.

Kastner, S., De Weerd, P., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in the human visual cortex. Journal of Neurophysiology, 86, 1398-1411.

Kastner, S., Nothdurft, H. C., & Pigarev, I. N. (1997). Neuronal correlates of pop-out in cat striate cortex. *Vision Research, 37*(4), 371-376.

Keysers, C., Xiao, D.-K., Földiák, P., & Perrett, D. I. (2005) Out of sight but not out of mind: The neurophysiology of iconic memory in the superior temporal sulcus. *Cognitive Neuropsychology, 22*(3/4), 316-332.

Klimesch, W., Doppelmayr, M., Schwaiger, J., Auinger, P., & Winkler, T. (1999). 'Paradoxical' alpha synchronization in a memory task. *Cognitive Brain Research, 7*, 493-501.

Landman, R., Spekreijse, H., & Lamme, V. A. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research, 43*(2), 149-164.

Levi, D. M. (2008). Crowding-An essential bottleneck for object recognition: A mini review. *Vision Research, 48*(5), 635-654.

Li, L., Miller, E. K., & Desimone, R. (1993). The representation of stimulus familiarity in anterior inferior temporal cortex. *Journal of Neurophysiology, 69*, 1918-1929.

Lin, P.-H., & Luck, S. J. (2009). The influence of similarity on visual working memory representations. *Visual Cognition, 17*(3), 358-372.

Linden, D. E. J., Bittner, R. A., Muckli, L., Waltz, J. A., Kriegeskorte, N., Goebel, R., Singer, W., & Munka, M. H. J. (2003). Cortical capacity constraints for visual working memory: Dissociation of fMRI load effects in a fronto-parietal network. *NeuroImage, 20*, 1518–1530.

Long, G. M., & Sakitt, B. The retinal basis of iconic memory: Eriksen and Collins revisited. *The American Journal of Psychology, 93*(2), 195-206.

Loomis, J. M. (1978). Lateral masking in foveal and eccentric vision. *Vision Research, 18*, 335-338.

Luck, S. J. (2008). Visual short-term memory. In S. J. Luck & A. R. Hollingworth (Eds.), *Visual Memory*. New York: Oxford University Press

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2 and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*(1), 24-42.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

Makovski, T. (2012). Are multiple visual short-term memory storages necessary to explain the retro-cue effect? *Psychonomic Bulletin & Review, 19*(3), 470-476.

Makovski, T., & Jiang, Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychonomic Bulletin & Review, 14*(6), 1072-1078.

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology: Learning Memory, and Cognition, 34*(2), 369-380.

Marshall, L., & Bays, P. M. (2013). Obligatory encoding of task-irrelevant features depletes working memory resources. *Journal of Vision, 13*(2):21, 1-13.

Matsukura, M., & Hollingworth, A. (2011). Does visual short-term memory have a high-capacity stage? *Psychonomic Bulletin & Review, 18*, 1098-1104.

McCarley, J. S., Mounts, J. R. W., & Kramer, A. F. (2004). Age-related differences in localized attentional interference. *Psychology and Aging, 19*(1), 203-210.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychol. Rev. 63*(2), 81–97.

Miller, E. K., & Desimone, R. (1994). Parallel neuronal mechanisms for short-term memory. *Science, 263,* 520-522.

Miller, E. K., Li, L., & Desimone, R. (1991). A neural mechanism for working and recognition memory in inferior temporal cortex. *Science, 254,* 1377-1379.

Moore, C. M. (2001). Inattentional blindness: Perception or memory and what does it matter? *Psyche, 7*(2).

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229,* 782-784.

Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M., & Stokes, M. G. (2013). Attention restores discrete items to visual short-term memory. *Psychological Science, 24*(4), 550-556.

Murray, A. M., Nobre, A. C., Astle, D. E., & Stokes, M. G. (2012). Lacking control over the trade-off between quality and quantity in visual short-term memory. *PLoS-ONE, 7*(8), e41223.

Neisser, U., & Becklen, R. (1975). Selective looking: Attending to visually specified events. *Cognitive Psychology, 7,* 480-494.

Nickerson, R. S. (2000). Null hypothesis significance testing: A review of an old and continuing controversy. *Psychological Methods, 5*(2), 241-301.

Oliver, C. N. L., Maijer, F., & Teeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology: Human Perception and Performance, 32*(5), 1243-1265.

Olson, I. R., Moore, K. S., Stark, M., & Chatterjee, A. (2006). Visual working memory is impaired when the medial temporal lobe is damaged, *Journal of Cognitive Neuroscience, 18*(7), 1087-1097.

Pelli, D. G., Palomares, M., & Majaj. N. J. (2004). Crowding is unlike ordinary masking: Distinguishing feature integration from detection. *Journal of Vision, 4,* 1136-1169.

Pessoa, L., Gutierrez, E., Bandettini, P. A., & Ungerleider, L. G. (2002). Neural correlates of visual working memory: FMRI amplitude predicts task performance. Neuron, 35, 975-987.

Phaf, R. H., & Wolters, G. (1997). A constructivist and connectionist view on conscious and nonconscious processes. *Philosophical Psychology, 10,* 287–307.

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception and Psychophysics, 16*(2), 283-290.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3*, 179-197.

Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception & Performance, 18*(3), 849-860.Reinhart, R. M. G., Heitz, R. P., Purcell, B. A., Weigand, P. K., Schall, J. D., & Woodman, G. F. (2012). Homologous mechanisms of visuospatial working memory maintenance in macaque and human: Properties and sources. *Journal of Neuroscience, 32*(22), 7711-7722.

Rensink, R. A. (2002). Change detection. *Annual Review of Psychology, 53*, 245-277.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience, 19*(5), 1736-1753.

Riches, I. P., Wilson, F. A., & Brown, M. W. (1991). The effects of visual stimulation and memory on neurons of the hippocampal formation and the neighbouring parahippocampal gyrus and inferior temporal cortex of the primate. *The Journal of Neuroscience, 11*(6), 1763-1779.

Rolls, E. T., & Deco, G. (2002). *Computational Neuroscience of Vision*. New York: Oxford University Press.

Sakitt, B. (1976). Iconic memory. *Psychological Review, 83*(4), 257-276.

Sauseng, P., Kimesch, W., Heise, K. F., Gruber, W. R., Holz, E., Karim, A. A., Gllennon, M., Gerloff, C. et al. (2009). Brain oscillatory substrates of visual short-term memory capacity. *Current Biology, 19*, 1846-1852.

Shallice T., & Warrington, E. K. (1970). Independent functioning of verbal memory stores: A neuropsychological study. *Quarterly Journal of Experimental Psychology, 22*(2), 261-273.

Shimi, A., Woolrich, M. W., Mantini, D., & Astle, D. E. (2015). Memory load modulates graded changes in distracter filtering. *Frontiers in Human Neuroscience, 8*, article 1025.

Simons D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception, 28,* 1059-1074.

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS-ONE, 3*(2), e1699.

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2009). V4 activity predicts the strength of visual short-term memory representations. *Journal of Neuroscience, 29*(23), 7432-7438.

Sligte, I. G., Vandenbroucke, A. R. E., Scholte, H. S., & Lamme, V. A. F. (2010). Detailed sensory memory, sloppy working memory. *Frontiers in Psychology, 1*, 175.

Smith, M. A. (2006). Surround suppression in the early visual system. *Journal of Neuroscience, 26*(14), 3624 –3625.

Smith, E. E., & Jonides, J. (1998). Neuroimaging analyses of human working memory. *Proceedings of the National Academy of Sciences, 95*, 12061-12068.

Smith, A. T., Singh, K. D., Williams, A. L., & Greenlee, M. W. (1991). Estimating receptive field size from fMRI data in human striate and extrastriate visual cortex. *Cerebral Cortex, 11*(12), 1182-1190.

Shapiro, K. L. & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

Shiffrin, R. M., & Atkinson, R. C. (1969). Storage and retrieval processes in long-term memory. *Psychological Review, 76*(2), 179-193.

Suchow, J. W., Fougnie, D., Brady T. E., & Alvarez, G. A. (2014). Terms of the debate on the format and structure of visual memory. *Attention, Perception & Psychophysics, 76*, 2071-2079.

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature, 428*, 751-754.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology, 12*(1), 97-136.

Tripathy, S. P., & Cavanagh, P. (2002). The extent of crowding in peripheral vision does not scale with target size. *Vision Research, 42*, 2357-2369.

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32*(7), 1349-1357.

Van den Berg, R., Sin, H., Chou, W.-C., George, R., & Ma, W. J. (2012). Variability in encoding precision accounts for visual short-term memory limitations. *PNAS, 109*(22), 8780-8785.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428,* 748-751.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature, 438,* 500-503.

Werblin, F. S. (1974). Control of retinal sensitivity II. Lateral interactions at the outer plexiform layer. *The Journal of General Physiology, 63*, 62-87.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120*(2), 272-292.

Wheeler, M. E. & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General, 131*(1), 48-64.

Xu, Y., & Chun, M.M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature, 440*, 91-95.

Xu, Y., & Chun, M.M. (2009). Selecting and perceiving multiple visual objects. *Trends in Cognitive Sciences, 13*(4), 167-174.

Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *Journal of Neuroscience, 29*(10), 3059-3066.

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453*, 233-236.

Zhang, W., & Luck, S. J. (2009). Sudden death and gradual decay in visual working memory. *Psychological Science, 20,* 423-428.

Zhang, W., & Luck, S. J. (2011). The number and quality of representations in working memory. *Psychological Science, 22,* 1434-1441.

2 Methods

As described in Chapter 1, the collection of experiments presented in this thesis explores the degree to which visual short-term memory (VSTM) performance may be influenced by competitive interactions between stimuli, occurring in both a top-down and bottom-up manner. This chapter aims to give background to the data acquisition and analysis methods used in the upcoming chapters, and detail benefits and limitations to be considered upon their interpretation.

2.1 Behavioural/Psychophysical Methods

2.1.1 Change Detection Tasks

The behavioural experiments primarily use a modified change detection task. Change detection tasks are commonly used to assess VSTM performance. First used by Phillips (1974), the paradigm was later adapted in Luck and Vogel's (1997) influential paper investigating VSTM capacity. Ihssen, Linden and Shapiro's (2010) sequential change detection paradigm (see Section 1.5 for further description) was adapted to form the basis of several experiments in this thesis.

A huge advantage of the change detection paradigm is that it allows confounds with verbal VSTM to be minimized, by allowing participants to report what they have seen in a non-verbal manner. Although they may lack some precision, change detection tasks allow a quicker judgement than tasks such as selecting a colour on a colour wheel (e.g., Lin & Luck, 2009). This is useful, especially given the nature of our experiments; we did not want competition to be increased by attending to colours not present in the memory display during the responding process. However, use of this method means that we are unable to make inferences about the precision with which items are represented, but rather the method results in a global measure of capacity.

2.1.2 Measures of performance

2.1.2.1 K-value: A measure of capacity

In many experiments I chose to quantify VSTM capacity using the k-value equation, a widely used method of calculating an estimate of VSTM capacity (e.g., Luck & Vogel, 1997; Ihssen, Linden & Shapiro, 2010; Vogel & Machizawa, 2004). Since k equations take set size into account, they are particularly useful for comparing

performance on a VSTM task across differing set size conditions, as was necessary in some experiments.

The k measure of VSTM capacity was originally devised by Pashler (1988; [k = ((Hit Rate – False Alarm Rate)/(1 – False Alarm Rate)) * Set Size]) and later adapted by Cowan (2001; [k = (Hit Rate – False Alarm Rate) * Set Size]). Cowan's version of the measure tends to be more commonly used, as is suggested to provide a more consistent capacity estimate over varying set sizes, as would be predicted by the slots model (Cowan, 2005). It was actually designed under the assumption that a single-item probe is used at test, rather than a full display of items (Rouder, Morey, Morey & Cowan, 2011). Nevertheless, due to the necessity to compare across set sizes in Chapter 6, and to allow direct comparison with results from Ihssen, Linden and Shapiro (2010) on which many of the experiments in this thesis were based, experiments testing VSTM capacity used Cowan's k calculation. Pashler's k was also calculated and produced similar patterns of results, which have not been reported here in the interest of brevity.

2.1.2.2 D-prime: Response sensitivity

Another calculation used in many studies is d-prime. D-prime is a measure of response sensitivity, which is important in discrimination tasks as it takes into account response bias (i.e., it considers both hits and false alarm responses). There is some controversy over the best way to calculate d-prime, with different calculations suggested in use for single item probe tasks than in two-alternative forced choice tasks (for a review, see MacMillan & Creelman, 2004). Many experiments in this thesis implemented two-alternative forced choice tasks, with participants responding whether a stimulus display was the same as or different to a previously presented display. Therefore in situations in which d-prime was used, it was calculated as follows: d-prime = z(Hit Rate) – z(False Alarm Rate). If any hit or false alarm rates was 1 or 0 they were corrected, to account for the fact that our observable data is only a sample of the participant's behaviour. The standard way to correct for this issue is to use 1/2N instead of 0, and 1 – (1/2N) in place of 1, with N being the maximum number of hits/false alarms possible). Due to use of hit/false alarm rates, d-prime correlates highly with Cowan's k, although it is not appropriate for comparing between conditions with different set sizes, since the equation does not include a set size parameter.

Although k and d-prime were both calculated in all VSTM experiments in which comparison across set size was not required, d-prime is reported only when it shows a

different pattern to k. Although these measures are strongly related, the primary variable of interest in these experiments was VSTM capacity.

2.2 Physiological Measures

2.2.1 ERPs

In some experiments, the event-related potential (ERP) technique was used. This is a cost-effective and non-invasive method, which involves taking electroencephalogram (EEG) measurements from the scalp and averaging together the EEG recorded over many trials, time locked to markers indicating the occurrence of an event. This procedure results in waveform for each electrode representing the mean electrical activity measured on the scalp in response to a type of event. When enough trials are averaged together to give sufficient signal/noise ratio, ERPs can be used to look at small variations in activation between conditions in which different events occurred.

The ERP technique typically examines "components", which are patterns of activation previously associated with cognitive functions or brain regions. Components can be used to make inferences about what processes are occurring in the brain. For example, as will be described in more detail (Section 2.2.1.1), there is strong evidence that the C1 component is closely associated with activity in primary visual cortex (V1; e.g., Jeffreys & Axford, 1972). Therefore, by looking at how its amplitude changes across different experimental conditions, researchers can gain insight into whether there are differences in V1 activation between the conditions of interest.

Since EEG is recorded from the electrodes on the scalp it has poor spatial resolution. This is due to several factors, including the folding of cortical tissue, diffusion of the electrical signal as it passes through the head (in particular the skull), and the somewhat crude summation of positive and negative activation across the different areas neighbouring the electrodes (see Luck, 2014). However, one of the major advantages of the ERP technique is its high temporal resolution, allowing measurement of changes in the brain to a timescale of milliseconds. This can give important insights into the order of occurrence of processes in the human visual system at a scale not possible to achieve with other neurophysiological techniques, such as fMRI.

It remains a long-standing (although controversial) convention to plot negative voltages upwards when plotting ERP waveforms. It is unclear why this practice developed, although Luck (2014) theorises that it may have emerged from a dated neurophysiological

convention. To reduce confusion, many ERP researchers are now beginning to plot positive upwards, in agreement with the vast majority of the scientific community. Throughout this thesis I will also be plotting ERP waveforms with positive voltages upwards.

2.2.1.1 C1 component

One of the components measured in the ERP experiments described in Chapter 3 is the C1. The C1 typically peaks around 80-100 ms post stimulus, and is largest at posterior midline sites (Luck, 2014). It is thought to reflect feedforward primary visual cortex (V1) activity (Clark, Fan & Hillyard, 1995; Jeffreys & Axford, 1972). In addition to source localization through dipole modelling (e.g., Di Russo, Martinez, Sereno, Pitzalis & Hillyard, 2002), further evidence of the cortical origin of C1 comes from its polarity in response to stimuli at different positions in the visual field. Specifically, the C1 is positive in response to stimuli present in the lower visual field and negative for those in the upper field, consistent with expectations given the folding of V1 around the calcarine fissure (Clark, Fan & Hillyard, 1995; Jeffreys & Axford, 1972). C1 is variable around the horizontal meridian, due to differences between individuals in the exact point of polarity change (Clark, Fan & Hillyard, 1995). Therefore, in studies in which stimuli are presented around the horizontal midline, or in which activation to upper and lower visual field stimuli is averaged together, the C1 tends to cancel out or merge with the P1.

In recent controversy about whether the C1 wave is certain to reflect activity in area V1 alone, Ales, Yates & Norcia (2010, 2013) revealed polarity inversions between upper and lower visual field stimulation, in simulated V2 and V3 topographical data. However, Kelly and colleagues suggest that although inversions are also present for topographies reflecting V2 and V3 generators, they are of a somewhat different scalp distribution and of opposite polarity on the scalp to that expected for the C1 (Kelly, Schroeder & Lalor, 2013; Kelly, Vanegas, Schroeder & Lalor, 2013). Further, they suggest that V2/V3 polarity reversal should onset tens of milliseconds after the C1. These studies suggest that although presence of a polarity reversal for upper- versus lower-field stimuli is not alone sufficient to discriminate between striate and extrastriate areas, the combination of the particular point in the visual field at which the polarity reverses, and the scalp topography and polarity of the reversal (Clark, Fan & Hillyard, 1995; Jeffreys & Axford, 1972), provide compelling evidence that the C1 is produced in area V1.

2.2.1.2 P1 component

Unlike the C1, the P1 has the same polarity on the scalp in response to stimuli presented in upper and lower visual fields, and is detected at highest amplitude at lateral occipital electrodes. Therefore, the P1 is generally calculated by averaging together the activation elicited by stimuli presented across the visual field. Stimulus characteristics such as contrast can affect the latency of P1, which typically onsets approximately 60-90 ms post-stimulus, and peaks at around 100-130 ms (Luck, 2014). Di Russo, Martinez, Sereno, Pitzalis and Hillyard (2002) suggest P1 to originate in extrastriate areas; more specifically early P1 is consistent with a dipole in V3/V3a and middle-occupital gyrus, and the late part of the P1 is consistent with anterior V4v activation. Unlike the C1, the P1 is thought to be amplified by selective attention to a stimulus (Hillyard, Vogel & Luck, 1998).

2.2.1.3 Source localisation

As previously mentioned, one of the limitations of the ERP technique is its poor spatial resolution. However, it is possible to make inferences about the neural sources of activation, using source localization techniques such as Brain Electrical Source Analysis (BESA; Scherg, 1990) and Low Resolution Electromagnetic Tomography (e.g., sLORETA; Pascual-Marqui, 2002). These techniques estimate activation within the brain, given the activation measured on the scalp. In conjunction with accurate volume conduction values for different parts of the head (ideally informed by structural MRI for each participant), source localisation techniques can provide useful, albeit tentative information.

The idea behind dipole localisation techniques such as BESA (Scherg, 1990) is to estimate brain activation given an observed scalp distribution, by modelling neural generators as a relatively small number of dipoles within the brain. If the brain did consist of several dipoles, and we knew how many, where they were located, and characteristics of the head and brain of each individual (from techniques such as structural MRI) it would be possible to predict the observed scalp distribution with a high degree of accuracy. In reality, these modelled dipoles represent the summation of small electrical potentials produced at many neurons. There are a potentially infinite number of dipole configurations which would produce exactly the same measurements on the scalp, and it is never possible to know how many dipoles truly exist, or their exact locations. Therefore, calculating the

neural generators underlying an observed scalp distribution is not a solvable problem (see Luck, 2014).

An alternative to dipole localisation is the distributed source approach, which models activation as a number of voxels, each containing three dipoles. This requires magnitudes of activation to be estimated for a large number of dipoles, and so again there are many possible solutions for a given scalp distribution. One technique used to discard some of the less likely solutions is the minimum norm approach, which adds the additional constraint that the magnitudes of solutions should not be too large. A particularly widely used method based on the minimum norm approach is Low Resolution Electromagnetic Tomography (LORETA; Pascual-Marqui, 2002), which makes the assumption that changes in voltages throughout the brain will be gradual. Although in some parts of the brain this would not be expected (e.g., between neighbouring but discrete brain structures) in general it is a reasonable assumption, and is especially useful for finding the midpoint of an area of activation (see Luck, 2014).

Another problematic aspect of source localisation is that it is not possible to calculate the statistical significance, and thereby know the likelihood that it is accurate. Once additional assumptions are used to constrain the solutions (as in LORETA, for example), it is possible to determine a margin of error, to get some idea of how accurate the localisation is. But although theoretically possible, techniques determining the accuracy of localisations are infrequently used (Luck, 2014). Source localisation techniques are also subject to researcher bias, with variables such as the number of and approximate locations of dipoles determined by the researcher to some extent. It is important to use impartial and scientifically informed methods to decide on these variables.

In summary, source localisation can be useful for verifying whether scalp distributions are potentially consistent with specified neural generators, and for ruling out inconsistent hypotheses. When combined with individual structural MRI data, it is possible to be a lot more confident about localisation, by taking brain structure into account on an individual level, rather than using a standard reconstruction. On the other hand, potential influence of the expectations and beliefs of the researcher, and an inability to know the accuracy of the solution mean that caution should be exercised when using source localisation techniques, and when interpreting results.

2.2.2 Magnetic Resonance Imaging (MRI)

In the experiments that constitute my thesis, I decided not to use MRI. MRI is another non-invasive technique, which is used to measure blood oxygen level dependent (BOLD) response in the brain. Reliance on BOLD response means that MRI is constrained by biological characteristics, such as the physical organisation of the vascular network. It also gives it a much poorer temporal resolution than ERPs; therefore, in general, this technique would not have been useful in answering questions we posed regarding the timing of competitive interactions in the visual system. However, its great spatial resolution means that functional MRI has been used in many other investigations into visual competition, in which timing was not a principle concern, but high spatial resolution was required (e.g. Kastner, De Weerd, Desimone & Ungerleider, 1998).

Ideally, it would have been useful to conduct structural MRI to allow us to run source localisations constrained by the brain characteristics of each individual, rather than using a standard reconstruction. We decided that in our studies the expense of structural MRI outweighed the potential benefits of its use. Due to carefully choosing ERP components of interest which had tight links to specific parts of the visual system, we were able to ascertain considerable information about the brain areas involved, and these findings were consistent with a sLORETA solution using a standard cortical reconstruction (see Section 3.2.2).

2.3 Analysis

2.3.1 Null Hypothesis Significance Testing

There are many disadvantages and controversies surrounding conventional null hypothesis significance testing (NHST), and ways in which results can be misinterpreted (for a review see Nickerson, 2000). The principle aim of NHST is to calculate the probability that the observed data occurred by chance, given that the null hypothesis is true. In order to do this, we initially assume the default hypothesis that there is no difference between the conditions, and then look for statistical evidence that this is unlikely (i.e., that there is less than a 5% chance that the data occurred by chance). One drawback is that even if there is insufficient evidence that the data were unlikely to occur by chance if the null hypothesis were true, it is still not possible to know to what extent the data actually reflect the null hypothesis (i.e., we cannot determine the probability that there is genuinely no difference between two populations). Another problem concerns how the

results of NHST are typically reported; traditionally researchers only report whether $p < .05$. Recent recommendations to report exact p-values (e.g., American Psychological Association, 2010) emphasise the importance of providing more detail about how close p-values are to the required threshold of significance. I will be reporting exact p-values throughout this thesis.

One part of NHST involves correcting for multiple comparisons, in order to avoid inflating our chances of incorrectly rejecting the null hypothesis. There are many ways in which this has been previously been achieved. One common but conservative correction is the standard Bonferroni correction. The basic principle is that the p-value which a comparison needs to achieve in order to be considered statistically significant is divided by the number of comparisons made, in order to keep the overall probability of making a type I error below 5%. One problem with this correction is that due to its conservative nature, it drastically increases the chance of making a type II error (i.e., the chance of failing to reject the null hypothesis when it is incorrect).

This lack of sensitivity makes alternatives, such as sequential modifications of Bonferroni corrections, particularly useful. One such example is the sequential Bonferroni procedure proposed by Holm (1979), which involves listing multiple p-values in order of size, and adjusting the p-value threshold required for significance, based on their magnitudes. Holm's sequential Bonferroni modification does decrease type II error chances, although some studies suggest that they remain unacceptably high (Nakagawa, 2004). Another alternative is the False Discovery Rate (FDR) correction particularly useful. FDR is another sequential p-value modification, which has shown particular usefulness in fMRI studies, where multiple comparisons are made between voxels (Bennett, Wolford & Miller, 2009). The primary reason for being less conservative is that the FDR correction is testing a slightly different assumption from Bonferroni. Bonferroni corrects the familywise error rate to <.05, whereas FDR ensures that <.05 of statistically significant results are false (Benjamini & Hochberg, 1995). This technique, which I have used when corrections were necessary, allows multiple planned comparisons to be made without unduly inflating the chance of a type II error.

2.3.2 Bayes Factor

In contrast to NHST, Bayesian model selection can evaluate the relative probabilities of the null and alternative hypotheses (e.g., Wetzels, Grasman & Wagenmakers, 2012). A Bayes Factor analysis provides the ratio of odds that the null and

alternative hypotheses are true. Bayes factor is based on a prior distribution, which is set in advance and informed by theoretical models. Setting the prior is extremely important: although the prior must be uninformative if there is little information available about the phenomenon of interest, it must not be too uninformative. If too uninformative, the null hypothesis will be overrepresented. A default prior which has been frequently and successfully used is the Jeffreys-Zellner-Siow Prior (see Wetzels, Grasman & Wagenmakers, 2012), which is based on a Cauchy distribution. In situations in which groups are compared to assess their similarity, the Bayes Factor calculation has been used.

2.4 References

Ales, J. M., Yates, J. L., & Norcia, A. M. (2010). V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *Neuroimage, 52*(4), 1401-1409.

Ales, J. M., Yates, J. L., & Norcia, A. M. (2013). On determining the intracranial sources of visual evoked potentials from scalp topography: A reply to Kelly et al. (this issue). *Neuroimage, 64*, 703-711.

American Psychological Association. (2010). *Publication manual of the American psychological association (6th ed).* Washington DC: American Psychological Association.

Bennett, C. M., Wolford, G. L., & Miller, M. B. (2009). The principled control of false positives in neuroimaging. *Social Cognitive and Affective Neuroscience, 4*(4), 417-422.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological). 57*(1), 289-300.

Clark, V. P., Fan, S., & Hillyard, S. A. (1995). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping, 2*, 170-187.

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

Cowan, N. (2005). *Working Memory Capacity.* New York, NY: Psychology Press.

Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95-111.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 353*, 1257-1270.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6(*2), 65-70.

Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17*(5), 680-686.

Jeffreys, D. A. & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked potentials. I. component of striate cortical origin. *Experimental Brain Research, 16*, 1-21.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282*, 108-111.

Kelly, S. P., Schroeder, C. E., & Lalor, E. C. (2013). What does polarity inversion of extrastriate activity tell us about striate contributions to the early VEP? A comment on Ales et al. (2010). *NeuroImage, 76*, 442-445.

Kelly, S. P., Vanegas, M. I., Schroeder, C. E., & Lalor, E. C. (2013). The cruciform model of striate generation of the early VEP, re-illustrated, not revoked: A reply to Ales et al. (2013). *NeuroImage, 82*, 154-159.

Luck, S.J. (2014). *An Introduction to the Event-Related Potential Technique* (2nd ed.). Cambridge, MA: MIT Press.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

MacMillan, N. A., & Creelman, C. D. (2004*). Detection theory: A user's guide.* Mahwah, NJ: Lawrence Erlbaum Associates.

Nakagawa, S. (2004). A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behavioral Ecology, 15*(6), 1044-1045.

Pascual-Marqui, R. D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, 24D, 5-12.

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics, 44*(4), 369-378.

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception and Psychophysics, 16*(2), 283-290.

Scherg, M. (1990). Fundamentals of dipole source potential analysis. In F. Grandori, M. Hoke, & G. I. Romani (eds.), *Auditory Evoked Magnetic Fields and Electric Potentials.* Basel, Switzerland: Karger.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428,* 748-751.

Wetzels, R., Grasman, R. P. P. P., & Wagenmakers, E.-J. (2012). A default Bayesian hypothesis test for ANOVA designs. *The American Statistician, 66*(2), 104-111.

3 The effect of stimulus proximity on early visual ERP components[2]

Objects in the external world are constantly competing for representation in the human brain at different scales and in different areas of cortex. The resolution of this competition is a vital mechanism serving to prevent information overload by prioritizing currently relevant information, as described in the highly influential theory of biased competition (Desimone & Duncan, 1995). As described in Chapter 1, recent studies suggest that competitive interactions in visual cortex are stronger between stimuli presented within the same visual receptive field (RF) than between stimuli presented in different RFs (Kastner, De Weerd, Desimone & Ungerleider, 1998; Reynolds, Chelazzi & Desimone, 1999).

Single cell recordings have been used to demonstrate the existence of competition in primate visual cortex, between stimuli presented within an individual RF (e.g., Reynolds, Chelazzi & Desimone, 1999). Reynolds et al. found that when an unattended stimulus pair was presented simultaneously within a single V4 RF, the firing rate was not simply the sum of the firing rates for each stimulus presented alone but was instead near the average of the firing rates for the individual stimuli. Further, when one stimulus of a pair was attended, the features of this stimulus alone determined the cell's firing rate. Similarly, Luck, Chelazzi, Hillyard and Desimone (1997) found that attention modulated V2 and V4 firing rates only when both the attended and ignored stimuli were inside the neuron's RF (and thus were in competition for control over that neuron). Moreover, when both stimuli were inside the RF, the attention effect was reduced when the stimuli were presented sequentially rather than simultaneously, presumably because sequential presentation reduces competition between the stimuli, as will be described presently. Other studies have also found large single-unit attention effects when both attended and ignored stimuli were simultaneously presented inside the neuron's RF (Treue & Maunsell, 1996; Moran & Desimone, 1985). It is important to note that single cell methods have been unable to investigate competitive interactions between two stimuli within the same V1 RF, due to small RF size.

Inter-stimulus competition has also been investigated in humans using fMRI. For example, Kastner, De Weerd, Desimone and Ungerleider (1998) presented the same four

[2] This chapter is the result of a collaboration with Professor Steven J. Luck, UC Davis. Much of this chapter, including Experiment 2, is based upon a previously published work (Miller, Shapiro & Luck, 2015). All data were collected and analysed by Claire E. Miller.

stimuli either simultaneously or sequentially in the periphery, while participants performed a task at fixation. They found decreased BOLD activity in response to simultaneous relative to sequential stimuli in areas V1, V2, V4 and area TEO in inferior temporal cortex, with the difference between the two conditions increasing with RF size. This outcome is consistent with strong competition between stimuli presented simultaneously within the same RF, with more items falling within a single RF in areas with large RFs than in areas such as V1 that have small RFs (see also Kastner et al., 2001). However, due to the low temporal resolution of the hemodynamic response measured using fMRI, it is unclear whether the findings of these studies reflect competition during feedforward processing, or competition in later visual areas feeding back to earlier areas. However, the high temporal resolution of the event-related potential (ERP) technique makes it ideal for assessing the different stages in visual processing at which competition can exert its effect in human neural populations. This chapter details experiments in which early visual ERP components were used to examine the effects of inter-stimulus competition in different areas of visual cortex.

The components of interest were: C1, thought to originate in primary visual cortex (Clark, Fan & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis & Hillyard, 2002; Jeffreys & Axford, 1972); C2 (Fortune & Hood, 2003; Kappenman & Luck, 2012), which we suggest to reflect V1 activity after feedback from extrastriate areas; and P1, thought to reflect extrastriate areas, including area V3 and middle-occipital gyrus, and anterior V4v (Di Russo et al., 2002). Our goal was to demonstrate that ERPs can provide a temporally sensitive index of early stimulus competition at varying levels of the early visual system. This is an important first step towards being able to study how competitive interactions in early visual activity depend on bottom-up factors such as stimulus similarity and top-down factors such as attention.

The experimental approach took advantage of the fact that voltages in the brain directly summate (Nunez & Srinivasan, 2006). Thus, if stimuli presented at two different locations are processed independently, the ERP response to the two stimuli presented simultaneously will be exactly the same as the sum of the ERP responses to the two stimuli presented individually. Consequently, if the observed ERP to two simultaneous stimuli differs from the sum of the ERPs to the individual stimuli presented separately, the two simultaneous stimuli must be interacting with each other. We therefore presented stimuli sequentially at various locations to obtain the responses to the individual stimuli and also presented the stimuli simultaneously at pairs of the same locations (see Figure 3.1). This

approach has been used extensively in research into binaural interactions between auditory stimuli presented simultaneously to the two ears compared with stimuli presented separately to each ear (see Pratt, 2012 for a review). We also varied the distance between simultaneously presented pairs, to test the hypothesis that interactions between stimuli would occur earlier for nearby locations than for more distant locations. Specifically, we predicted that the near stimuli would compete beginning in V1, leading to interactions between simultaneous stimuli beginning with the C1 wave. The far stimuli were predicted to compete only in later visual areas, leading to interactions in the P1 wave but not in the C1 wave.

3.1 Experiment 1

3.1.1 Method

3.1.1.1 Participants.

Fifteen participants were recruited from the UC Davis Center of Mind and Brain ERP participant pool, and each took part in a testing session lasting approximately 2.5 hours in exchange for payment of $10/hour. Two were later excluded after detection of artefacts in a proportion of trials exceeding our a priori criterion of >30%, resulting in a final sample size of N = 13 (ages 19-33, mean age = 22.4, 8 females).

3.1.1.2 Stimuli.

Stimuli were presented using 'Presentation' experimental control software (Neurobehavioral Systems, Albany, CA) on a 21" CRT monitor with a black background and a continuously visible white fixation point. Each display contained one or two small wedge-shaped checkerboards. As shown in Figure 3.1, each wedge extended from 5.5° to 9.5° of visual angle from the fixation point. Each had a width of 15° of polar angle, which was equivalent to 2° of visual angle in the centre of each checkerboard (0.5° x 0.5° visual angle per check).

Each display contained either a single checkerboard or two simultaneously presented checkerboards in a single quadrant of the screen. On 10% of trials, one checkerboard was a target, in which two of the central checks were black instead of white (see Figure 3.1, bottom left panel). Participants performed a target detection task (as

described below), which allowed continual assessment of their attention to the task. Trials containing target stimuli were excluded from all analyses.

The presentation of stimuli in upper versus lower quadrants was designed to help isolate the C1 wave, which is positive for lower-field stimuli and negative for upper-field stimuli due to the folding pattern of area V1 around the calcarine fissure (Clark, Fan & Hillyard, 1995; Jeffreys & Axford, 1972). No stimuli were presented in the 7.5° (polar angle) adjacent to the vertical meridian, or the 22.5° (polar angle) adjacent to the horizontal meridian of each quadrant (see Figure 3.1) where there is likely to be substantial variation in individuals' C1 polarity (Clark, Fan & Hillyard, 1995). The remaining 60° of each quadrant were divided into 4 equal sectors, with each stimulus centred at an eccentricity of 7.5° of visual angle.

Three different trial types were presented in a random order (each occurring in 1/3 of trials): 'dual-near' stimuli, in which two checkerboards were presented simultaneously in adjacent sectors (0.16° visual angle gap, 1.88° center-to-center), 'dual-far' stimuli, in which two checkerboards were presented simultaneously separated by one sector (2° gap, 3.72° center-to-center), and 'single' stimuli, in which a single checkerboard was presented. For each trial type, the target checkerboards appeared in each sector with equal probability, and stimuli were presented in each quadrant of the screen with equal probability. In the dual-near trials, the stimuli were separated by a gap of 0.16° visual angle, which is smaller than the size of a V1 RF at an eccentricity of 7.5° (approx. 0.6°; Hubel & Wiesel, 1974). Near stimuli should therefore frequently be represented in the same V1 RFs. In the dual-far trials, the inter-stimulus gap measured 2°. Therefore, two far stimuli should be too far apart to fall within the same RF in V1, but should frequently fall within the same RF in extrastriate cortex (for example V4, with RFs approximately 5° wide at eccentricity 7.5°; Gattass, Sousa & Gross, 1988). In addition, the two dual-near stimuli should always compete in V4 RFs.

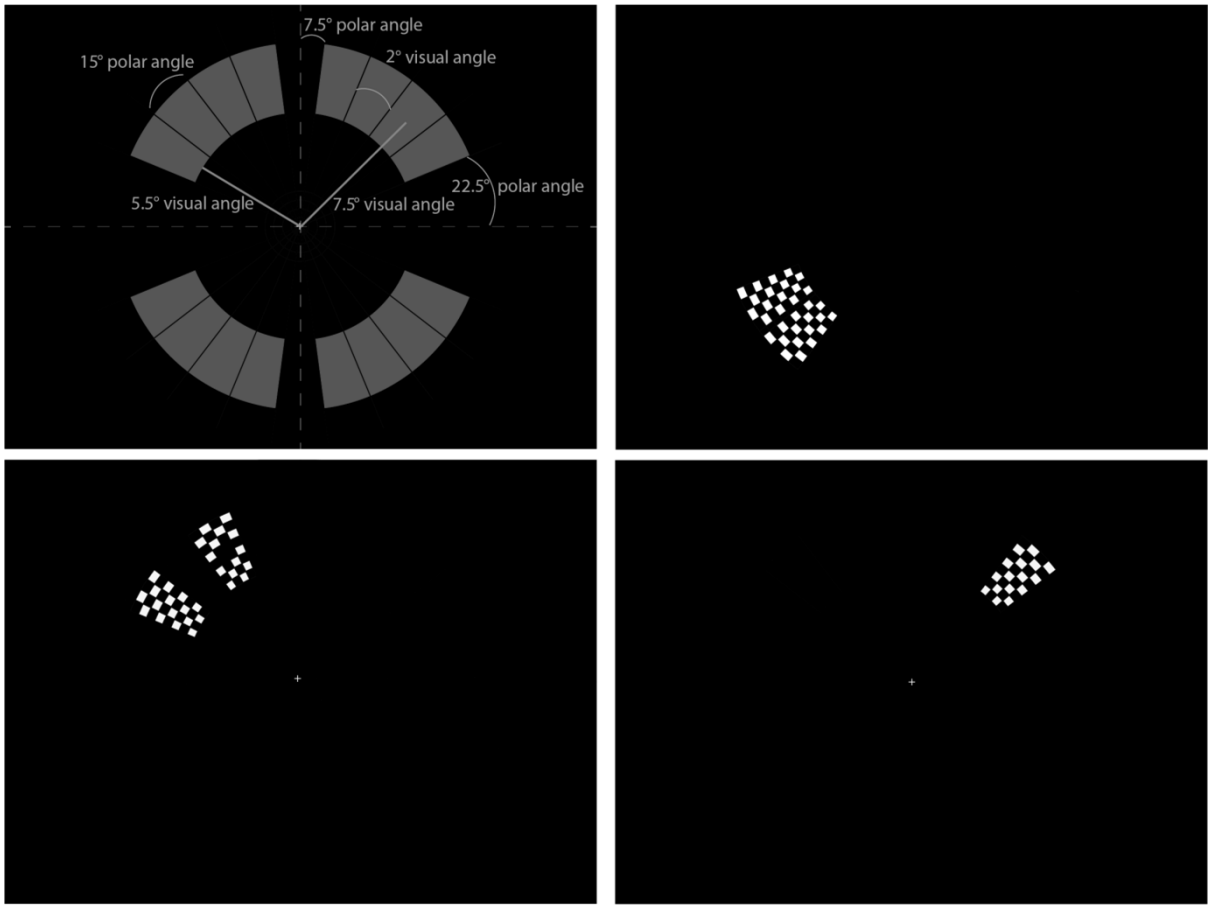


Figure 3.1. Top Left: Locations in which stimuli could be presented (grey segments) with measurements indicating size and position. Top Right: Example of experimental screen layout for a dual-near target absent trial. In each trial type, the stimuli could be presented above or below fixation (each occurring on 50% of trials). Bottom Left: Dual-far trial, with target present (upper stimulus). Bottom Right: Single stimulus target absent trial.

3.1.1.3 Procedure.

Participants were presented with a sequence of 3840 stimulus displays, divided into 8 blocks of equal length. Each stimulus display was presented for a duration of 100 ms, separated by a blank inter-stimulus interval between 600 and 800 ms (rectangular distribution). Participants were instructed to press a key with the index finger of the right hand if a target was detected in any location and to withhold their response if a target was not detected. As an incentive to attend fully to the task, participants earned 5 points for each correctly identified target stimulus and lost 5 points for each incorrect response. At the end of the experiment, participants received $1 extra for every 100 points they had scored.

3.1.1.4 EEG acquisition/processing.

BioSemi ActiveTwo active Ag/AgCl electrodes (BioSemi, Amsterdam, Netherlands) were used to record the EEG. Thirty-two scalp electrodes were used, distributed across the whole head but with a higher density in parietal and occipital areas (see Figure 3.2). EEG recordings were also taken from the left and right mastoids, and electrooculogram (EOG) recordings were taken from electrodes placed above and below the right eye and adjacent to the outer canthus of each eye. These signals were recorded in single-ended mode, low-pass filtered with a 5th-order sinc function (half-power cutoff at 208 Hz), and digitized at 512 Hz. A photosensor was used to assess timing delays; all timings were within 12 ms, with a small discrepancy of approximately 5 ms between stimuli presented in the upper and lower portions of the screen.

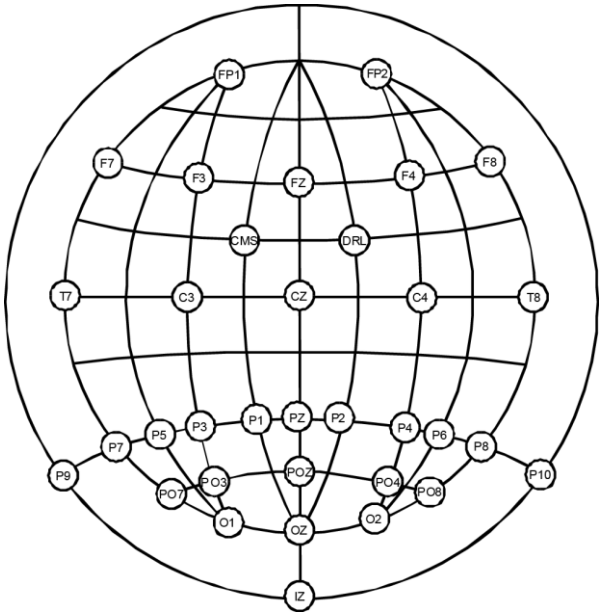


Figure 3.2. Electrode locations.

The data were processed using ERPLAB (Lopez-Calderon & Luck, 2014) and EEGLAB (Delorme & Makeig, 2004), which are open source, Matlab-based toolboxes. The EEG and EOG signals were band-pass filtered using a noncausal Butterworth infinite impulse response filter with half-amplitude cut-offs of 0.5 and 30 Hz (12 dB/octave), down-sampled to 256 Hz, and re-referenced to the average of the mastoid electrodes. The data were epoched into 600 ms segments, including a 100 ms pre-stimulus baseline.

The EOG was referenced into bipolar horizontal and vertical derivations and used in the detection of eyeblinks and saccades. The analyses were limited to non-target stimuli,

to which the participant's response was successfully withheld. In addition, trials were automatically rejected if a change in voltage exceeding 100 μV was detected in any channel (or 50 μV in the vertical EOG channel) within a moving window of 200 ms. Trials were also rejected if a step function detected changes of more than 50 μV in the vertical EOG channel or more than 10 μV on the horizontal EOG channel (Luck, 2014). The EEG was then visually examined for each participant, and thresholds were adjusted where necessary to ensure that all artefacts were rejected. In the final sample, an average of 10.26% of trials was rejected (SD = 6.09).

For each trial type, all trials remaining after artefact rejection were averaged, collapsing over stimulus locations except that the upper and lower visual field trials were kept separate. The C1 component was isolated by subtracting the ERPs elicited by stimuli presented in the lower visual field from those elicited by stimuli in the upper visual field. This difference wave takes advantage of the fact that the upper and lower field representations in area V1 are located in the lower and upper banks of the calcarine fissure respectively. The dipoles for the lower and upper fields therefore point in opposite directions, causing the scalp ERP to have opposite polarities for lower and upper field stimuli (Jeffreys & Axford, 1972; Clark, Fan & Hillyard, 1995). An upper-minus-lower difference wave therefore accentuates activity arising from V1, and activity that does not differ systematically in response to upper and lower visual field stimulation is cancelled out. Although other visual areas may also exhibit different activity for upper and lower field stimuli (Ales, Yates, & Norcia, 2010), the timing, scalp distribution, and precise reversal point of the C1 wave provide converging evidence that it arises from area V1 (Clark, Fan & Hillyard, 1995; Kelly, Schroeder & Lalor, 2013b). For the P1 wave, we averaged across upper and lower visual field stimuli.

3.1.1.5 EEG Statistical Analyses.

In analysing the EEG, the waveforms elicited by dual-near and by dual-far trials were compared with both the average of the two single-stimulus waveforms ('single average') and with the sum of the two single-stimulus waveforms ('single sum' average). As illustrated in Figure 3.3, the single sum waveforms provide an estimate of the response that would be obtained if the two simultaneous stimuli were processed completely independently, with no competition, and the single average waveforms provide an estimate of what might be expected if the two stimuli strongly compete (Reynolds et al., 1999). For each component, statistical analyses were conducted to compare the following trial types:

dual-near vs. dual-far stimuli, both dual-near and dual-far vs. single average, and dual-near and dual-far vs. single sum.

Our method of analysis relies on a number of assumptions. Firstly, as previously suggested, we assume that two stimuli presented simultaneously should, in the absence of competition, elicit activation equal to the sum of the same two stimuli presented individually (e.g., Nunez & Srinivasan, 2006). Secondly, we assume that our identified peaks will reflect components each corresponding to a separate and distinct stage in visual processing, and that measureable differences between these peaks therefore reflect differences in processing. This is a common assumption, necessarily underpinning the majority of research into cognitive processes using the ERP technique (see Luck, 2005). These assumptions will be discussed further with regard to the current study in section 3.3.

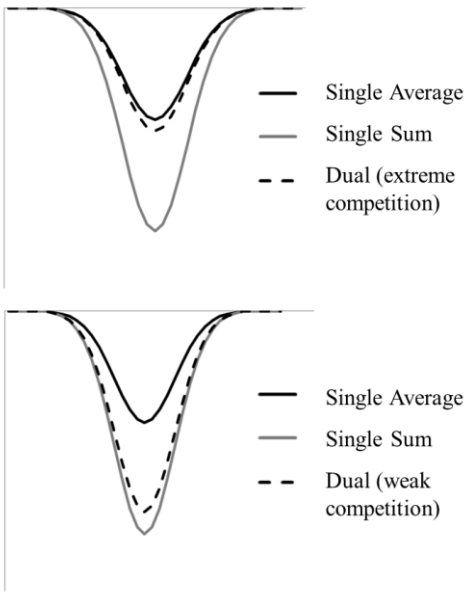


Figure 3.3. Expected ERP waveforms given weak competition (top panel) and extreme competition (lower panel) between two simultaneous stimuli.

We created two a priori clusters of electrodes, one for the C1 and C2 waves and one for the P1 wave. Informed by previous research, the C1/C2 cluster included the electrodes at or near the posterior midline (P1, O1, Iz, Pz, P2, POz, Oz, O2). The remaining posterior sites were used for the P1 cluster (P3, P5, P7, P9, PO7, PO3, P4, P6,

P8, P10, PO8, PO4). The ERP waveforms were averaged across the sites within a cluster prior to quantification of component amplitudes.

We chose our time windows with the main aim of minimizing the influence of overlap from other components on our components of interest. For the C1 and C2 we planned to use the signed area approach (Sawaki, Geng & Luck, 2012; Luck, 2014), in which the area either above or below the baseline is measured within the specified time window (with points of the opposite polarity effectively set to zero). This approach is ideal for components measured from a difference wave because it is not necessary to define a narrow measurement window to avoid cancellation of one component by an opposite-polarity component. We therefore chose wide windows within which each component of interest has been found in previous studies. Specifically, we used the negative area between 50 and 150 ms for the C1 wave (Di Russo, Martinez, Sereno, Pitzalis & Hillyard, 2002; Jeffreys & Axford, 1972; Fu, Fedota, Greenwood & Parasuraman, 2010) and the positive area between 50 and 250 ms for the C2 wave (Fortune & Hood, 2003; Kappenman & Luck, 2012). The signed area method was unsuitable for the P1 because it was not measured from a difference wave. We instead measured the mean amplitude within a specific time window. To avoid biasing the results by using differences between conditions to define the time window, we collapsed across conditions and then defined the time window as the time between P1 onset and P1 peak (thereby minimizing overlap from the N1 wave). Specifically, we computed a grand average across all trial types and used the 20% fractional peak latency to define P1 onset latency (Kiesel, Miller, Jolicoeur & Brisson, 2008) and the time of the maximum positive voltage to define P1 peak latency. This resulted in a measurement window of 66-102 ms for Experiment 1. Statistical analyses were conducted with analysis of variance (ANOVA), and all *p* values presented below reflect the Huynh-Feldt correction for heterogeneity of covariance.

3.1.2 Results

3.1.2.1 Behavioural Analyses.

D-prime scores (see Section 2.1.2.2) were calculated to compare participants' response sensitivity to targets between conditions. A one-way repeated measures ANOVA comparing single stimulus (M=4.89, SD=0.60), dual-near (M=4.70, SD=0.51) and dual-far (M=4.51, SD= 0.80) conditions revealed a significant main effect, $F(2,24) = 5.51$, $p =$

.011. Follow-up paired samples t-tests revealed a significant difference between dual-far and single stimulus conditions, $t(12) = 3.50$, $p = .004$, but no significant difference between dual-near and single stimulus, $t(12) = 1.84$, $p = .090$, nor dual-near and dual far $t(12) = 1.48$, $p = .164$.

3.1.2.2 Electrophysiological Analyses.

EEG data from the 13 participants remaining after artefact rejection were averaged, to produce grand average waveforms isolating the P1 and C1 components. The C1 can be seen in Figure 3.4 as the initial difference between the negative activation for stimuli presented in the upper visual field and the positivity to stimuli in the lower field (approximately 40-80 ms post stimulus). The C1 was unfortunately small and not distinct enough from baseline noise to analyse; however, a clear reversal in polarities followed, culminating in a large difference between upper and lower visual fields, which we termed the 'C2' wave (see also Fortune & Hood, 2003; Kappenman & Luck, 2012). The reversal in polarity of the C2 around the horizontal meridian, which is shown more clearly in Figure 3.5A, is consistent with V1 activation, and its timing is consistent with that of feedback into V1 from extrastriate areas (e.g., Fahrenfort, Scholte & Lamme, 2008). This suggests that the C2 reflects feedback signals arriving into V1, although we cannot be certain of this.

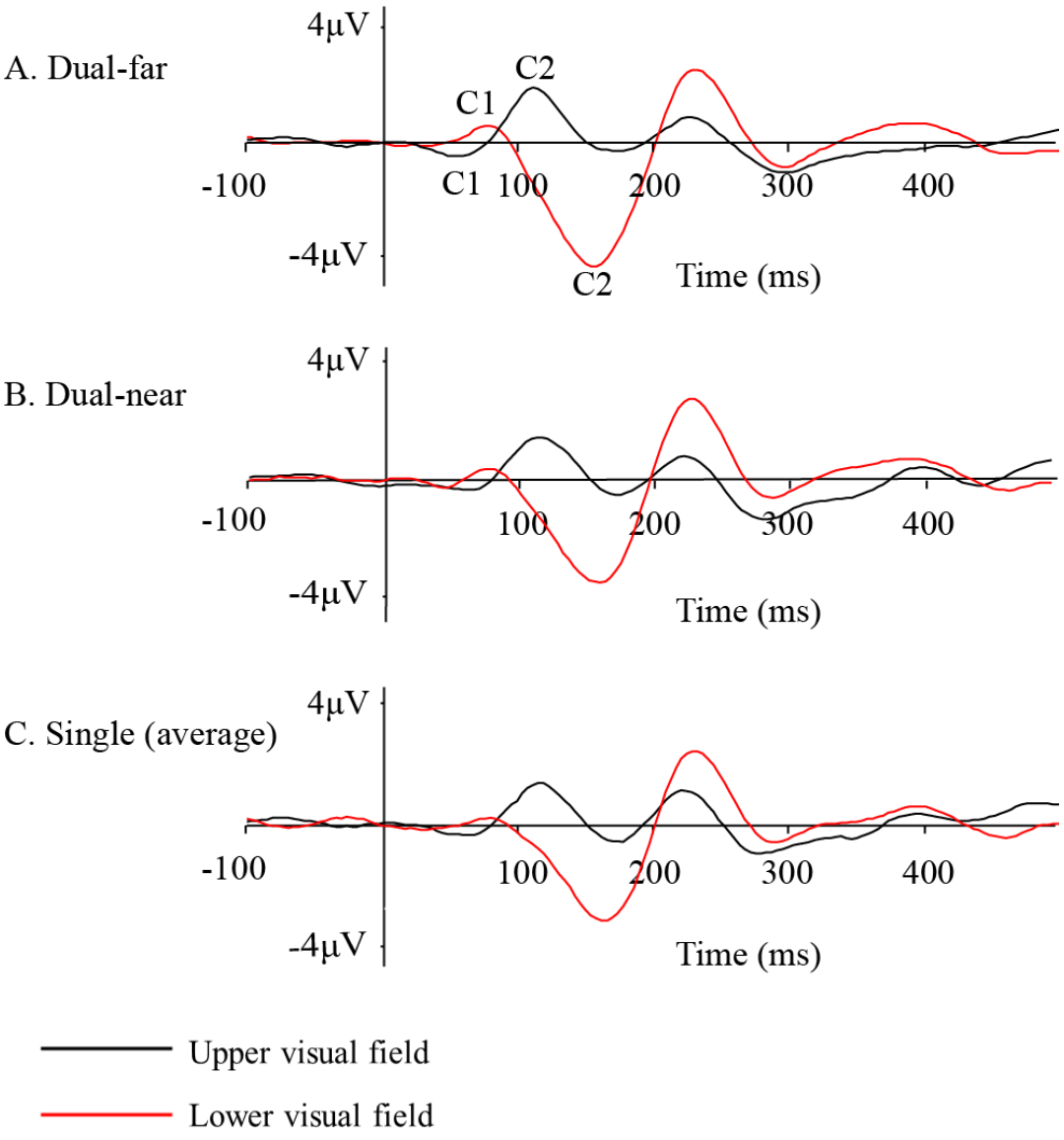


Figure 3.4. Experiment 1 grand average ERP waveforms from the C1/C2 electrode cluster (P1, O1, Iz, Pz, P2, POz, Oz, O2, referenced to the averaged mastoids) for upper- and lower-field stimuli in each of the stimulus configurations.

3.1.2.2.1 C2 Analyses.

Initially, a repeated measures ANOVA was conducted on the C2 component, between dual-near, dual-far and single average trial types, revealing a significant main effect, $F(2, 24) = 11.92$, $p < .001$. Further planned two-tailed paired-samples t-tests were then conducted (Figure 3.5B), with the aim of quantifying where on the spectrum between no competition (two simultaneous stimuli producing similar activation to two sequential stimuli) and extreme competition (two simultaneous stimuli producing similar activation to one single stimulus) the dual-near and dual-far conditions occurred.

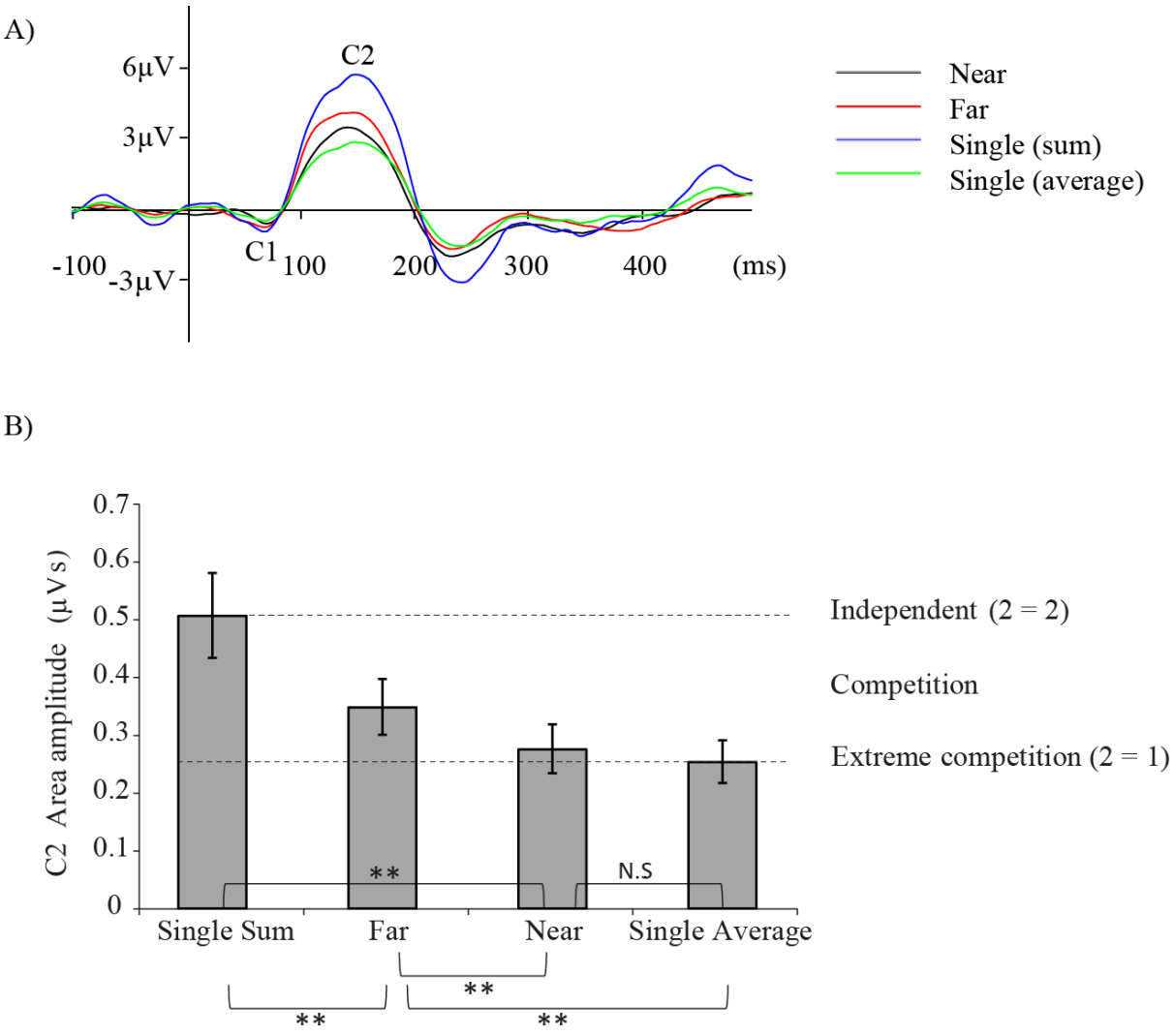


*Figure 3.5. A) Grand average upper-minus-lower difference waves from the C1/C2 electrode cluster (P1, O1, Iz, Pz, P2, POz, Oz, O2, referenced to the averaged mastoids) in each of the stimulus configurations. B) Area of the positive region in the C2 time window for the 4 trial types, with pairwise significance levels and error bars representing the standard error of the mean. * = $p < .05$. ** = $p < .01$.*

First, we tested the hypothesis that greater competition would occur between simultaneous stimuli when the gap between the stimuli was small, by comparing the dual-near and dual-far trial types. We found that the C2 was significantly smaller for the dual-near stimuli than for the dual-far stimuli, $t(12) = -3.69$, $p = .003$, confirming this prediction.

Next, to determine the extent of the competition between dual-far stimuli, we compared the C2 in this trial type with the single sum and single average C2 waveforms. The C2 in the dual-far waveforms was significantly smaller than the C2 in the single sum waveforms, $t(12) = -4.16$, $p = .001$, which is what would be expected if competition was

present between the two stimuli in the dual-far trials. Additionally, the C2 for the dual-far trials was significantly greater than the single average C2, $t(12) = 4.12$, $p = .001$, suggesting that the stimuli were not competing to the extent of being treated as a single stimulus.

The same comparisons were performed for the dual-near stimuli. The dual-near stimuli elicited significantly less activation than single sum, $t(12) = -5.85$, $p < .001$, providing evidence for competition between the near stimuli. The C2 to dual-near stimuli was not significantly different to than the single average C2, $t(12) = 1.24$, $p = .240$[3], suggesting that two near stimuli were under extreme competition, competing to the extent of producing similar activation to one single stimulus. Scalp maps (Figure 3.6A) show activation in central occipital areas, providing support for the hypothesis that the C1 reflects V1 activity.

[3] All of the planned comparisons that were significant in this chapter remained significant after False Discovery Rate (FDR) correction for multiple comparisons, unless otherwise specified.

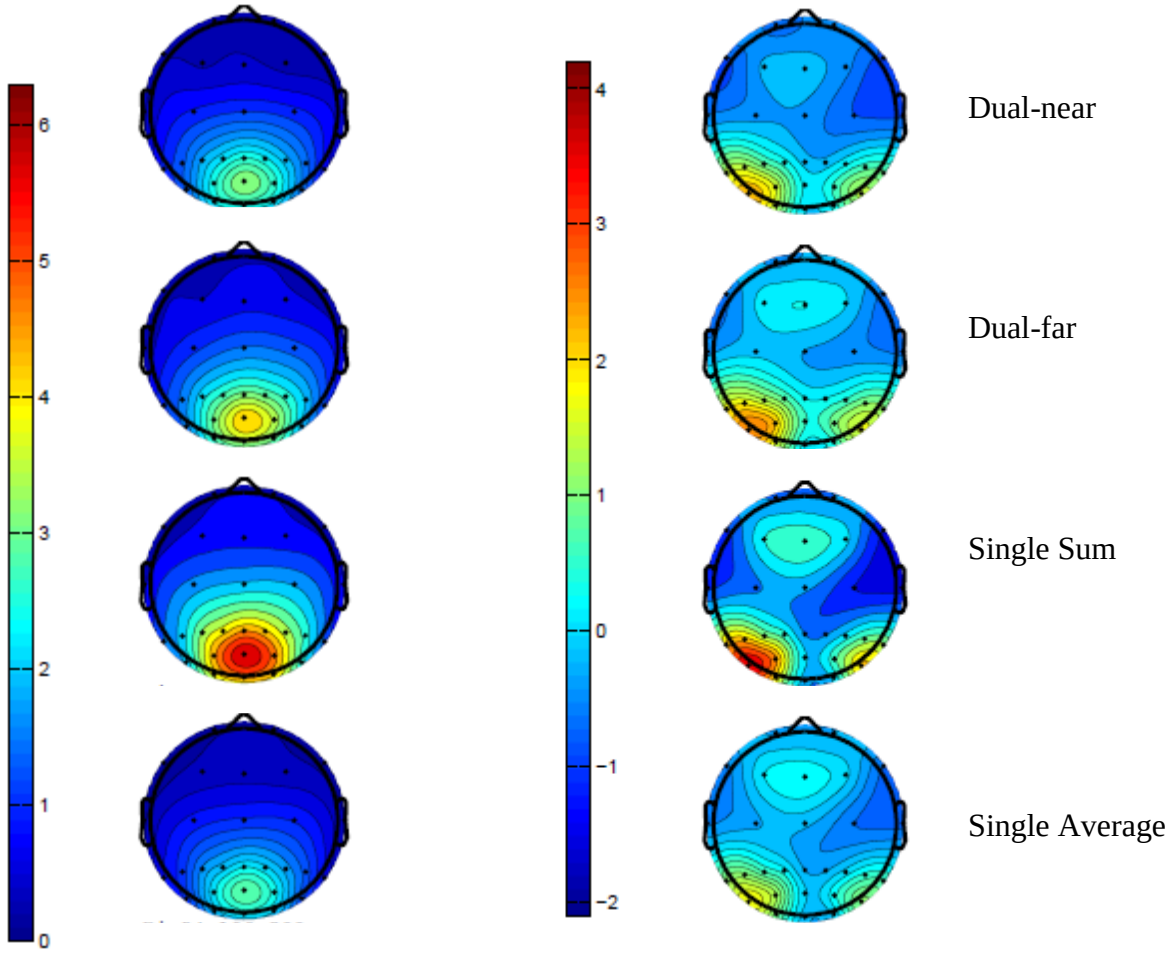


Figure 3.6. A) C2 scalp maps, showing the distribution of voltage in the upper minus lower difference waves from 100-200 ms. B) P1 scalp maps, showing the distribution of voltage in the time range of the early portion of the P1 wave (66-102 ms).

3.1.2.2.2 P1 Analyses.

The P1 wave can be easily observed in the waveforms from the lateral occipital electrode sites, collapsed across upper and lower fields (Figure 3.7A). In line with this, scalp maps for the individual conditions (Figure 3.6B) show bilateral lateral occipital activation in all conditions. P1 amplitude differed only slightly between the dual-near, dual-far, and single average waveforms, but it was much smaller for these waveforms than for the single sum waveforms. This suggests the presence of competition between the two simultaneous stimuli.

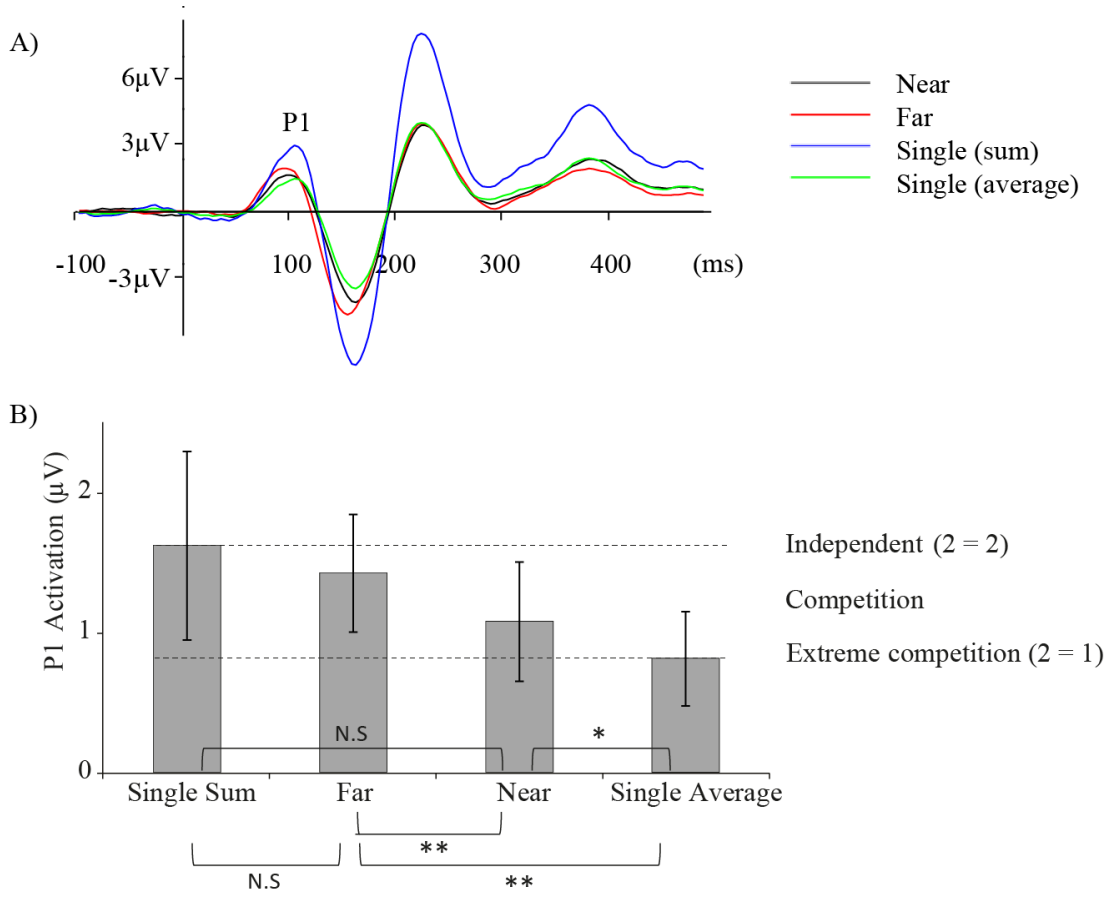


*Figure 3.7. A) Grand average ERP waveforms from the P1 electrode cluster (P3, P5, P7, P9, PO7, PO3, P4, P6, P8, P10, PO8, PO4, referenced to the averaged mastoids), collapsed across upper- and lower-field locations in each of the stimulus configurations. B) Mean amplitude in the P1 time window for the 4 trial types, with pairwise significance levels and error bars representing the standard error of the mean. * = p < .05. ** = p < .01.*

A repeated measures ANOVA between dual-near, dual-far and single average trial types revealed a highly significant main effect, $F(2, 24) = 13.93$, $p < .001$. Planned paired-samples t-tests were therefore conducted (Figure 3.7B). The dual-near P1 wave was revealed to be significantly smaller than dual-far, $t(12) = -3.34$, $p = .006$, suggesting increased competition for the near stimuli relative to the far at the P1 stage.

A marginally significant difference was found between the dual-near and single sum waveforms, $t(12) = -2.03$, $p = .066$, but there was no significant difference between the dual-far and single-sum waveforms, $t(12) = -0.68$, $p = .51$. This suggests possible competition between the two stimulus locations in dual-near trials, but not in dual-far trials.

The P1 was also significantly larger for the dual-near than the single average waveform, $t(12) = 2.29$, $p = .041$, although this comparison did not retain significance after FDR correction for multiple comparisons. There was, however, a significant difference between the dual-far and single average waveforms, $t(12) = 4.78$, $p < .001$. This indicates that, at least in the dual-far condition, competition was not extreme enough to reduce P1 amplitude to the level of a single stimulus.

It is important to note that the P1 component in Experiment 1 was fairly small, and standard errors were relatively large. This is especially noticeable in the single sum condition, where the doubling of the single stimulus activation also doubled the error present. Therefore the null results in these t-tests should be viewed with particular caution.

3.1.3 Discussion

The significant difference in P1 activation between single average and dual-far stimuli suggests that little inter-stimulus competition was present in extrastriate cortex in response to far stimuli in Experiment 1, with activation significantly greater than that elicited by a single stimulus alone. The lack of significant difference between dual-far and single sum conditions suggests a lack of extrastriate competition for stimuli in the dual-far trials. However, the difference between dual-near and single sum stimuli was approaching significance. When viewed together with the significant difference between dual-near and dual-far stimuli, this suggests the presence of weak competition for near stimuli, but little or no competition for far stimuli, contrary to our hypothesis of strong competition in extrastriate RFs for both near and far stimuli. Unfortunately, the C1 elicited in Experiment 1 was very small, and not adequately different from baseline noise to justify analysis. However, analysis of the following positive deflection, which we termed the 'C2', revealed a significant difference between activation to near and far stimuli, as predicted to occur in the presence of inter-stimulus competition. Viewed with the hypothesis that the C2 arises from V1 after extrastriate feedback, this suggests that competition elicited by item proximity is influencing activation after this feedback, but still very early in the information processing hierarchy. Interestingly, there was also a significant difference between the far and single average conditions, and between both near and far conditions and single sum (see Figure 3.5). This suggests that the stimuli are neither processed independently (for which we would expect near or far = single sum), nor do they produce the same level of activation regardless of the number of stimuli (near or far = single average). Instead, by the time feedback from extrastriate areas reaches striate cortex, pairs

of stimuli produce an intermediate level of activation, likely due to the combination of competition mechanisms and feedback.

However, behavioural target-detection results revealed a significant difference in response sensitivity (d-prime) between the dual-far and single stimulus conditions, which may indicate the presence of another variable which differed between these conditions. For example, it is possible that the reduced dual-far d-prime relative to single average is associated with the requirement to extend attentional focus across a larger area. It is also worth noting that the standard deviation for the dual-far condition was higher than the single average and dual-near conditions (0.80 vs 0.60 and 0.51 respectively). Despite the general robustness of ANOVA in response to differences in standard deviation, these results should therefore be treated with additional caution.

In Experiment 2 we aimed to assess the replicability of these findings and also to increase the size of the C1 component, by presenting the stimuli bilaterally to increase V1 stimulation (Fu, Fedota, Greenwood & Parasuraman, 2010). The bilateral stimulus presentation also forced participants to attend across the whole top/bottom half of the screen, eliminating the previously mentioned difference in extent of attentional focus required between the three conditions.

3.2 Experiment 2

3.2.1 Methods

Methods were as described for Experiment 1, except as detailed below.

3.2.1.1 Participants.

Twenty participants were recruited from the Bangor University participant pool, and each took part in a testing session lasting approximately 2.5 hours in exchange for either course credit or payment of £6/hour. Three were later excluded, two due to the detection of artefacts exceeding an a priori criterion of >30% of trials, and one due to a target hit rate of lower than 2 SD below the mean. This resulted in a final sample of N = 17 (ages 18-31, mean age = 21.2, 8 females).

3.2.1.2 Stimuli.

Stimuli were presented on a 24” Samsung LCD monitor. They were as described for Experiment 1 except that, to maximize the size of the C1, in addition to presenting

either a single checkerboard or two simultaneous checkerboards in each display additional (non-target) stimuli were presented simultaneously in mirror-image positions in the opposite visual field (Fu, Fedota, Greenwood & Parasuraman, 2010). Note that the classical RFs of neurons in V1 and V4 do not cross far into the ipsilateral side, so there should be minimal direct competition between the mirror-image stimulus pairs used in Experiment 2.

3.2.1.3 Procedure.

During the task, participants earned points for correctly identifying missing checks and lost points for incorrect responding, and those reaching the highest point total were awarded £10 online shopping vouchers.

3.2.1.4 EEG acquisition/processing.

The signals were recorded in single-ended mode, low-pass filtered with a 5th-order sinc function (half-power cutoff at 410 Hz), and digitized at 2048 Hz. All timings were within 2 ms, and there were no timing differences between the different stimulus locations (which is an advantage of the LCD display over the CRT display used in Experiment 1). In the final sample, an average of 13.65% of trials was rejected (SD = 7.43).

3.2.1.5 Statistical Analyses.

We used the signed area approach (Sawaki, Geng & Luck, 2012; Luck, 2014) for measurement of both C1 and C2. As in Experiment 1, we collapsed across conditions and locations before defining the P1 time window as the time between P1 onset and P1 peak. The resulting measurement window was 78-117 ms. In addition to the analyses described for Experiment 1, the interaction between component and condition was assessed, using a series of 2 x 2 ANOVAs comparing C1 and C2 for pairs of conditions. It was hypothesised that if competition had a significant influence upon the changes in activation between C1 and C2, the interaction between single average and dual conditions should be significant.

3.2.1.6 Source Analyses.

To obtain information about the possible neural sources of the data, we applied low resolution electromagnetic tomography (sLORETA; Pascual-Marqui, 2002) to the C1, C2, and P1 measurements, using a cortical surface reconstruction of the standard MNI152 brain to constrain the solutions. These analyses were performed on the grand average data,

to maximize signal-to-noise ratio. The goal of these analyses was not to provide definitive evidence regarding the neural generators, but simply to determine whether the scalp distributions were at least consistent with the assumed generator locations of the C1, C2, and P1 waves.

3.2.2 Results

3.2.2.1 Behavioural Analyses.

Participants' response sensitivity was compared between conditions using a one-way repeated measures ANOVA assessing single stimulus (M=4.66, SD=0.47), dual-near (M=4.56, SD=0.55) and dual-far (M=4.58, SD=0.51) conditions. In contrast with Experiment 1, the main effect was not significant, $F(2,32) = .66$, $p = .525$. Critically, this suggests that participants could discriminate between targets and non-targets similarly in each condition, ruling out differences between participants' ability to perceive stimuli in the different conditions.

3.2.2.2 Electrophysiological Analyses.

Data from the final sample of 17 participants were averaged, as described for Experiment 1. The C1/C2 upper- and lower-field waveforms are shown in Figure 3.8, where the C1 is clearly visible between approximately 60-100 ms as the initial difference between the negative activation for stimuli presented in the upper visual field and the positive activation to lower field stimuli.

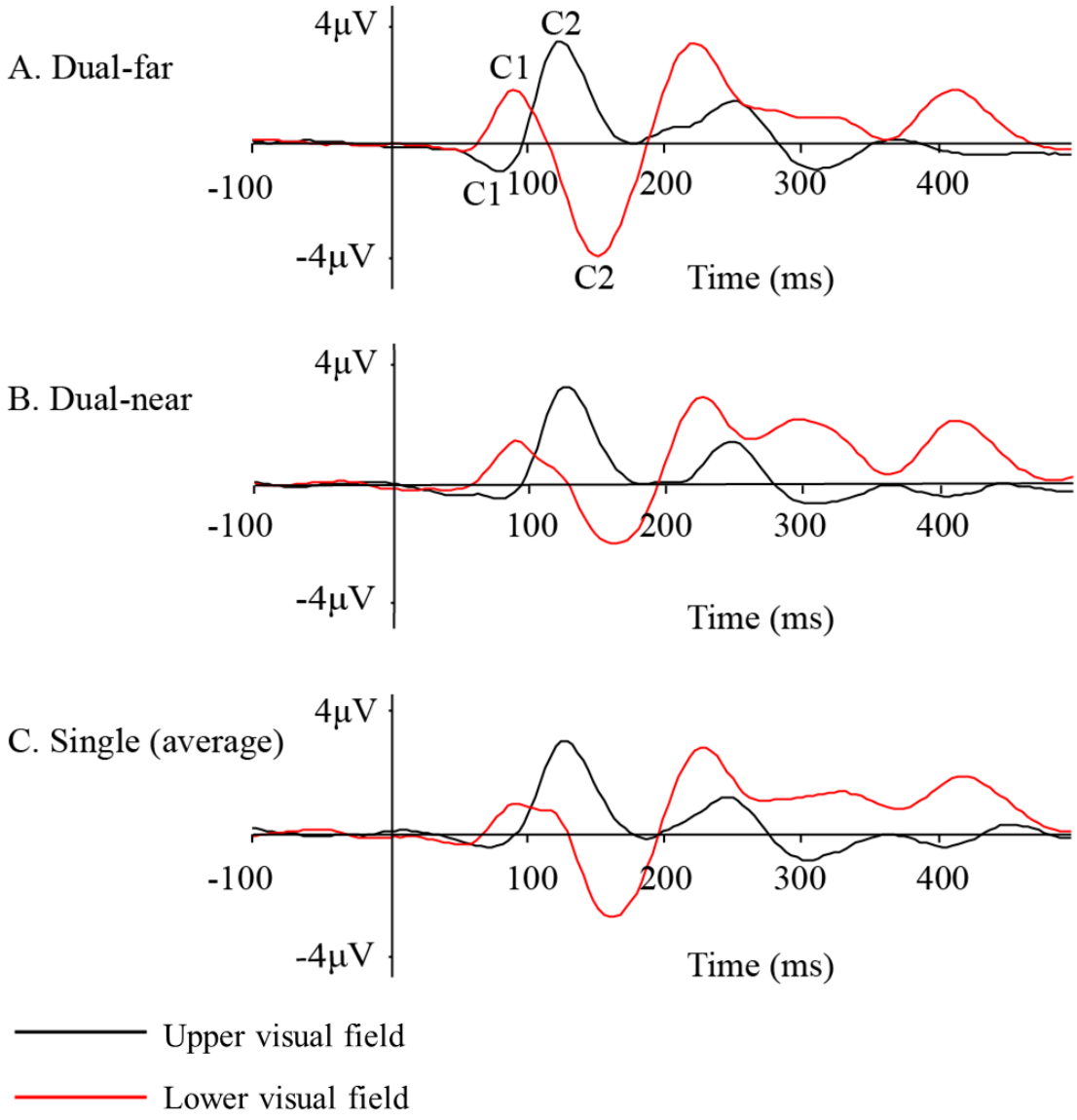


Figure 3.8. Grand average ERP waveforms from the C1/C2 electrode cluster (P1, O1, Iz, Pz, P2, POz, Oz, O2, referenced to the averaged mastoids) for upper- and lower-field stimuli in each of the stimulus configurations.

3.2.2.2.1 C1 Analyses.

The C1 in the upper-minus-lower grand average was smallest in response to the single stimuli (when averaged rather than summed), larger for the dual-near stimuli, and even larger for the dual-far stimuli (Figure 3.9A). The C1 for the dual-far stimuli was similar in size to that of the single sum waveform, suggesting that the far stimuli were processed largely independently at this stage. In contrast, the C1 for the dual-near stimuli

was approximately midway between the C1 for the single sum and single average stimuli, consistent with competition between the two dual-near locations.

The C1 amplitude measurements for dual-near, dual-far and single average conditions were submitted to a one-factor repeated measures ANOVA, which revealed a significant main effect, $F(2, 32) = 12.67$, $p < .001$. As in Experiment 1, planned two-tailed paired-samples t-tests were then conducted (Figure 3.9B) to test specific hypotheses. First, we tested the hypothesis that greater competition would occur between simultaneous stimuli when the gap between the stimuli was small, by comparing the dual-near and dual-far trial types. We found that the C1 was significantly smaller for the dual-near stimuli than for the dual-far stimuli, $t(16) = -2.41$, $p = .028$, confirming this prediction.

Next, to determine the level of competition between the dual-far stimuli, we compared the C1 in this trial type with the single sum and single average C1 waveforms. The C1 in the dual-far waveforms was nearly identical to the C1 in the single sum waveforms, $t(16) = -1.07$, $p = .299$, which is what would be expected if the two stimuli in the dual-far trials were processed completely independently. Consistent with this, the C1 for the dual-far trials was significantly greater than the single average C1, $t(16) = 4.38$, $p < .001$.

The same comparisons were performed for the dual-near stimuli. The dual-near stimuli elicited significantly less activation than single sum, $t(16) = -2.38$, $p = .030$, providing further evidence for competition between the near stimuli. The C1 to dual-near stimuli was also significantly greater in amplitude than the single average C1, $t(16) = -2.96$, $p = .009$, suggesting that two near stimuli did not compete to the extent of producing the same activation as a single stimulus.

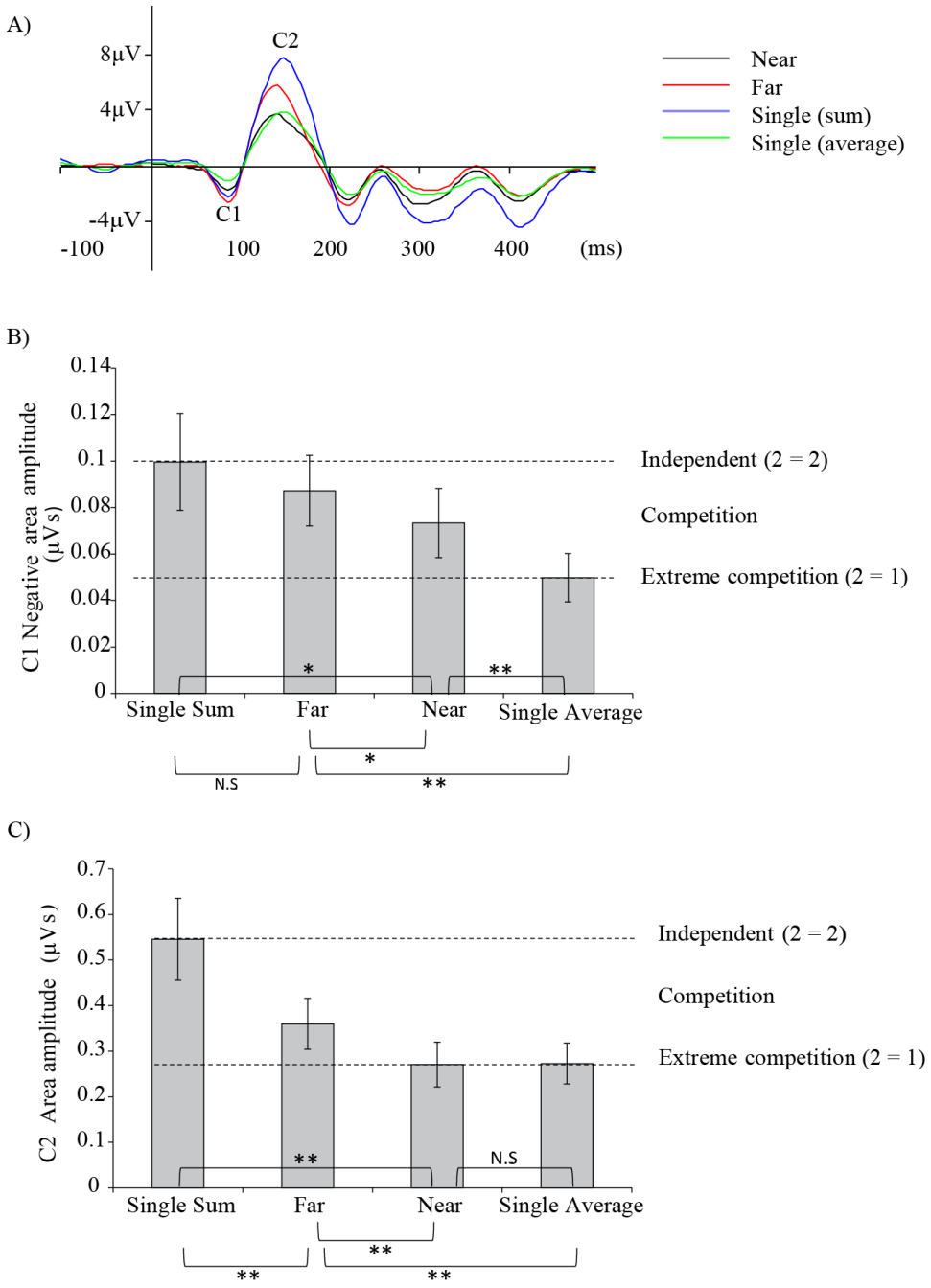


*Figure 3.9. A) Grand average upper-minus-lower difference waves from the C1/C2 electrode cluster (P1, O1, Iz, Pz, P2, POz, Oz, O2, referenced to the averaged mastoids) in each of the stimulus configurations. B) Area of the negative region in the C1 time window for the 4 trial types, with pairwise significance levels and error bars representing the standard error of the mean. * = p < .05. ** = p < .01. C) Area of the positive region in the C2 time window for the 4 trial types, with pairwise significance levels and error bars representing the standard error of the mean. * = p < .05. ** = p < .01.*

Figures 3.10A and 3.10B show the scalp distributions of the upper-minus-lower difference waves from 50-100 ms (C1) and 100-200 ms (C2) respectively. Both of these scalp distributions exhibited a focus over the occipital pole, consistent with a generator in area V1 (but not ruling out other potential generators, such as V2).

Figure 3.11A shows the sLORETA solution for the C1 wave, based on the upper-minus-lower difference waves for the dual-far trials, for which the C1 was largest (solutions were similar for the other trial types). The estimated current flow was maximal along the occipital midline, which is the location of area V1. The Talairach coordinate of the maximum current flow was (X= -5, Y= -96, Z= 19), which is similar to the average coordinates of the C1 dipoles (X= 1, Y= -85, Z= 12) reported by Di Russo et al. (2002), which in turn closely matched the location of area V1 determined from fMRI data. Note that some differences in V1 coordinates would be expected due to differences in stimulus location between studies.

We also conducted an sLORETA analysis on a difference wave that focused on the independence of the C1 when processing two simultaneous stimuli in the same hemifield. Specifically, we took the upper-minus-lower difference waves and subtracted the average-single condition from the dual-far condition. Any difference between these two upper-minus-lower difference waves reflects independent (additive) contributions of the stimuli in the dual-far displays. Figure 3.11B presents the sLORETA solution for this double difference wave, showing that like the basic C1 itself, the estimated current flow for this "independence effect" is maximal along the occipital midline. The present data do not provide the precision needed to distinguish between area V1 and the surrounding extrastriate areas, but these results demonstrate that the scalp distributions of the C1 wave and the C1 independence effect are at least consistent with a generator in area V1.

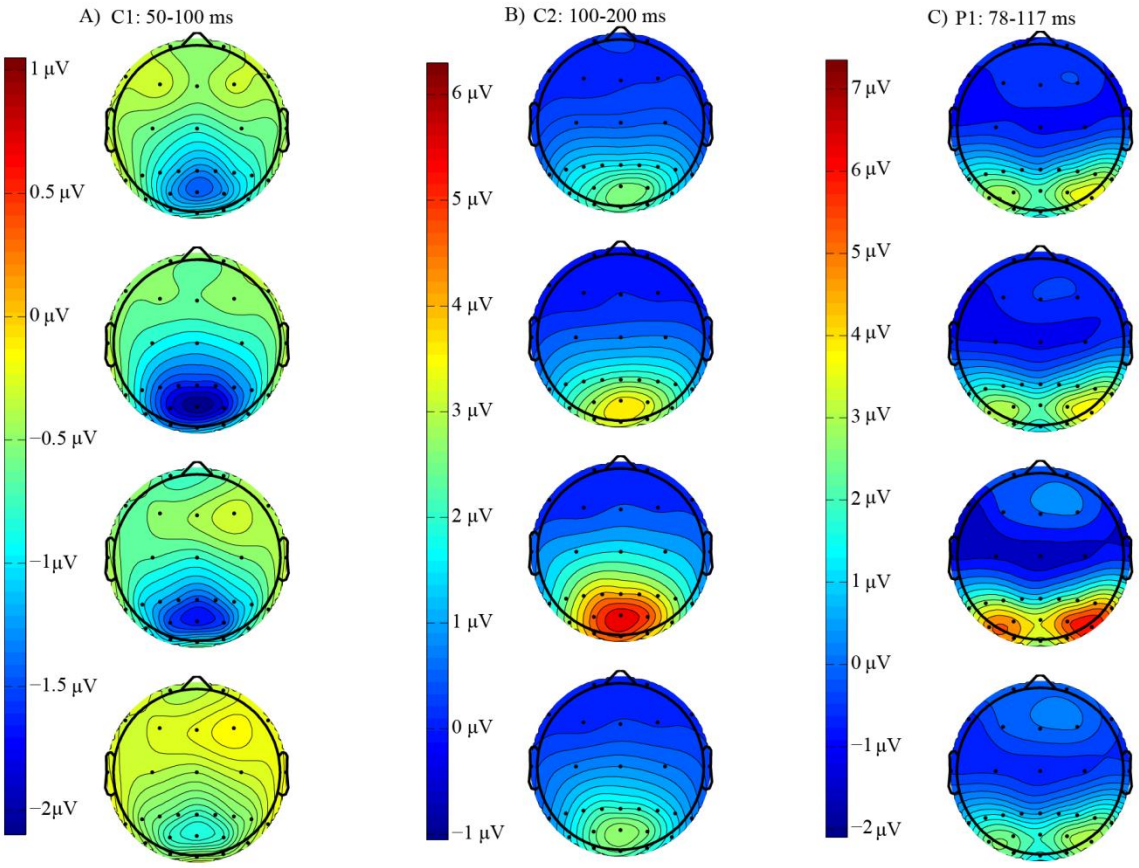


Figure 3.10. A) C1 and B) C2 scalp maps, showing the distribution of voltage in the upper minus lower difference waves from 50-100 ms, and 100-200 ms respectively. C) P1 scalp maps, showing the distribution of voltage in the time range of the early portion of the P1 wave.

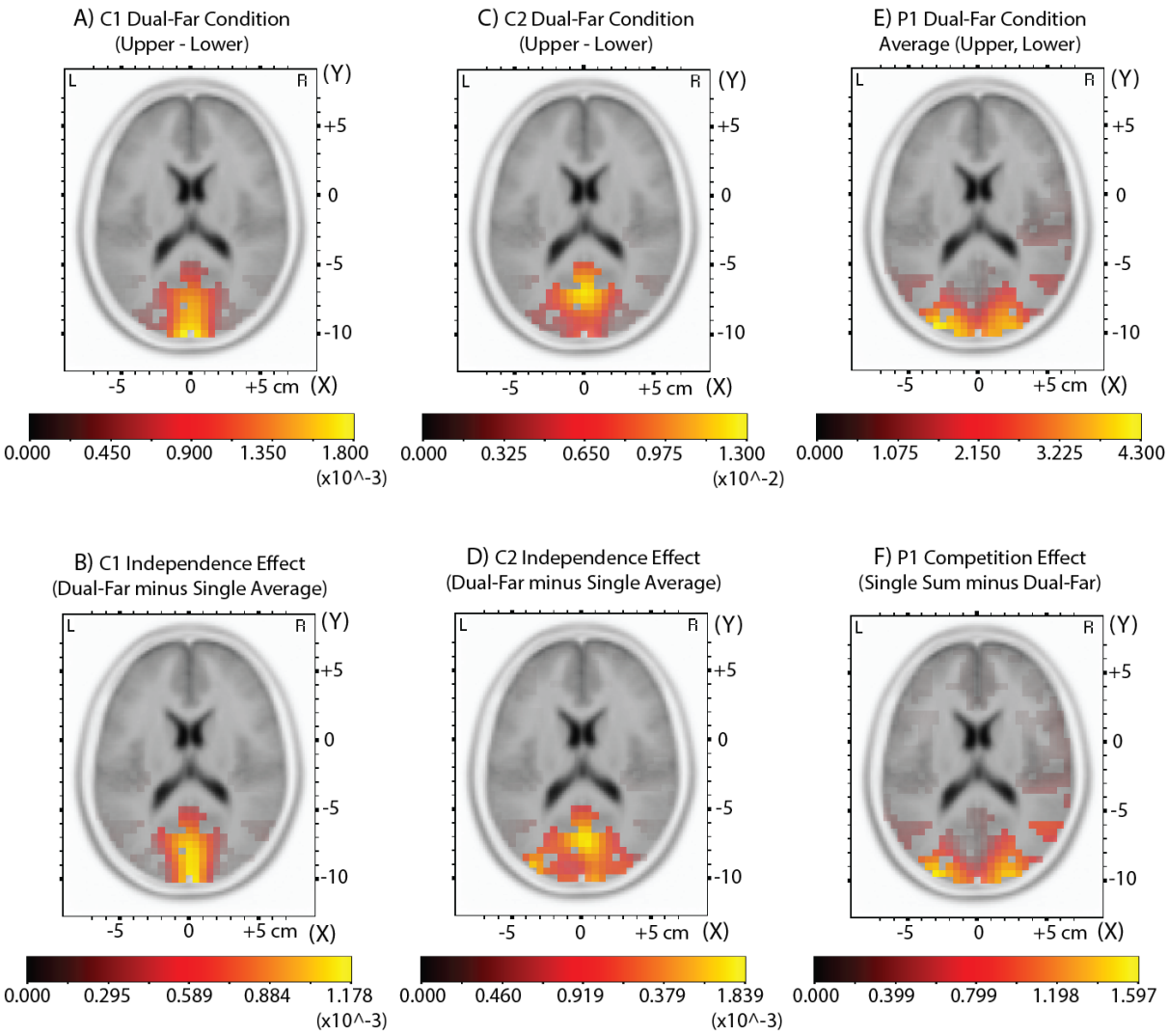


Figure 3.11. Estimated distribution of current flow over the cortical surface for A) Dual-Far upper minus lower difference wave, B) C1 Dual-Far difference wave minus Single Average difference wave, C) C2 Dual-Far upper minus lower difference wave, D) C2 Dual-Far difference wave minus Single Average difference wave, E) P1 Dual-Far average, F) P1 Single Sum average minus Dual-Far average. Note that each map has a separate scale to maximize the visibility of the estimated current distribution.

3.2.2.2.2 C2 Analyses.

For the C2 wave, a repeated measures ANOVA between dual-near, dual-far and single average trial types again revealed a significant main effect, $F(2, 32) = 7.85$, $p=.002$. The follow-up paired t-test between the dual-near and dual-far trial types was significant, $t(16) = -3.98$, $p = .001$, once again demonstrating significantly greater competition between the dual-near stimuli than between the dual-far (Figure 3.9C).

However, for both the dual-near and dual-far stimuli, the C2 wave showed greater evidence of competition between the simultaneous stimuli than was observed for the C1 wave. This can be seen by comparing Figures 3.9B and 3.9C, in which the amplitudes for the simultaneous stimuli were closer to the "extreme competition" level for the C2 wave than for the C1 wave. This greater degree of competition was also evidenced in the statistical comparisons. Paired t-tests indicated significant differences in C2 amplitude between the dual-far and single sum waveforms, $t(16) = -3.79$, $p = .002$, and between the dual-far and single average waveforms, $t(16) = 3.20$, $p = .006$. These effects indicate a moderate level of competition between the far locations at the C2 stage. Paired t-tests also yielded a significant difference between the dual-near and single sum trial types, $t(16) = -4.95$, $p < .001$, but not between the dual-near and single average trials, $t(16) = -0.82$, $p = .936$. These effects suggest fairly extreme competition between the two locations in the dual-near stimuli at the C2 stage. Note that these results support and replicate results from the Experiment 1 C2 analyses.

The sLORETA solutions for the C2 wave (based on the upper-minus-lower difference wave for the dual-far trials) and the C2 independence effect (dual-far minus single average) are shown in Figures 3.11C and 3.11D. Like the C1 solutions, the maximal current flow was along the occipital midline, consistent with a generator in area V1. However, the C2 solutions were more broadly distributed, suggesting that the C2 wave and C2 independence effect may involve surrounding extrastriate areas as well as striate cortex.

The Talairach coordinates of the maximum current flow for the C2 wave was (X= 0, Y= -67, Z= 26), which is reasonably close to the coordinates of the maximum current flow for the C1 component, as described above. Moreover, it was right on the midline rather than being on the lateral surface of the brain, which is also consistent with a generator in V1.

3.2.2.2.3 P1 Analyses.

A repeated measures ANOVA between dual-near, dual-far and single average trial types revealed a marginally significant main effect, $F(2, 32) = 3.67$, $p = .050$. Planned paired-samples t-tests (Figure 12B) yielded significant differences between the dual-near and single sum waveforms, $t(16) = -3.18$, $p = .006$, and also between the dual-far and single sum waveforms, $t(16) = -3.17$, $p = .006$. This suggests that competition was present between the two stimulus locations in both the dual-near and dual-far trials. In addition,

the dual-near and dual-far P1 waves were nearly identical, with no significant difference between them, $t(16) = -0.34$, $p = .737$, providing evidence that competition is equivalent between these two distances at the P1 stage. The P1 was also significantly larger for the dual-near waveform than for the single-average waveform, $t(16) = 2.61$, $p = .019$ indicating that activation for the near stimuli was not reduced to the level of a single stimulus. The magnitude of this difference was nearly identical when the dual-far waveforms were compared with the single average waveforms, but this difference did not quite reach significance, $t(16) = 1.95$, $p = .070$. This small difference in *p*-values presumably reflects noise rather than any real difference between the dual-near and dual-far conditions. In any case, the pattern of results clearly indicates that the two locations compete with each other at the stage of the P1 wave in both dual-near and dual-far configurations, but it is likely that the competition does not bring the P1 amplitude all the way down to the level observed for a single stimulus.

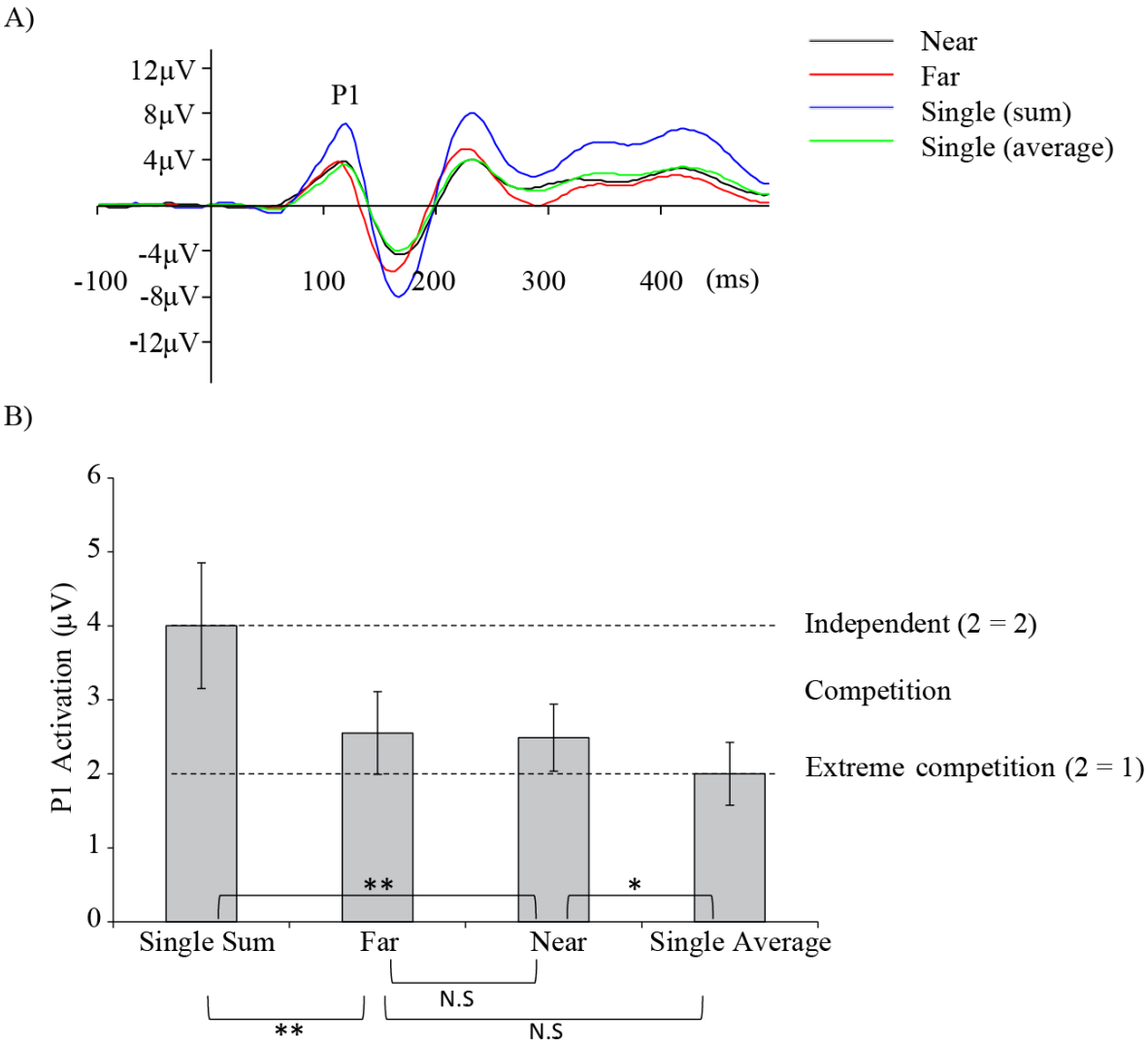


*Figure 3.12. A) Grand average ERP waveforms from the P1 electrode cluster (P3, P5, P7, P9, PO7, PO3, P4, P6, P8, P10, PO8, PO4, referenced to the averaged mastoids), collapsed across upper- and lower-field locations in each of the stimulus configurations. B) Mean amplitude in the P1 time window for the 4 trial types, with pairwise significance levels and error bars representing the standard error of the mean. * = p < .05. ** = p < .01.*

For the P1 wave, sLORETA was applied to the data from the dual-far trials after averaging across upper- and lower-field stimuli. As shown in Figure 3.11E, the estimated distribution of current flow was more lateral for the P1 wave than for the C1 and C2 waves. sLORETA was also applied to the difference in P1 amplitude between the single sum waveforms and the dual-far waveforms, which is a means of quantifying the effect of competition on the P1 wave. In other words, this amplitude increases as the dual-far waveform becomes less and less like the sum of the activity to the individual stimuli. As

shown in Figure 3.11F, the estimated current flow for this "competition effect" was also maximal over lateral occipital cortex.

The maximal current flow for the P1 wave had coordinates of (X= -20, Y= -97, Z=5) in the left hemisphere and (X= 15, Y= -97, Z= 5) in the right hemisphere. These are fairly close to the average coordinates of the early P1 dipole (X= ±32, Y= -84, Z= 10) identified by Di Russo et al. (2002), which was localized on the basis of fMRI-based topographical mapping to areas V3/V3a and surrounding areas of the middle occipital gyrus. Again, it should be noted that some differences in coordinates would be expected between studies due to differences in stimulus location. Thus, we cannot say that the P1 in the present study had exactly the same generator as the P1 in the Di Russo et al. (2002) study, but the two studies yielded reasonably similar estimates.

3.2.2.2.4 C1/C2 interaction analyses.

Three further 2 x 2 ANOVAs were conducted, to ascertain the significance of the interaction effect between C1 and C2 components and several pairs of conditions. The first ANOVA revealed a significant interaction between dual-near and dual-far conditions and C1/C2 components, $F(1,16)= 10.67$, $p = .005$. However, neither the ANOVA involving single average and dual-near conditions nor that including single average and dual-far conditions revealed significant interactions, $F(1,16)= 0.61$, $p = .447$ and $F(1,16)= 2.33$, $p = .146$ respectively. This suggests that although competition does influence the change in activation between the pairs of stimuli at different proximities, it is not the main factor explaining the difference between the dual conditions and the single stimulus (average) condition.

3.2.3 Discussion

The significant difference in C1 amplitude between the near and far conditions suggests that competition is occurring in primary visual cortex prior to extrastriate feedback. Moreover, this competition appears to be stronger in the near stimulus condition than the far, consistent with predictions given the small RF sizes in V1.

As in Experiment 1, a significant difference between C2 activation elicited by near and far stimuli suggests that inter-stimulus competition is influencing activation in V1 after extrastriate feedback. By this stage in processing, a moderate amount of suppression is present in the far stimuli condition, as shown by significant main effects in both far Vs single average and far Vs single sum t-tests. In contrast, stimuli in the near condition

appear to be under stronger competition in V1 after feedback, evidenced by the lack of a significant difference between the near and single average conditions.

In addition, analysis of the interaction between condition (dual-near/dual-far) and C1/C2 magnitude shows a significant increase in the difference in activation between near and far stimuli, as activation passed between areas indexed by the C1 and C2 components. This was expected, given a larger predicted increase in competition for far stimuli (which should not compete in V1 as indexed by the C1 component) than for the near stimuli (which should show moderate competition in the C1). This significant interaction further supports the idea that competition for far stimuli was present in the C2 wave.

Analysis of the P1 suggests that in extrastriate cortex, pairs of stimuli produce similar levels of activation regardless of proximity. By this stage in processing a moderate amount of competition occurs, with pairs of stimuli neither being processed as though two sequential stimuli, nor as one single stimulus.

Importantly, the lack of significant main effect of condition for response sensitivity suggests that participants could discriminate between targets and non-targets similarly in each condition, ruling out confounds due to differences between participants' ability to perceive the different conditions.

3.3 General Discussion

Overall, the pattern of results from these experiments suggests that the spatial range of competition between simultaneous stimuli increases between the initial C1 wave (likely reflecting V1 neurons) and the P1 wave (which likely reflects neurons in extrastriate cortex). This pattern is consistent with decades of single cell neurophysiological research (e.g., Luck, Chelazzi, Hillyard & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Chelazzi & Desimone, 1999; Treue & Maunsell, 1996) as well as human fMRI research (Kastner, De Weerd, Desimone & Ungerleider, 1998; Kastner et al., 2001), and it demonstrates that the present experimental approach provides a sensitive and valid means of assessing competitive interactions at specific time points and inter-item distances. This approach therefore provides a valuable tool that can be used to assess how these interactions vary as a function of stimulus properties (e.g., similarity) and cognitive manipulations (e.g., attention) in human subjects. An analogous approach has been used in fMRI experiments (e.g., Kastner, De Weerd, Desimone & Ungerleider, 1998; Kastner et

al., 2001), but the present approach can isolate competition at specific time points rather than collapsing across hundreds or thousands of milliseconds.

We found that the C1 response to two individually presented stimuli (i.e., the single sum condition) was nearly equivalent to the sum of the C1 responses to the two individual stimuli when they were separated by a 2° gap, indicating minimal competition at this distance in primary visual cortex. However, when the separation was reduced to 0.16°, the C1 response to the two simultaneous stimuli was significantly less than the response to the two stimuli presented individually (and smaller than the response to two stimuli presented simultaneously with a 2° gap). This provides strong evidence of competition between the two stimuli at this close proximity. However, the C1 response to the dual-near stimuli was still larger than the response to a single stimulus, indicating that the competition was only moderate. This likely reflects the fact that, although some V1 receptive fields contained parts of both stimuli, many other V1 receptive fields presumably contained just one of the two stimuli.

It is important to note the recent controversy about whether the C1 wave necessarily reflects activity in area V1 (Ales et al., 2010, 2013; Kelly et al., 2013a, 2013b; See Section 2.2.1.1). The most plausible conclusion from these papers is that a polarity reversal for upper- versus lower-field stimuli is not by itself sufficient to discriminate among V1, V2, and V3, but the combination of the particular point at which the polarity reverses (Clark, Fan & Hillyard, 1995; Jeffreys & Axford, 1972) and the polarity and scalp distribution of the C1 provide strong evidence that it arises from area V1. The present C1 results therefore very likely reflect V1, with little or no contribution from V2 and V3.

The C2 component showed a different pattern to that of the C1. Less is known about this component, but the fact that its polarity reverses for upper- versus lower-field locations suggests that it may arise in area V1, and its timing suggests that it reflects feedback from later visual areas. Its scalp distribution is also consistent with a generator in striate and/or early extrastriate areas (Figure 3.10B). Like the C1 wave, the C2 wave was smaller for dual-near than for dual-far stimuli, indicating that competition can be reduced by a spatial gap of only 2° at this stage. However, like the P1 wave, the C2 wave was significantly smaller for dual-near stimuli than for the sum of the single-location stimuli, indicating that at least some competition was present even with a 2° gap between the stimuli. This pattern may reflect the combination of an anatomically early generator source (V1 and perhaps V2/V3) along with a relatively late time of occurrence (after the P1 wave). This combination may allow differential competition between our near and far

stimulus pairs (separated by a 0.16° gap versus a 2° gap) owing to the small RFs in area V1, while still providing substantial interactions between the stimuli owing to feedback from areas with larger receptive fields.

However, if the change in activity between the C1 and C2 components were owing solely to increases in inter-stimulus competition, we would expect a significant interaction between single average C1/C2 activation and dual (-near and -far) conditions' activation. The lack of a significant interaction suggests the additional influence of another related variable, such amount of visual stimulation present. Furthermore, further research is needed to determine the anatomical generator of the C2 wave and to assess the hypothesis that it reflects feedback from higher-level extrastriate areas into striate and early extrastriate areas.

The pattern of results was different again for the P1 wave, which likely arises in extrastriate cortex (Di Russo, Martinez, Sereno, Pitzalis & Hillyard, 2002), with Experiments 1 and 2 showing slightly different results. As hypothesized, pairs of stimuli in Experiment 2 produced similar P1 amplitudes regardless of the inter-item distance, although in Experiment 1 this was not the case, with near stimuli producing a smaller P1 than far. This suggests that in Experiment 1, near stimuli were under stronger competition in extrastriate cortex than far stimuli, whereas in Experiment 2 stimuli in each trial type was under similar levels of competition. In support of this idea, the amplitudes for near pairs were substantially reduced relative to the sum of the single-stimulus P1 responses in both experiments, suggesting the presence of extrastriate competition in the near trial type. However, for the far pairs there was a substantial reduction only in Experiment 2.

In both experiments, regardless of the amount of competition present, P1 amplitude for stimulus pairs was not reduced all of the way to the level of the response to a single stimulus. The P1 was always substantially larger in the dual trial types than in the single average condition. This suggests that competition in either proximity condition does not bring the P1 amplitude down to single stimulus level. This difference in results between experiments may indicate an interaction due to the presence of the mirror-image stimuli in Experiment 2, although this is unlikely, since V3/V4 receptive fields do not extend far across the vertical midline (e.g., Gattass, Sousa & Gross, 1988).

In general, these results indicate the presence of substantial and similar competition between locations in dual-near and dual-far trials. Note, however, that the distance between stimuli was only 2° in the dual-far trials, and the amount of competition would likely be reduced if the distance between the stimuli were increased further.

However, there are a number of assumptions which affect should be considered when interpreting this data. We are assuming, in line with previous research (e.g., Nunez & Srinivasan, 2006), that two simultaneously presented stimuli will elicit activation equivalent to the sum of activation to the same two stimuli presented individually, in the absence of competitive interactions. Additionally, as with the majority of ERP studies, we make the assumption that the peaks we are measuring reflect individual components each corresponding to a separate and distinct stage in visual processing. This is never going to be entirely accurate, as the observed ERP signal consists of a number of components superimposed upon one another (Luck, 2005). However, we took steps during analysis to minimise the overlap of the main neighbouring components as much as possible, for example by using difference waves for the C1 and C2, and by strategically choosing the portion of the P1 which should be least effected by such overlap. We are also assuming that differences between these peaks reflect differences in processing. In addition, the use of ERP components to infer what is going on in different areas of the visual system relies heavily on previous research into these components and from which areas they are likely to arise. This includes the previously described studies into the C1. Although there is converging research using many different techniques, it is still not possible to be 100% certain from which brain areas the C1, C2 and P1 arise.

Although competition in primate visual cortex has previously been investigated using single cell recordings (e.g., Moran & Desimone, 1985; Luck, Chelazzi, Hillyard & Desimone, 1997; Chelazzi, Duncan, Miller & Desimone, 1998; Reynolds, Chelazzi & Desimone, 1999), V1 cannot easily be investigated using this approach due to its extremely small RF sizes. In contrast and underscoring the importance of the present findings, the ERP approach allows measurement of activation of neural populations in human visual cortex with excellent temporal resolution. Previous studies by Kastner et al. (1998) found BOLD activation in V1 and extrastriate cortex to be modulated by manipulating the extent to which stimuli compete within a RF. To our knowledge, ours is the first study of human brain activity to demonstrate that this competition begins in the initial, presumably feedforward, V1 response. Further competition for items of both high and low proximity appears to be enabled by feedback into V1 from extrastriate areas, which have RFs representing a larger proportion of the visual field (Kastner et al., 2001).

Inter-stimulus competition plays an important role in many perceptual and cognitive processes, including crowding, visual attention (e.g., Desimone & Duncan, 1995) and visual short-term memory (e.g., Shapiro & Miller, 2011). For example, Lavie's

perceptual load theory proposes that attention can operate at an early stage only when competition produces a high perceptual load (Lavie, 1995; 2005). However, studies of this sort typically lack an independent measure of the degree of competition between the stimuli. The approach outlined in this study will therefore be useful in testing specific predictions of how, and at which stage in processing, competition influences these perceptual and cognitive processes.

3.4 References

Ales, J. M., Yates, J. L., & Norcia, A. M. (2010). V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *Neuroimage, 52*(4), 1401-1409.

Ales, J. M., Yates, J. L., & Norcia, A. M. (2013). On determining the intracranial sources of visual evoked potentials from scalp topography: A reply to Kelly et al. (this issue). *Neuroimage, 64*, 703-711.

Alpern, M. & David, H. (1959). The additivity of contrast in the human eye. *The Journal of General Physiology, 43*, 109-126.

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of neurons in inferior temporal cortex during memory-guided visual search. *Journal of Neurophysiology, 80*(6), 2918-2940.

Clark, V. P., Fan, S., & Hillyard, S. A. (1995). Identification of early visual evoked potential generators by retinotopic and topographic analyses. *Human Brain Mapping, 2*, 170-187.

Cook, P. B., & McReynolds, J. S. (1998). Lateral inhibition in the inner retina is important for spatial tuning of ganglion cells. *Nature Neuroscience, 1*(8), 714-719.

Delorme, A. & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*, 9-21.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193-222.

Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Human Brain Mapping, 15*, 95-111.

Fahrenfort, J. J., Scholte, H. S., & Lamme, V. A. F. (2008). The spatiotemporal profile of cortical processing leading up to visual perception. *Journal of Vision, 8*(1):12, 1-12.

Flom, M. C., Weymouth, F. W., & Kahneman, D. (1963). Visual resolution and contour interaction. *Journal of the Optical Society of America, 53*(9), 1026-1032.

Fortune, B. & Hood, D. C. (2003), Conventional pattern-reversal VEPs are not equivalent to summed multifocal VEPs. *Investigative Ophthalmology & Visual Science, 44*, 1364-1375.

Fu, S., Fedota, J. R., Greenwood, P. M., & Parasuraman, R. (2010). Dissociation of visual C1 and P1 components as a function of attentional load: An event-related potential study. *Biological Psychology, 85*(1), 171-178.

Gattass, R., Sousa, A. P. B., & Gross, C. G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. *The Journal of Neuroscience, 8*(6), 1831-1845.

Hartline, H. K., Wagner H. G., & Ratliff, F. (1956). Inhibition in the eye of limulus. *The Journal of General Physiology, 39*(5), 651-673.

Hubel, D. H., & Wiesel, T. N. (1974). Uniformity of monkey striate cortex: A parallel relationship between field size, scatter and magnification factor. *Journal of Comparative Neurology, 158*, 295-306.

Jeffreys, D. A. & Axford, J. G. (1972). Source locations of pattern-specific components of human visual evoked potentials. I. component of striate cortical origin. *Experimental Brain Research, 16*, 1-21.

Kappenman, E. S., & Luck, S. J. (2012). Manipulation of orthogonal neural systems together in electrophysiological recordings: The MONSTER approach to simultaneous assessment of multiple neurocognitive processes. *Schizophrenia Bulletin, 38*(1), 92-102.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282*, 108-111.

Kastner, S., De Weerd, P., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in the human visual cortex. *Journal of Neurophysiology, 86*, 1398-1411.

Kelly, S. P., Schroeder, C. E., & Lalor, E. C. (2013a). What does polarity inversion of extrastriate activity tell us about striate contributions to the early VEP? A comment on Ales et al. (2010). *NeuroImage, 76*, 442-445.

Kelly, S. P., Vanegas, M. I., Schroeder, C. E., & Lalor, E. C. (2013b). The cruciform model of striate generation of the early VEP, re-illustrated, not revoked: A reply to Ales et al. (2013). *NeuroImage, 82*, 154-159.

Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology, 45*, 250-274.

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance, 21*(3), 451-468.

Lavie, N. (2005). Distracted and confused?: Selective attention under load. *TRENDS in Cognitive Sciences, 9*(2), 75-82.

Levi, D. M., Hariharan, S., & Klein, S. A. (2002). Suppressive and facilitatory spatial interactions in peripheral vision: Peripheral crowding is neither size invariant nor simple contrast masking. *Journal of Vision, 2*, 167-177.

Loomis, J. M. (1978). Lateral masking in foveal and eccentric vision. *Vision Research, 18*, 335-338.

Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience, 8*, 213.

Luck, S. J. (2005). Ten simple rules for designing ERP experiments. In T. C. Handy (Ed.) *Event-related potentials: A methods handbook*. Cambridge, MA: MIT Press.

Luck, S. J. (2014). *An Introduction to the Event-Related Potential Technique* (2nd ed.). Cambridge, MA: MIT Press.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2 and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*(1), 24-42.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229*, 782-784.

Nunez, P.L., & Srinivasan, R. (2006). *Electric Fields of the Brain* (2nd ed.). New York: Oxford University Press.

Pascual-Marqui, R. D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): Technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, 24D, 5-12.

Pratt, H. (2012). Sensory ERP components. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford Handbook of ERP Components* (pp. 89-114). New York: Oxford University Press.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience, 19*(5), 1736-1753.

Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *The Journal of Neuroscience, 32*(31), 10725-10736.

Shapiro, K. L., & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

Treue, S., & Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature, 382*, 539-541.

Werblin, F. S. (1974). Control of retinal sensitivity II. Lateral interactions at the outer plexiform layer. *The Journal of General Physiology, 63*, 62-87.

4 An optimal stimulus ratio for improved VSTM performance[4]

The experiments described in Chapter 3 lend support to the theory that items represented in the same visual receptive field (RF) in visual cortex exert particularly strong suppressive influence upon each other, leading to a net decrease in activation relative to the same stimuli falling in multiple, different RFs (e.g., Reynolds, Chelazzi & Desimone, 1999; Luck, Chelazzi, Hillyard & Desimone, 1997; see Section 1.4.3). Previous studies sought to reduce the extent of these interactions, by separating items such that they fall within the same RFs less frequently.

Kastner, De Weerd, Pinsk, Elizondo, Desimone and Ungerleider (2001) employed a spatial separation technique in their study, concluding that extent of suppressive interactions (indexed by BOLD response) increased between early visual areas (e.g., V1) and later areas (e.g., V4). This is highly consistent with competition predominantly between stimuli within a single RF; as RFs got larger, more stimuli shared single RFs, leading to increased overall suppression. Kastner, De Weerd, Desimone and Ungerleider (1998) used temporal separation of stimuli, comparing simultaneously presented items to the same stimuli presented sequentially. They found a significant BOLD difference between simultaneous and sequential conditions, suggesting the presence of competition between stimuli represented in a single RF.

As Figure 4.1 demonstrates, both spatial and temporal manipulations can lead stimuli to share RFs in fewer visual areas (i.e., beginning later in visual processing), reducing the extent of competitive interactions. The current chapter considers the effect of temporal stimulus separation on VSTM, as explored previously by Ihssen, Linden and Shapiro (2010). Their study saw eight items presented in either two 4-item sequential memory displays, one 8-item simultaneous (baseline) display, or a repeated 8-item display (repetition condition; see Figure 4.2). They demonstrated that reducing competition by presenting 8 items in two 4-item displays led to improved performance on a VSTM task.

However, VSTM capacity also increased relative to baseline when the entire 8-item display was presented twice. It is possible that the offset of the 8-item repetition display allowed disengagement of attention from some of the stimuli and re-engagement on others, allowing the display to be treated similarly to the sequential condition. A follow-up fMRI study (Ihssen, Linden, Miller & Shapiro, 2015) supported this hypothesis, finding increased BOLD activity in visual cortex in both sequential and repetition conditions

[4] Data from Experiment 2 have previously been published (Ihssen, Linden, Miller & Shapiro, 2015). All data were collected and analysed by Claire E. Miller.

relative to simultaneous, but also increased frontal BOLD in the repetition condition suggesting increased use of top-down mechanisms.

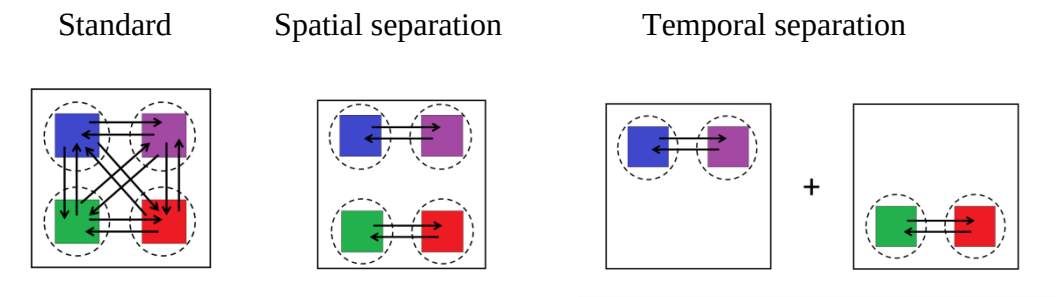


Figure 4.1. Example of how separating a 4-item display spatially (assuming separated pairs fall within different visual RFs) or temporally (in two sequential displays) could reduce overall competition present. Each arrow represents one 'unit' of competition; in this hypothetical example competition is reduced from 12 units to 4 units.

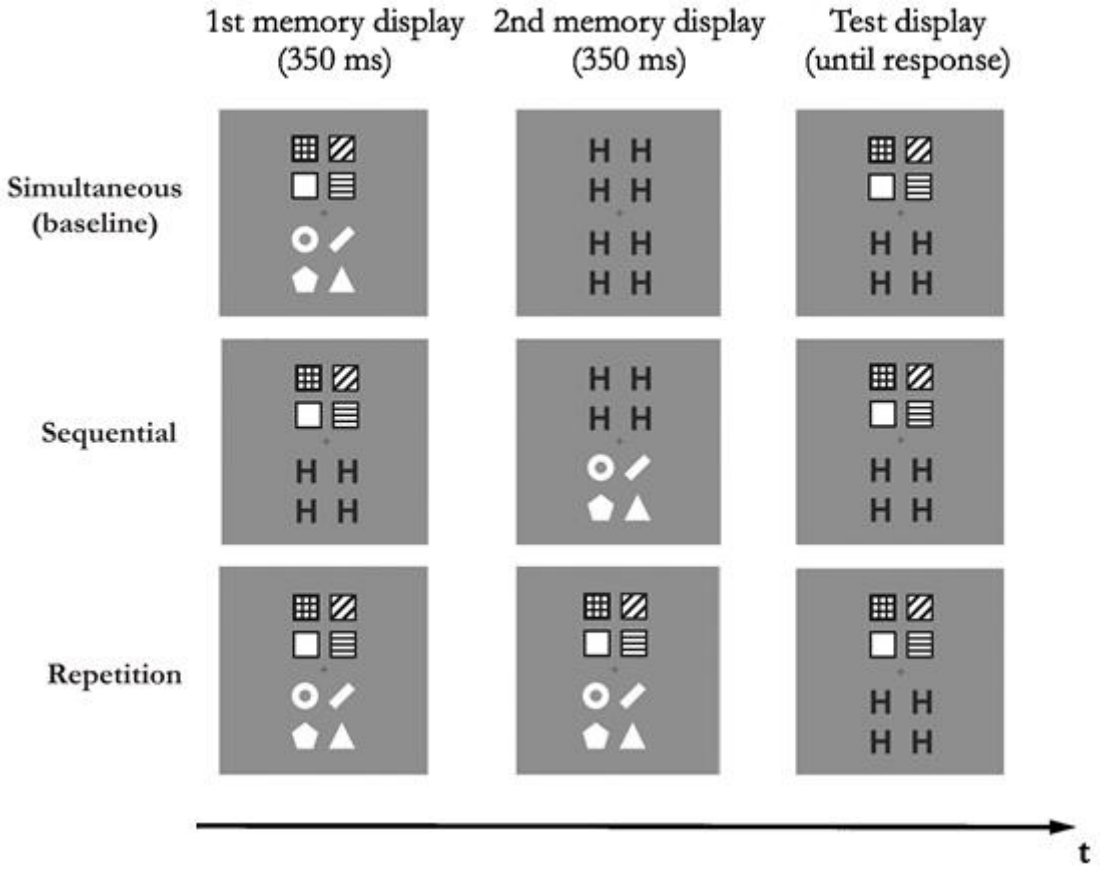


Figure 4.2. The baseline, sequential and repetition conditions, presented by Ihssen, Linden and Shapiro (2010). Figure created by Claire E. Miller, previously published (Shapiro & Miller, 2011).

Extending these findings, we predicted that presenting similar numbers of stimuli in each sequential display would minimise overall competition, optimising VSTM performance. The rationale behind this prediction is based on the number of strong competitive interactions between stimuli represented within the same receptive field (Figure 4.3). By separating 4 stimuli into sequential displays, competition could be thought of as reduced from 12 inter-stimulus interactions when 4 items are presented together, to 6 interactions with 3 items in the first display and 1 in the second, to only 4 interactions with 2 items per display. We tested this hypothesis by varying the number of items in each of two sequential displays between being approximately equal to being larger in one display than the other. The effect of set size was also investigated, through use of both high and low set size arrays.

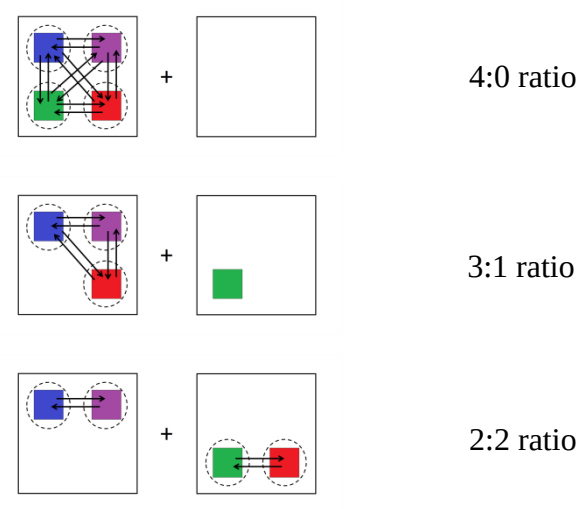


Figure 4.3. Example of how presenting a 4-item array in sequential displays of similar size could reduce inter-stimulus competition. Each arrow represents one 'unit' of competition, so this hypothetical example sees competition reduced from 12 units with all items presented together, to 6 units with 3 items in one display and 1 in the other, to 4 units with 2 items per display.

4.1 Experiment 1

4.1.1 Methods

4.1.1.1 Participants.

Sixteen undergraduate students aged 18-29 (M = 20.38, SD = 3.10; 10 females) were recruited through the Bangor University participant panel, and consented to participate in exchange for course credits. One participant was removed prior to analysis, due to consistently poor task performance. All participants had normal or corrected-to-normal vision, and reported no colour perception problems.

4.1.1.2 Stimuli.

A 19" computer monitor with a 100Hz screen refresh rate was used to display several stimuli per trial, each subtending 1.47° x 1.47° visual angle, at a viewing distance of 70cm. Stimuli comprised coloured squares and white shapes, presented using 'Presentation' stimulus control software (Neurobehavioral Systems, Albany, CA) in separate displays above and below fixation respectively (see Figure 4.4). Stimuli were presented in two 350 ms sequential displays containing 0 to 6 items, followed by a test display testing VSTM for one sequential display. Each display subtended a maximum visual angle of 6.38° x 4.50°, when six items were present. Ratios of items between the two displays were on a continuum, between the same number of items in each display (termed n : n) and four more items in one display than the other (n : n+/-4). Set size was also varied, with either a high or low set size of items presented across the two displays, as detailed in Table 4.1.

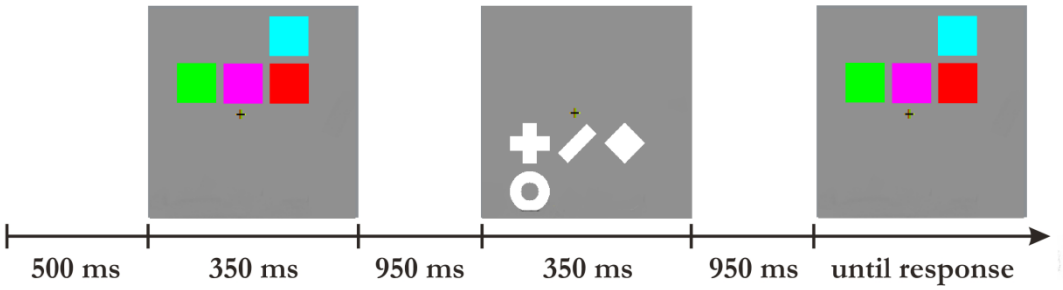


Figure 4.4. Example of a high set size trial, ratio n : n, with no change in the test display.

Table 4.1. The interaction between ratio and set size in Experiment 1

	n : n	n : n +/-1	n : n +/-2	n : n +/-3	n : n +/-4
Low set size (3, 4)	2 : 2	1 : 2 or 2 : 1	1 : 3 or 3 : 1	0 : 3 or 3 : 0	0 : 4 or 4 : 0
High set size (7, 8)	4 : 4	3 : 4 or 4 : 3	3 : 5 or 5 : 3	2 : 5 or 5 : 2	2 : 6 or 6 : 2

4.1.1.3 Design.

The task contained 480 experimental trials, comprising 48 per ratio condition. Trials were presented within-participants, with independent variables of set size (high, low) and ratio of items (near, far) between the sequential displays, and a dependent variable of VSTM capacity (Cowan's k; Cowan, 2001). Trials types were presented to each participant pseudo-randomly, to prevent participants' development of strategies. Items were allocated to the appropriate display in a uniform manner, beginning at one side of the screen and working across the display (see Figure 4.4). Displays containing no items were indicated by the presentation of an empty rectangle in the area in which items would otherwise have been displayed (Figure 4.5), to keep the rhythm of the presentations regular and ensure participants were not confused by thinking they had missed a display of items. Each display contained only one stimulus type (i.e., only colours or only shapes). This follows from previous studies using the sequential display method of stimulus presentation. The reason for single stimulus types per display in Ihssen, Linden and Shapiro's study (2010) was to try to equate grouping potential between the 2 array and 1 array conditions as far as possible. It was acknowledged that splitting the array into two displays may have made participants more able to use grouping strategies to remember them, so they wanted this to be similarly possible in the one-display condition (see Section 4.3 for further discussion of the implications of this design decision).

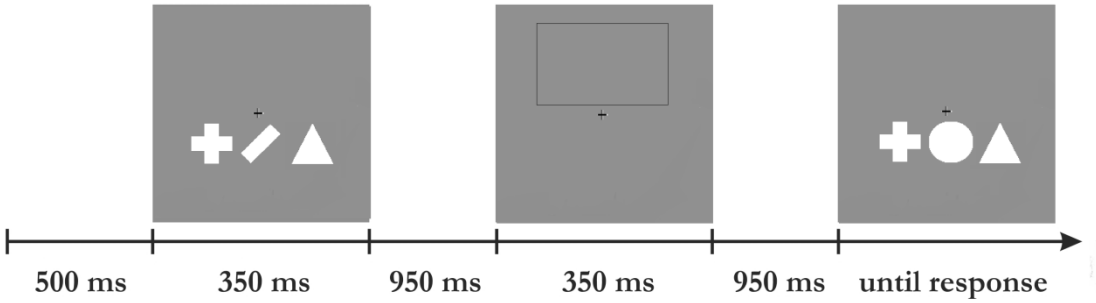


Figure 4.5. Example of a low set size trial, ratio n : n+/-3, with a change in the test display.

4.1.1.4 Procedure.

Participants were shown a series of arrays of coloured squares and white shapes, each split into two sequential 350 ms 'memory' displays of varying ratios and followed by a 'test' display probing memory for one of the presented displays. The display to be probed was selected at random, forcing participants to remember both displays of stimuli until presentation of the test display. Participants were asked to maintain fixation on a small cross in the centre of the screen throughout each trial, and to indicate for each test display whether all stimuli were exactly the same as in either of the preceding sequential displays or whether any item had changed, by pressing S (same) or D (different) on a standard QWERTY keyboard. Only one item in the 'test' array was ever changed on a 'different' trial and was changed to a same-category item not shown in the encoding array. During the task, participants repeated a pre-defined three-syllable word, to prevent the use of verbal strategies to remember the stimuli. After the experiment they were fully debriefed.

4.1.2 Results

To control for decay and recency effects, k-values were averaged over display order (e.g., 1:3 and 3:1 averaged) to produce a single estimate for each ratio. A 2 (set size; high, low) x 5 (ratio to n; n, n+/-1, n+/-2, n+/-3, n+/-4) repeated measures ANOVA revealed a significant main effect of set size, $F(1,14)=14.60$, $p=.002$, and a significant main effect of ratio, $F(4,56)=2.78$, $p=.035$ (see Figure 4.6). There was no significant interaction between these two factors, $F(4,56)=1.77$, $p=.147$.

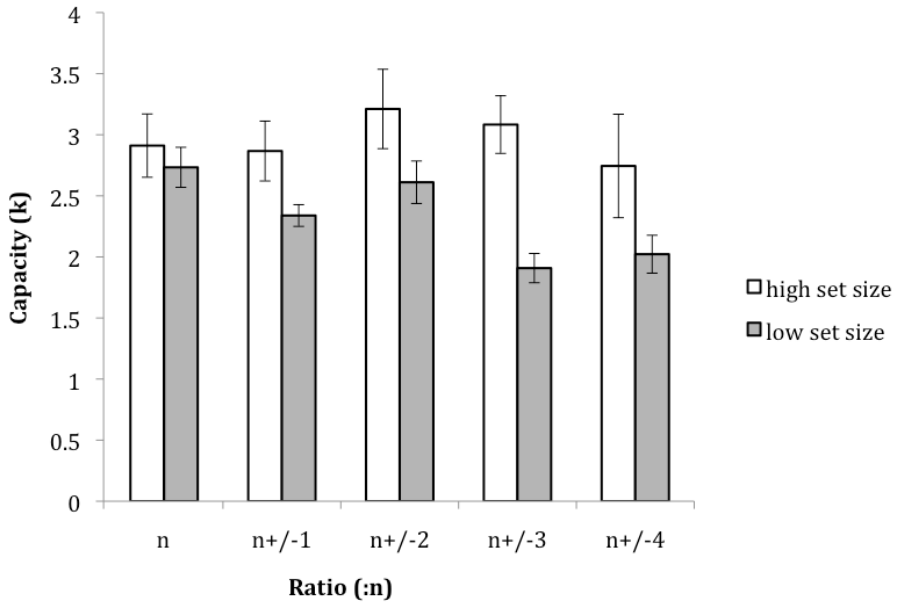


Figure 4.6. The mean capacity for each condition, averaged over the 15 participants.

A planned one-tailed repeated measures t-test was conducted on average k-values for near (n : n and n : n+/-1) and far ratios (n : n+/-3 and n : n+/-4) collapsed over set size (Figure 4.7). In support of our hypothesis, VSTM capacity in the near ratio condition was significantly higher than that for the far ratios, $t(14)=1.96$, $p=.036$.

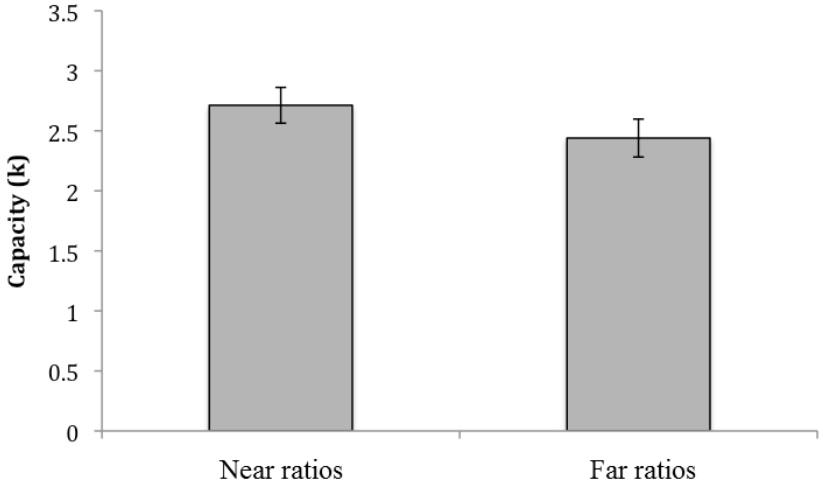


Figure 4.7. Capacity levels for the near (n : n, n : n+/-1) and far (n : n+/-3, n : n+/-4) ratio conditions.

4.1.3 Discussion

In Experiment 1, performance was significantly improved near relative to far item ratios. This suggests that minimising inter-stimulus competition by presenting items in approximately equal-sized displays (e.g., Figure 4.3) also elicits optimal VSTM performance. These results provide support for the involvement of inter-stimulus competition in VSTM capacity; however, it is interesting to note that within more uneven ratios, the low set size condition produced a markedly lower capacity than the high set size condition: visibly lower than in any of the other ratio conditions (see Figure 4.6). This could be attributed to the fact that in the low set size condition of these two ratios, one of the displays contained no items. Although our primary interest is in the main effect of ratio, rather than set size, confounds in these conditions will affect the capacity averages for far ratios (Figure 4.7).

Presenting stimuli across two displays in every condition would also address a potential confound in Ihssen, Linden and Shapiro's (2010) simultaneous and repetition performance increase. It may be that providing two 'episodes' by presenting stimuli in two displays (whether in the repetition or sequential condition) allowed participants to attend and encode them into VSTM more effectively (e.g., Bowman & Wyble, 2007; See Section 1.1.3 & 4.1.3).

Experiment 2 aimed to address these possible confounds. The number of items in the low set size condition was increased, such that no displays contained no stimuli. This meant that two encoding episodes were presented on every trial, addressing possible temporal episodic explanations of the lower capacity measured in the low set size condition. We suggest that if bottom-up inter-stimulus competition is a factor in VSTM, performance should still be better in the near than the far ratio condition, even when two displays of items are always presented per trial.

4.2 Experiment 2

4.2.1 Methods

The methods were the same as reported in Experiment 1, apart from the following details.

4.2.1.1 Participants.

Twenty undergraduate students were recruited through the Bangor University participant panel (mean age= 19.6, SD= 4.84; 16 female).

4.2.1.2 Stimuli.

Across the two displays, each low set size trial contained 4-5 items and high set size trials contained 7-8 items (see Table 4.2). This change allowed set size to be varied whilst retaining at least one item per display. For the same reason, ratios of items between the displays were this time on a continuum between n : n and n : n+/-3.

4.2.1.3 Design/Procedure.

The task contained 384 experimental trials, comprising 48 per ratio condition.

Table 4.2. The interaction between ratio and set size in Experiment 2.

	n : n	n : n +/-1	n : n +/-2	n : n +/-3
Low set size (4, 5)	2 : 2	2 : 3 or 3 : 2	1 : 3 or 3 : 1	1 : 4 or 4 : 1
High set size (7, 8)	4 : 4	3 : 4 or 4 : 3	3 : 5 or 5 : 3	2 : 5 or 5 : 2

4.2.2 Results

As in Experiment 1, k-values were calculated for each condition averaged over display order, and then similar and dissimilar ratios were averaged separately to get the near and far ratio conditions (Figure 4.8). A 2 (set size; high, low) x 2 (ratio; near, far) repeated measures ANOVA revealed a significant main effect of ratio, $F(1,19)=4.65$, $p=.044$. The main effect of set size was not significant, $F(1,19)=1.76$, $p=.200$, and there was no significant set size x ratio interaction, $F(1,19)=0.03$, $p=.874$. To consider the impact of untested display on performance (and thereby draw conclusions about whether the sequential displays were viewed as whole arrays or two separate memory tasks) a further analysis investigated the influence of untested display size on performance. A subset of conditions were chosen for analysis by selecting test display sizes which had been presented alongside 2 different display sizes, of consecutive magnitudes (e.g., 1:3 and 1:4). A 2 (untested display; small, large) x 4 (ratio; 1:3/4, 3:1/2, 3:4/5, 5:2/3) ANOVA revealed a significant main effect of untested display, $F(1, 19) = 4.40$, $p = .050$, and no significant interaction, $F(3,57) = .91$, $p = .420$. This suggests that the number of items in the untested

display did influence performance.

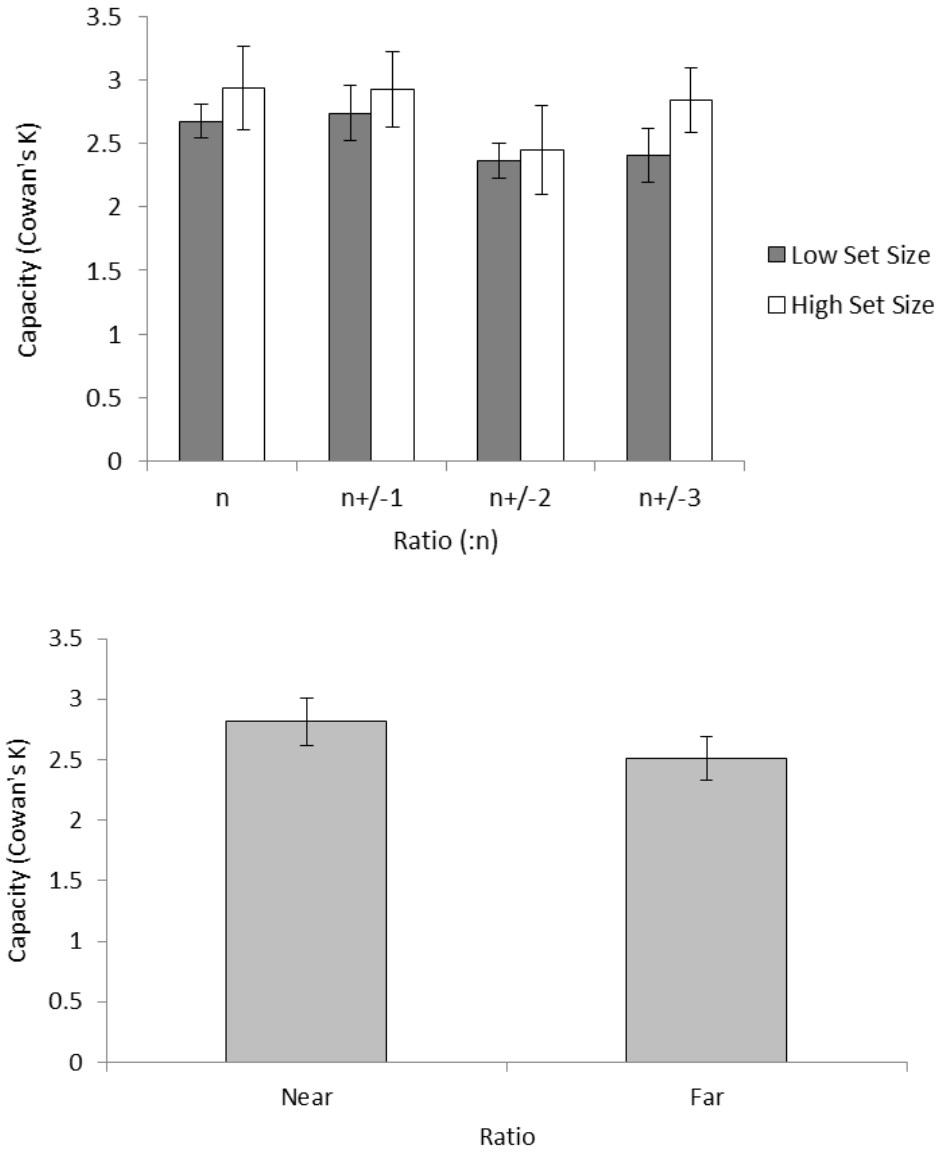


Figure 4.8. Upper pane: Mean capacity for each condition, averaged over the 20 participants. Lower pane: Capacity levels for the near (n : n, n : n+/-1) and far (n : n+/-2, n : n+/-3) ratio conditions.

4.2.3 Discussion

As in Experiment 1, there was a significant difference in performance between near and far ratios, indicating that ratio of items between sequential displays had an effect on VSTM capacity, with more equal sized displays being optimal. This supports the hypothesis that inter-stimulus competition underlies VSTM performance.

The lack of a significant main effect of set size suggests that presenting more than 4-5 items per trial does not significantly increase the number of items that can be recalled,

as would be expected based on a VSTM capacity limit of 3-4 simple items (Luck & Vogel, 1997). It is possible that this was not the case in Experiment 1 due to the confound of the 0-item displays within the low set size condition. Additionally, the smaller difference between the number of stimuli presented in the 'high' and 'low' set size conditions in Experiment 2 may have contributed to this different outcome.

A further analysis found a significant difference between performance on a given display presented alongside an untested display of n items, compared with an untested display of n+1 items. This difference suggests that participants were treating the two sequential displays as one large array, rather than as two separate memory tasks.

4.3 General Discussion

The experiments discussed in this chapter varied the ratios of items displayed across sequential displays between 'near' (i.e., similar number of items in each display) and 'far' (more items in one display than the other). In both experiments, participants showed significantly improved VSTM performance for displays containing similar numbers of items, relative to dissimilar. This is consistent with our hypothesis, given previous research into competition within RFs (e.g., Luck, Chelazzi, Hillyard & Desimone, 1997; Reynolds, Chelazzi & Desimone, 1999), which predicts that the more similar displays are in size, the fewer competitive interactions will be present in each to-be-remembered array overall (Figure 4.3). This reduction in competitive interactions at stimulus encoding appears to be related to performance in our VSTM task.

The results extend work by Ihssen, Linden and Shapiro (2010) into the effect of bottom-up inter-stimulus competition, manipulated through temporal stimulus separation, on VSTM. A potential competing explanation of Ihssen et al.'s finding of increased VSTM performance in the sequential and repetition conditions relative to the simultaneous baseline is also addressed. In addition to the amount of competition present differing between the 8-item display and two 4-item displays presented, there were also more temporal episodes presented in the two-display than the one-display condition. Bowman and Wyble's STST model (2007, see Section 1.1.3) differs from the biased competition account in that it is primarily a temporal model, explaining attention and memory over time at one spatial location. Although it is not yet clear exactly how such temporal models may interact with spatial competition between stimuli, previous results did have the potential to be explained by a similar episodic account. This also had the potential to confound results from Experiment 1, where stimuli could be presented across just one

episode (e.g., 3:0/4:0 conditions). In contrast, although stimuli in Experiment 2 were always presented in two episodes (maximising encoding potential according to episodic accounts) there was still a significant difference in VSTM likely related to the extent of inter-stimulus competition.

The current results lend support to the hypothesis that low-level inter-stimulus competition influences VSTM. However, there are competing explanations which are not competition-based. For example, it may be that participants viewed each stimulus display as a separate task, and so were able to allocate their resources more efficiently. It is important to note that in the absence of competition/display size effects this should have occurred similarly in each condition of Experiment 2, since there were always two displays presented. Nevertheless, to shed further light upon whether participants viewed the sequential display pairs as whole arrays or as separate tasks, a subset of the conditions from Experiment 2 were further analysed. A significant difference was found between performance on a given display size which had been presented alongside an untested display of size n compared with an untested display of size n+1. This would not be expected if participants were treating each pair of sequential displays as two separate memory tasks, rather than one large memory array However, further studies would be needed to investigate this further with a larger variety of set sizes.

Indeed, there are some aspects of the current experimental design which may encourage participants to view the displays as distinct, such as the presentation of colours and shapes in separate displays rather than intermixed and the probing of just one of the displays rather than the whole large memory array. Probing just one display may encourage participants to discard the irrelevant display as soon as the test display appears, and either episodic or categorical grouping of the stimuli may have enabled this to happen more easily. This is not a problem in terms of the validity of our task, as the full array of stimuli must be held in VSTM throughout the maintenance period until the test display appears. However, future studies should consider whether this style of strategy influences memory performance, and whether presenting a different item category per sequential display is necessary for the improved performance observed in low competition conditions.

Further studies will also be required to pinpoint whether competition (if this is indeed what drives the observed memory differences) primarily affects VSTM during the initial encoding of stimuli (explored in Chapter 3), or at later stages such as maintenance or retrieval. Additionally, these experiments do not address the influence of the top-down

factors hypothesised to underlie Ihssen et al.'s repetition benefit (Ihssen, Linden & Shapiro, 2010; Ihssen, Linden, Miller & Shapiro, 2015). This will be the main focus of Chapter 5.

4.4 References

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

Bowman, H., & Wyble, B. (2007). The simultaneous type, serial token model of temporal attention and working memory. *Psychological Review, 114*(1), 38-70.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual *Review of Neuroscience, 18*, 193-222.

Ihssen, N., Linden, D. E. J., Miller, C. E., & Shapiro, K. L. (2015). Neural mechanisms underlying visual short-term memory gain for temporally distinct objects. *Cerebral Cortex, 25*(8), 2149-2159.Ihssen, N., Linden, D. E., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17*, 680-686.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282*, 108-111.

Kastner, S., De Weerd, P., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in the human visual cortex. Journal of Neurophysiology, 86, 1398-1411.

Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2 and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*(1), 24-42.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *The Journal of Neuroscience, 19*(5), 1736-1753.

Shapiro, K. L., & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

5 Top-down control over VSTM[5]

Top-down goals are vital to success in everyday tasks, allowing us to select desired objects, switch attention between items in response to task demands, and ignore task irrelevant stimuli. For example, if we could not ignore irrelevant items, selecting a required coin from a handful of change would be challenging. Similarly, finding a required book would be difficult if we could not switch efficiently between library shelves in response to newly obtained cues such as shelf labels and call numbers. These examples point out that the interplay between top-down, goal-directed processes and visual short-term memory (VSTM) allows us to function in the everyday world.

As described in Chapter 1, previous research suggests that top-down processes can exert control over both activity in visual cortex and a range of cognitive behaviours including thoughts and memory. First, evidence for top-down modulation of visual activity includes a single-unit recording study by Chelazzi, Miller, Duncan and Desimone (1993), in which macaque monkeys attended a previously defined 'target' stimulus, presented along with a distractor (one stimulus 'good', eliciting a high cell firing rate when presented alone, and the other 'poor'). By 200 ms post-stimulus, firing of cells in inferior temporal cortex was determined by whether the target stimulus was good or poor. Similar results were found in area V4 (Chelazzi, Miller, Duncan & Desimone, 2001). This highlights the ability of top-down processes to suppress visual activation, if required by task-demands, biasing competition in favour of relevant stimuli.

Second, the importance of top-down processes in regulating thoughts and memory by resolving competition has been demonstrated EEG and fMRI studies (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005). Sequentially presenting two scenes and two faces per trial, and varying only participant instructions (to "remember" or "ignore" stimuli), they found increased fusiform gyrus and parahippocampal gyrus activation to to-be-remembered faces and scenes respectively, relative to those to-be-ignored. Participants also showed greater N170 magnitude to to-be-remembered than to-be-ignored faces. Evidence of both enhancement and suppression of BOLD signal and N170 was found, relative to a passive viewing baseline condition, as was a later N170 to to-be-ignored faces. These findings indicate both increased activation to and faster processing of stimuli, when task demands require them to be remembered.

[5] This chapter was aided by a collaboration with Professor Anna C. Nobre, University of Oxford. Experiments 2 and 3 are currently under review for JEP:HPP (Miller & Shapiro). All data were collected and analysed by Claire E. Miller.

Additionally, an ERP study by Kuo, Rao, Lepsien and Nobre (2009) suggested activation towards task relevant VSTM representations to be biased in a spatially specific way, as towards perceptual stimuli. Similar characteristics of N2PC were observed when participants performed a visual search task and a task requiring search through VSTM, suggesting the topographic organisation of VSTM and the operation of similar target-selection mechanisms in these two situations (see also Dell'Acqua, Sessa, Toffanin, Luria & Jolicoeur, 2010; Eimer & Kiss, 2010).

Indeed, attentional control is thought to strongly influence VSTM performance, as demonstrated by Ihssen, Linden and Shapiro (2010) in their study employing a modified change-detection paradigm (cf. Luck & Vogel, 1997). As described in Section 1.5, presenting 8 to-be-remembered items in two 4-item 'sequential' displays improved participants' VSTM performance relative to a simultaneously presented baseline. In another ('repetition') condition, in which the entire array was presented twice with constant encoding time maintained, a similar increase in VSTM capacity was found. The authors suggest that in both conditions, the increase arose due to attentional control: In the 'sequential' condition the control was enforced by the displays themselves, whereas in the repetition condition the control was manifest by strategically reallocating attention to a different part of the display.

The influence of directing this top-down control specifically to stimuli within VSTM is illustrated in retro-cuing studies (Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003). Griffin and Nobre, for example, showed that 'retro-cue' trials, which cue a memory array item after the both the array and its iconic memory representation have disappeared, elicit similar VSTM performance and reaction times as 'pre-cue' trials, where the cue is presented before memory array onset. In 'neutral' trials, in which stimuli were not cued, participants' performance and reaction times were significantly worse.

In addition, Landman, Spekreijse and Lamme (2003) found that relative to one 100% predictive retro-cue, participants performed similarly when given two retro-cues: a 'fake' cue which misdirected participants to a subsequently un-probed item, followed by a 'real' cue. This emphasises the durability of memory traces in this paradigm, suggesting that after the initial shift in attention, all non-attended items are still maintained. However, Makovski and Jiang (2007) report that although retro-cueing 1 item enabled significantly increased performance relative to cuing all or no items, cueing 2 or 3 items simultaneously produced no such benefit.

Although the research discussed above suggests humans have control over VSTM, the extent of this control is still unclear. Several studies suggest that presenting irrelevant visual information after to-be-remembered stimuli can reduce performance, relative to presenting only the to-be-remembered items (Logie & Marchetti, 1991; Quinn & McConnell, 1996; Woodman & Luck, 2009). However, in these studies participants knew the irrelevant nature of the distracting information in advance. The present study used pre-cues and retro-cues in a modified change-detection task, to compare participants' performance when they were able to prepare in advance to encode relevant stimuli, relative to their performance when control was required mid-task.

Previous studies suggest that cueing the first display (i.e., presenting to-be-remembered items followed by irrelevant information) should elicit lower performance than cueing the second display (Logie & Marchetti, 1991; Woodman & Luck, 2009). However, these studies only tested one-way interference, whereas we aimed to also test participants' ability to drop the first display and encode the second. In addition, to our knowledge, previous studies always made participants aware from the beginning of the trial of the irrelevance of the intervening information. We tested the flexibility of top-down control, using a paradigm which has not previously been implemented. Exerting efficient top-down control over the contents of VSTM should enable similar performance whether participants can fully prepare in advance or are required to exert control mid-trial.

5.1 Experiment 1

5.1.1 Method

5.1.1.1 Participants.

Sixteen undergraduate students aged 18-23 (M = 18.94, SD = 1.24; 12 females) were recruited through the Bangor University participant panel, and participated in exchange for course credits. All participants gave informed consent to participate in the study, which was approved by Bangor University's ethics committee. All participants had normal or corrected-to-normal vision, and reported normal colour perception. One participant was excluded prior to analyses, due to consistently poor performance.

5.1.1.2 Stimuli.

Stimuli were presented using 'Presentation' experimental control software (Neurobehavioral Systems, Albany, CA), on a 19" monitor with 100Hz screen refresh rate, at a viewing distance of 70cm. Coloured squares and white shapes, each randomly selected from eight alternatives used by Ihssen, Linden and Shapiro (2010), were presented in separate displays above and below fixation respectively. Trials consisted of two 350 ms 4-item sequential encoding displays (whole display: 3.93° x 3.93° visual angle, each stimulus: 1.47° x 1.47°), followed by a test display (Figure 5.1).

5.1.1.3 Design.

The experiment was conducted within-participants, with independent variables of trial type (pre-cue, mid-cue, baseline) and display tested (1, 2; each occurring on 50% of trials) and dependent variable of VSTM capacity (Cowan's k; Cowan, 2001). Each participant performed 480 experimental trials, comprising two 80-trial blocks per condition, presented in a pseudo-random order.

5.1.1.4 Procedure.

The experiment used a modified change-detection task (Luck & Vogel, 1997), with each trial comprising two sequential 350 ms encoding displays followed by a test display (Figure 5.2). Participants completed 3 conditions (blocked), two of which cued whether the first or second memory display should be encoded, by presentation of a digit 1 or 2 either prior to display 1 ('pre-cue' condition) or between displays ('mid-cue' condition). Cues were 100% predictive. The critical condition was the mid-cue condition, in which participants either held display 1 in VSTM and attempted to ignore the presentation of display 2, or attempted to forget display 1 mid-trial and encode display 2. In the third ('baseline') condition, participants were presented with just one encoding display (first or second) and the other display contained four letter H placeholders.

Participants were asked to fixate a small, central cross throughout each trial, and to indicate for each test display whether the stimuli were exactly the same as in the cued (or only) sequential display or whether any item had changed, by pressing S (same) or D (different) on a standard QWERTY keyboard. Only one item in the test array was ever changed on a 'different' trial, and when this occurred the item always changed to another same-category item not shown in the relevant encoding display. Participants performed the

concurrent articulatory suppression task of repeating a pre-defined 3-syllable word throughout each block. They were fully debriefed at the end of the experiment.

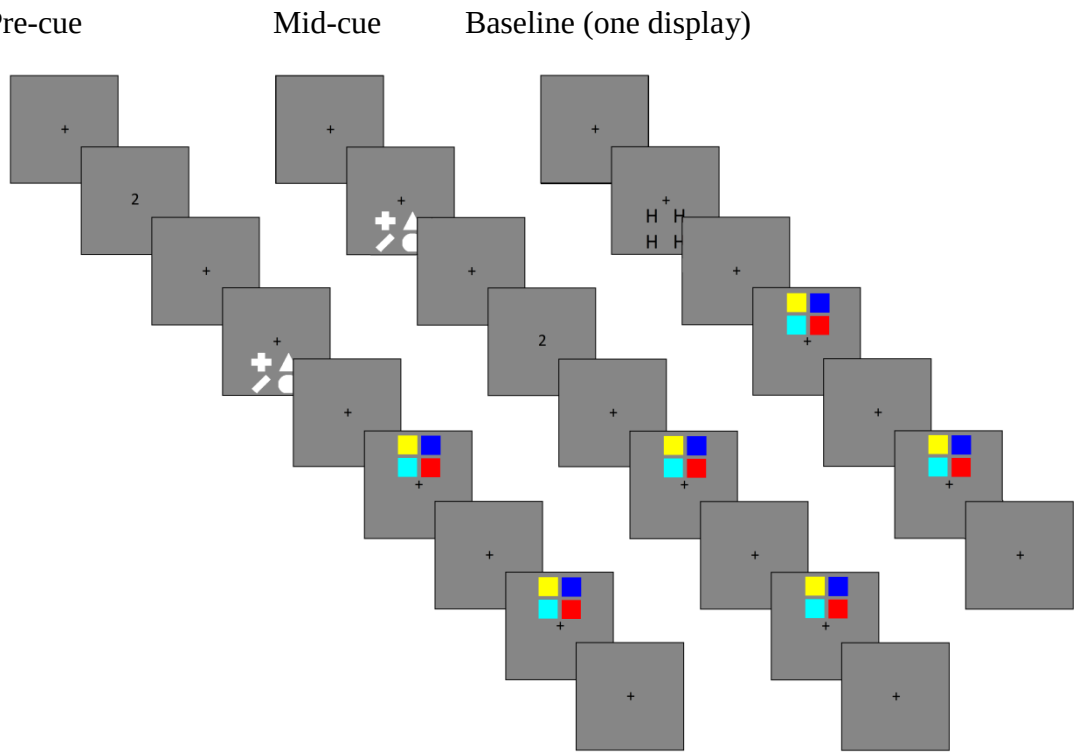


Figure 5.1. Diagram of Experiment 1 stimuli. In the pre-cue and mid-cue conditions, the fixation cross changed to either 1 or 2, to indicate which display would be tested. In the baseline condition, placeholders could be presented in place of either memory display 1 or 2.

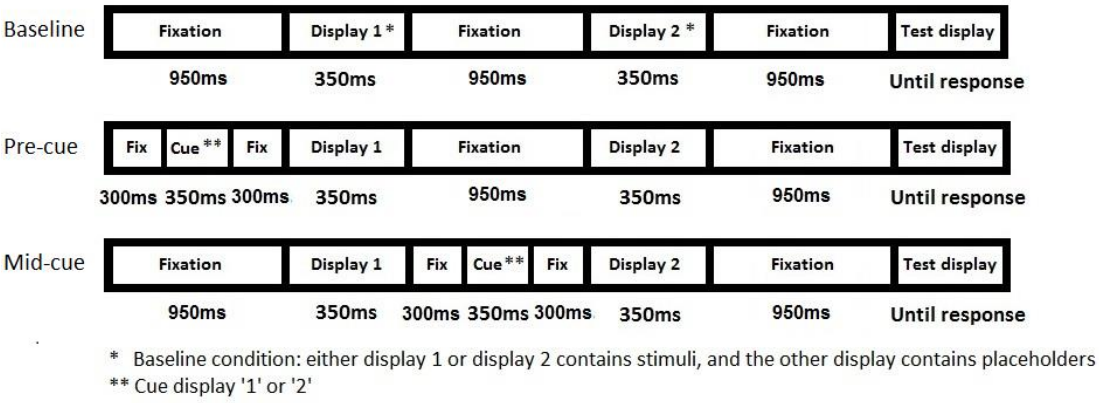


Figure 5.2. Diagram of Experiment 1 event timings for each condition.

5.1.2 Results

The mean capacity estimate (Cowan's k) for each condition is shown in Figure 5.3. A 2 (display tested; 1, 2) x 3 (trial type; pre-cue, mid-cue, baseline) repeated measures ANOVA revealed a significant interaction, $F(2,28) = 16.55$, $p < .001$. A two-tailed paired samples t-test between the pre-cue (M=2.15, SD=0.73) and mid-cue (M=1.47, SD=0.42) conditions for display 1 was found to be significant, $t(14) = 5.02$, $p < .001$. A further t-test conducted between these conditions for display 2 (pre-cue M=2.32, SD=0.53; mid-cue M=2.41, SD=0.60) was not significant, $t(14) = -.785$, $p = .446$. To ascertain the likelihood of the null effect being true, a Bayes Factor analysis was run with a Jeffrey-Zellner-Siow (JZS) prior. Results suggested a 3.85:1 likelihood of the null hypothesis being correct. The two conditions presenting cues before the tested display (display 1 pre-cue and display 2 mid-cue) were also compared; the increase in performance with cues prior to display 2 relative to display 1 approached significance, $t(14) = -1.89$, $p = .079$. Additionally, no significant difference was found between the display 1 and display 2 baseline conditions (display 1 M=2.38, SD=0.66; display 2 M=2.36, SD=0.60), $t(14) = 0.195$, $p = .848$, with JZS Bayes Factor analysis suggesting a 5.05:1 likelihood of no effect. This suggests that decay and recency effects did not play a large role.

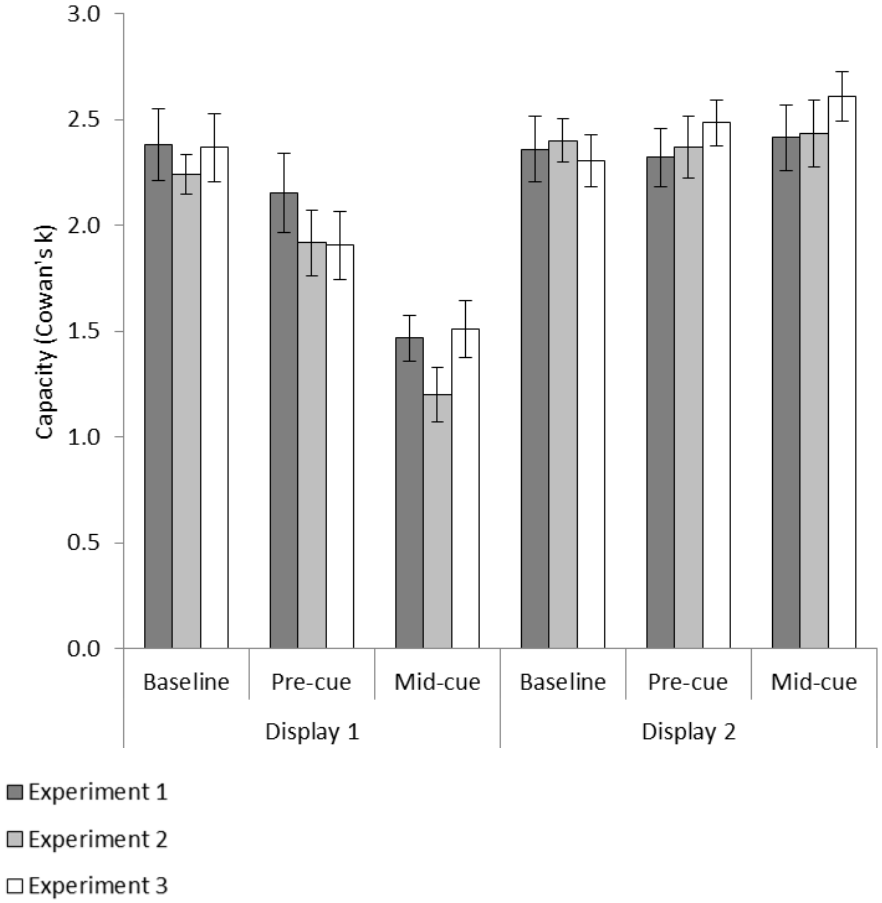


Figure 5.3. The mean VSTM capacity (Cowan's k) calculated for each condition of Experiments 1-3.

5.1.3 Discussion

If participants have efficient top-down control over the contents of VSTM, they should perform similarly in the mid-cue and pre-cue conditions when probed on the contents of display 1. In contrast, the significant difference in capacity between the pre-cue and mid-cue conditions when display 1 was tested suggests incomplete control; participants are better able to hold items in VSTM if they know from the start of the trial that they will be tested on the first display, than if this is only indicated after the first display has been presented. In trials testing display 2, participants performed equally well whether they were cued at the start of the trial, or only informed mid-trial, although in these cases both the pre-cue and the mid-cue came before the cued display. Taken together, these results suggest participants are more able to forget display 1 when required to encode display 2 at short notice (i.e., when the second display is cued) than they are able to remember display 1 and ignore display 2 at short notice.

Performance was also compared between trials in which display 1 was cued, immediately before its presentation, and those where this occurred for display 2 (pre-cue display 1 and mid-cue display 2 respectively). The marginally significant difference suggests that participants are better able to use cues prior to display 2, despite already holding display 1 items in VSTM, requiring these items to be quickly ignored or forgotten and new items encoded.

The above outcome raised the concern that participants may have strategically waited until after the (display 1) mid-cue to fully encode items previously seen in display 1, rather than encoding them 'online' as expected. Repeated failure of such strategy could contribute to the lower performance in the display 1 Mid-cue condition, and in turn the increased performance in the display 2 Mid-cue condition. Experiment 2 addressed this concern by presenting a mask 50 ms post-stimulus to force online encoding. We also increased each display's duration to ensure sufficient encoding time, and reduced the cue duration and fixation duration prior to cue, to keep trial lengths similar to Experiment 1.

5.2 Experiment 2

5.2.1 Method

5.2.1.1 Participants.

Fifteen undergraduate students aged 18-24 (M = 19.87, SD = 1.64; 10 females) with normal or corrected-to-normal vision were recruited through the Bangor University participant panel.

5.2.1.2 Stimuli/Design/Procedure.

The stimuli, design and procedure were the same as those in Experiment 1, with the following exceptions. The duration of each stimulus display was increased from 350 ms to 600 ms, to allow participants sufficient encoding time. Participants performed 384 experimental trials, comprising two 64-trial blocks per condition. On each trial participants were shown two sequential encoding displays, each masked after a 50 ms interval (see Figure 5.4). Masks were presented after all displays, including the placeholder-filled baseline display, to maintain consistency of timings and visual input. The interval before each cue was decreased to 150 ms, with each cue presented for 200 ms, to avoid significantly lengthening the trials.

Figure 5.4. Example of Experiment 2 stimuli and associated masks. In the Baseline condition, where placeholders were presented in place of stimuli in either memory display 1 or 2, masks were still presented after each display, to maintain consistency of visual input.

5.2.2 Results

The mean capacity measured for each condition is shown in Figure 5.3. The results of Experiment 2 paralleled those of Experiment 1. The 2 (display tested) x 3 (trial type) repeated measures ANOVA revealed a significant interaction, $F(2,28) = 9.53$, $p = .001$. A paired samples t-test comparing pre-cue (M=1.92, SD=0.60) and mid-cue (M=1.20, SD=0.50) k-values for display 1 trials was found to be significant, $t(14) = 4.21$, $p = .001$. A t-test comparing the same conditions for trials in which display 2 was tested (pre-cue M=2.37, SD=0.57; mid-cue M=2.43, SD=0.60) was not significant, $t(14) = -0.41$, $p = .686$, with JZS Bayes Factor analysis suggesting a 4.75:1 likelihood of the null being true.

The difference between the display 1 and display 2 baseline conditions (M=2.24, SD=0.37 and M=2.40, SD=0.40 respectively) was not significant, $t(14) = 1.21$, $p = .247$, with JZS Bayes Factor analysis suggesting a 2.64:1 likelihood of the null being true. This suggests that decay and recency effects did not significantly influence the data. The difference between the two conditions with to-be-tested displays occurring immediately following the cue (display 1 pre-cue and display 2 mid-cue) was significant, $t(14) = -3.75$, $p = .002$.

5.2.3 Discussion

By presenting a mask 50 ms post-stimulus, participants were forced to attempt encoding display 1 into VSTM prior to the cue. Nevertheless, Experiment 2 supports the conclusion that participants have limited control over the ability to retain items in VSTM. When display 2 was tested, participants once again performed equally well whether the cue appeared before the first or second display.

Experiment 2 also revealed significantly better performance when the cue directly preceded the (to-be-remembered) second display compared with that preceding the (to-be-remembered) first display, a comparison which approached significance in Experiment 1. Alongside the lack of significant differences between the two baseline displays, implying that decay and recency do not play a significant role, these results suggest participants are unable to protect the contents of VSTM at short notice (i.e., when they only learn they must do so after display 1), by avoiding interference from display 2.

Although previous studies suggest endogenous cues can be utilised within 300 ms (e.g., Müller & Rabbitt, 1989), the nature of the cues in the current study may require additional processing before they are acted upon. In addition, Oberauer's (2001) study into forgetting word lists found that up to 600 ms after being told to forget it, an irrelevant word list was still contributing to reaction times in a memory task. Insufficient processing time could result in impaired performance in pre-cue trials for display 1, which occurs shortly after the cue. Reduced performance may also occur in the mid-cue condition, especially when display 1 is cued, as this requires participants to actively ignore display 2 after processing the cue meaning. If cue processing takes too long, there may be insufficient time to inhibit encoding of part or all of display 2, and consequently VSTM capacity may be overloaded. In Experiment 3 the pre- and post-cue intervals were increased, to ensure sufficient time to process cues before display onset.

5.3 Experiment 3

5.3.1 Method

5.3.1.1 Participants

Sixteen undergraduate students aged 18-29 (M = 20.56, SD = 3.48; 11 females) with normal or corrected-to-normal vision were recruited through the Bangor University participant panel.

5.3.1.2 Stimuli/Design/Procedure

Experiment 3 stimuli, design and procedure were as Experiments 1 and 2, except that fixation periods before and after each cue were doubled, to 300 ms and 600 ms respectively.

5.3.2 Results

As in Experiments 1 and 2, a 2 (display tested) x 3 (trial type) repeated measures ANOVA revealed a significant interaction, $F(2,30) = 13.89$, $p < .001$ (see Figure 5.3). A follow up paired samples t-test comparing pre-cue (M=1.91, SD=0.65) and mid-cue (M=1.51, SD=0.54) k-values for display 1 trials was found to be significant, $t(15) = -2.45$, $p = .027$. A t-test comparing the same conditions for trials in which display 2 was tested (pre-cue, M=2.48, SD=0.43; mid-cue, M=2.61, SD=0.47) was not significant, $t(15) = 1.07$, $p = .300$, with JZS Bayes Factor analysis suggesting a 3.12:1 likelihood of null being true. There was also no significant difference between the display 1 and display 2 baseline conditions (display 1, M=2.37, SD=0.64; display 2, M=2.30, SD=0.50), $t(15) = 0.45$, $p = .660$, with JZS Bayes Factor analysis suggesting a 4.81:1 likelihood of the null being true.

5.3.3 Discussion

By increasing the SOA between the cue and the following display to 800 ms, participants were allowed sufficient time to process the cue. Nevertheless, VSTM capacity was significantly reduced in the display 1 mid-cue condition relative to display 1 pre-cue, thereby replicating the results of the previous experiments. Further, a 3 (Experiment; 1, 2, 3) x 3 (trial type; pre-cue, mid-cue, baseline) x 2 (display tested; 1, 2) mixed ANOVA revealed no significant interaction between experiment and cue type, $F(4) = .714$, $p = .585$, suggesting that neither increasing the SOA (Experiment 3) or introducing a mask (Experiment 2) changed the relationship between the cue conditions significantly. Additionally, a one-way ANOVA found no significant main effect of block order, $F(5) = 1.225$, $p = .298$, suggesting the absence of order effects.

5.4 General Discussion

The experiments in this chapter sought to investigate the extent of control over VSTM contents, by comparing change-detection performance when cued in advance with performance when cued mid-task. We hypothesised that efficient top-down control over VSTM, should allow similar capacity regardless of when participants are cued to indicate which of two displays to encode.

The significant difference in capacity between display 1 pre-cue and mid-cue conditions suggests that participants are better able to hold display 1 items in VSTM if they know they will be tested on display 1 from the start of the trial, than if this is only indicated after display 1 presentation. In other words, participants have difficulty inhibiting

encoding of an immediately upcoming (display 2) irrelevant display, whilst holding display 1 in VSTM. It is unlikely that this difficulty arose strategically (e.g., waiting to fully encode display 1 until after the cue was presented), since a significant difference was still found after masking the stimuli and providing additional time to process the cue. The lack of significant difference between pre-cue and mid-cue conditions for display 2 indicates similar performance whether participants know from the start that display 2 will be tested, or are told mid-trial to clear previous information from memory and remember upcoming items. This suggests that participants could efficiently ignore or forget irrelevant information mid-trial, allowing them to essentially perform a regular one-display change-detection task.

Since the baseline (one display only) condition in the present experiment revealed no difference in performance between display 1 and 2, the observed better performance for display 2 was unlikely due to pure decay and/or recency effects.

Taken together, these results suggest presence of interference from intervening stimulus displays and a disconfirmation of the hypothesis that humans can efficiently control VSTM contents. Specifically, performance was impaired when participants were quickly (between displays, i.e., midcue condition) required to protect display 1 and prevent interference or updating from display 2.

Our 'no cue' baseline condition was intended to assess cue effectiveness, allowing comparison between performance with and without the presence of a cue. In typical retro-cue tasks, participants remember a set number of items in all conditions, and performance is compared with a baseline containing the same number of items, but no cues. The cueing benefit is calculated by comparing the baseline condition with the conditions in which stimuli were cued. However, since the cues in our study were 100% valid (in contrast with the majority of the retro-cueing literature) the cue conditions only required participants to hold 4 items in memory at any one time. A baseline condition in which 8 items were presented without cues would therefore not be comparable to our experimental conditions; we would be comparing a condition in which participants held 8 items in memory, with a condition in which 4 items were held.

Although the current baseline shows that decay and recency effects are not contributing to differences between first and second display conditions, it does not provide an effective baseline for the mid-cue condition. Essentially, we use the pre-cue condition of each display as a baseline of sorts for the mid-cue condition. This introduces a confound; in the display 1 pre-cue condition the cue functions as a pre-cue, whereas in the

mid-cue condition it functions as a retro-cue. A more useful baseline would present one display followed by a mid-cue (i.e., a retro-cue) cueing that display, but no display 2. This would show the effect of the second display on memory for the retro-cued first display, allowing further investigation into the low performance in the display 1 mid-cue condition.

Expanding on previous evidence of top-down control over the transfer of items into VSTM using the retro-cueing paradigm (e.g., Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003), the current experiments suggest that participants can easily update VSTM, removing old items and encoding new ones. In contrast, during maintenance of stimuli, they experience difficulty inhibiting the encoding of new stimuli at short notice. Results further suggest that retro-cues are unable to ensure a successful behavioural outcome under all circumstances.

The lack of usefulness of the display 1 retro-cue may be due to the cueing of a whole display, rather than a single item. Previous work by Makovski and Jiang (2007) suggests that retro-cueing multiple items simultaneously does not produce the VSTM benefit typically seen when one item is cued. Additionally, in typical retro-cue tasks, updating/overwriting by a subsequent array does not occur; the present results may reflect a limited ability to protect items in VSTM from new incoming information. Finally, many retro-cueing experiments use arrow cues, which likely reflect both top-down and bottom-up properties (Berryhill, Richmond, Shay & Olson, 2012). It is possible that top-down cues such as numbers exert their influence in a different way.

In summary, the current study suggests that the contents of VSTM can be manipulated through top-down control, although its effectiveness is limited. Knowledge of varying effectiveness at different time points will be vital in developing stimulus-presentation strategies for optimal VSTM storage, and in informing future VSTM models.

5.5 References

Berryhill, M. E., Richmond, L. L., Shay, C. S., & Olson, I. R. (2012). Shifting attention among working memory representations: Testing cue type, awareness, and strategic control. *The Quarterly Journal of Experimental Psychology, 65*(3), 426-438.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*, 345-347.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. *Cerebral Cortex, 11*(8), 761-772.

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

Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicoeur, P. (2010). Orienting attention to objects in visual short-term memory. *Neuropsychologia, 48*(2), 419-428.

Eimer, M., & Kiss, M. (2010). An electrophysiological measure of access to representations in visual working memory. *Psychophysiology, 47*(1), 197-200.

Gazzaley, A., Cooney, J. W., McEvoy, K., Knight, R. T., & D'Esposito, M. (2005). Top-down enhancement and suppression of the magnitude and speed of neural activity. *Journal of Cognitive Neuroscience, 17*(3), 507-517.

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*(8), 1176-94.

Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17,* 680-686.

Kuo, B.-C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for targets within the spatial layout of visual short-term memory. *The Journal of Neuroscience, 29*(25), 8032-8038.

Landman, R., Spekreijse, H., & Lamme, V. A. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research, 43*(2), 149-164.

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive. In R. H. Logie & M. Denis (Eds.), *Mental Images in Human Cognition* (pp. 105-115). Amsterdam: North Holland Press.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390,* 279-281.

Makovski, T., & Jiang, Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychonomic Bulletin & Review, 14*(6), 1072-1078.

Müller, H. J., & Rabbitt, P. M. A. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance, 15*(2), 315-330.

Oberauer, K. (2001). Removing irrelevant information from working memory: a cognitive aging study with the modified Sternberg Task. *Journal of Experimental Psychology: Learning, memory and cognition, 27*(4), 948-957.

Quinn, J. G., & McConnell, J. (1996). Irrelevant pictures in visual working memory. Quarterly Journal of Experimental Psychology. *A, Human Experimental Psychology, 49A*(1), 200-215.

Woodman, G. F., & Luck, S. J. (2009). Why is information displaced from visual working memory during visual search? *Visual Cognition, 18,* 275-295.

Wetzels, R., Grasman, R. P. P. P., & Wagenmakers, E.-J. (2012). *The American Statistician, 66*(2), 104-111.

6 Sequential stimulus displays improve VSTM in older adults

As adults age, declines are seen in many areas, including memory and cognitive control, which can lead tasks previously taken for granted to become challenging (Buckner, 2004; De Luca et al., 2003; Myerson, Emery, White & Hale, 2003). Investigating the nature of ageing-related impairment and finding ways to alleviate the difficulties they cause is therefore becoming a high priority research area.

Jost, Bryck, Vogel and Mayr (2011) quantified VSTM capacity decline, estimating that although young adults (aged 19-38) have a capacity of approximately 2.99 items, older adults (64-92 year old) remember on average only 2.05 items. In addition, in comparing CDA, it appeared that older adults did not have similar VSTM characteristics to those of low capacity younger adults. Instead, they exhibited difficulties when filtering irrelevant stimuli early in the retention interval. Gazzaley, Cooney, Rissman and D'Esposito (2008) also suggest that reduced VSTM performance in older adults is associated with impaired inhibition of irrelevant information in early visual processing.

In contrast, the frontal control hypothesis (e.g., West, 1996) suggests that older adults have an impairment specific to frontal control. Indeed, Braw, Aviram, Bloch and Levkovitz (2011) found an association between ageing and decreases in frontal lobe related cognitive functions (see also Cabeza & Dennis, 2012).

McCarley, Mounts and Kramer (2004) suggest that inter-item competition in older adults is increased, due to reductions in neurons available for item representation. In their task, participants were required to attend to two items, and judge whether they were the same or different in shape. Although younger participants (M = 20.31 years old) showed only a small decline in performance as items were presented at closer separations, older adults (M age= 70.92) showed a much larger increase in errors. McCarley et al. suggest that increase in errors at closer separations for older participants may be due to reductions in neural resources available to represent and recognise the items in cortex, and/or reduced effectiveness of the inhibitory processes underlying competition (see also McCarley, Yamani, Kramer & Mounts, 2012)

VSTM performance is often measured using change detection tasks (e.g., Luck & Vogel, 1997) in which participants are typically shown a 'memory display' of items, and asked to remember as many as possible. They are then shown a 'test display' and are asked to indicate whether or not any of the items has changed. The measure of VSTM gained

through this procedure can be used to compute an estimated VSTM capacity for each participant (k; Cowan, 2001).

Ihssen, Linden and Shapiro's study (2010; see Section 1.5) tested participants aged between 18 and 30 (mean age = 24) and found mean change detection task performance was improved when items were presented in two 4-item sequential displays, relative to one 8-item simultaneous display. They suggested that this may be due to decreased inter-item competition in the sequential condition, enabling an increase in VSTM capacity (see also Shapiro & Miller, 2011). However, participants also showed improved performance in a repetition condition, which saw the 8-item display presented twice. A further study associated the increased performance in the repetition condition with increased BOLD in DLPFC, which was suggested to reflect a top-down attentional shift supported by PFC (Ihssen, Linden, Miller & Shapiro, 2015).

Ihssen et al. suggest that the observed benefit may have a top-down influence, with the offset of the first repetition display allowing disengagement from some of the items, and reallocation of attention to other stimuli. The sequential displays did this automatically, without need for increased top-down control.

The current study aimed to ascertain whether the increase in VSTM performance shown by Ihssen, Linden and Shapiro (2010) is also observable in older adults. Older adults were predicted to show greater benefits in the sequential condition than younger adults, due to the increased inter-item competition associated with resource reduction due to neural loss (McCarley, Mounts & Kramer, 2004). According to the frontal lobe hypothesis of ageing (e.g., West, 1996), the sequential condition would be predicted to elicit higher performance than the repetition condition, where greater frontal control is required.

This chapter describes two pilot experiments which tested 60-70 year olds on simultaneous and sequential displays, and repeated and sequential displays respectively. In Pilot 1, we tested 8 healthy 60-70 year old adults, to see whether the same differences emerge between simultaneously and sequentially presented items as found previously in young adults (Ihssen, Linden & Shapiro, 2010). In Pilot 2, we tested 8 further participants, comparing the repetition and sequential conditions. Several of the Pilot 1 participants also participated in Pilot 2, due to recruitment limitations. Through these pilot studies, we hoped to get an idea of the level at which older adults could perform on the tasks, and the amount of testing we could expect to achieve within one session. The main experiment (Experiment 1) tested 18 participants aged 70-80 years old on all three conditions.

6.1 Pilot 1

6.1.1 Method

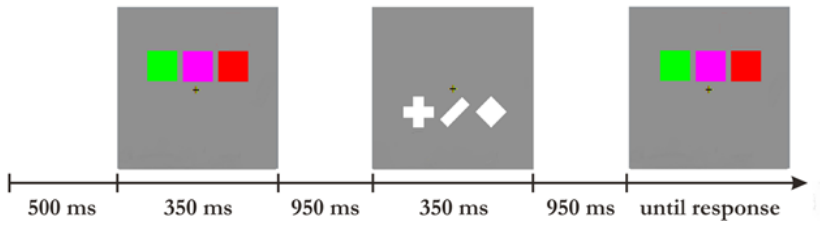
6.1.1.1 Participants.

Eight healthy older adults (aged 61-68, mean 64.75, 4 Females) were recruited through the Bangor University community participant panel. They were compensated £6/hour for the experimental session, which lasted between 60 and 90 minutes. They reported between 11 and 19 years of education (mean 16), and had normal or corrected-to-normal vision. When administered the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), all participants performed at a higher level than that suggestive of mild cognitive impairment.

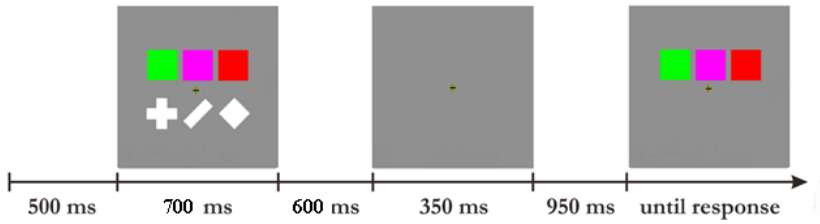
6.1.1.2 Stimuli.

'Presentation' experimental control software (Neurobehavioral Systems, Albany, CA) was used to present stimuli at a viewing distance of 70cm, on a 19" monitor (100Hz screen refresh rate). For the majority of participants (as explained in Section 6.1.1.4), the main experimental trials consisted of 3 white shapes and 3 coloured squares (Figure 6.1). These were randomly selected from eight alternatives used previously by Ihssen, Linden and Shapiro (2010), and were presented below and above fixation respectively. Trials contained a memory array, presented in either two 350 ms sequential encoding displays (whole display: 5.52° x 2.37° visual angle, each stimulus: 1.47° x 1.47°) or one 700 ms simultaneous encoding display (whole display: 5.52° x 3.93°). This was followed by a test display which remained on screen until participants responded "same" or "different" using a standard QWERTY keyboard.

A.



B.



C.

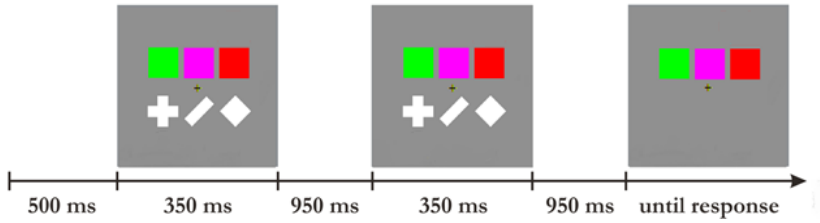


Figure 6.1. Screen layout throughout the trials in the three conditions. A. Sequential condition (presented in Pilot Experiments 1 and 2, and Experiment 1). B. Simultaneous condition (Pilot Experiment 1 and Experiment 1). C. Repetition condition (Pilot Experiment 2 and Experiment 1).

6.1.1.3 Design.

A blocked repeated measures design was employed, with independent variable of 'display type' (simultaneous, sequential) and dependent variable of 'VSTM capacity' (estimated using Cowan's k; Cowan, 2001).

6.1.1.4 Procedure.

Participants performed a modified change detection task (Luck & Vogel, 1997), comprising four 32-trial blocks in each of 2 conditions (sequential and simultaneous). In the sequential condition, each trial comprised two 350 ms sequentially presented 3-item

'encoding' displays, and in the simultaneous condition, participants were presented with one 700 ms 6-item encoding display per trial. Each encoding display / pair of displays was followed by a 'test' display, in which either the 3 colours or 3 shapes were presented once again, either exactly the same, or with one item changed (each occurring on 50% of trials). Participants responded 'same' or 'different' to the test display via keypress.

Prior to the task, participants were given a series of practice phases to slowly introduce them to the task. For the sequential practice, first one item was presented per display, and when the participant was performing to a high level of accuracy 2 items per display were presented. If they achieved higher accuracy than a pre-defined level of 65%, we continued to the highest set size of 3 items per display. For the simultaneous practice trials, two items were first presented, and this was slowly built up to six items in the same way. One participant was unable to complete the set size 4 practice trials with an accuracy of greater than 65%, and so they completed the rest of the experiment at set size 4, and the remaining 7 participants completed the experiment at set size 6.

Participants were tested for as long as they were comfortable to continue, finally completing two (2 participants), three (2 participants) or four (4 participants) 32-trial blocks of each condition. Simultaneous and sequential blocks were alternated, in a counterbalanced design. The blocks each lasted approximately 3 minutes (self-paced), and there were short breaks between and during each block, for participants to relax and rest their eyes.

6.1.2 Results

Capacity was calculated using Cowan's k formula (Cowan, 2001). This formula allowed for the best possible comparison between participants who had been tested at different set sizes (see Section 2.1.2.1). In the sequential condition, k was calculated separately for each display and then summed, as per the method previously used by Ihssen, Linden and Shapiro (2010). A paired samples t-test revealed no significant difference between the simultaneous and sequential conditions, $t(7)=0.06$, $p=.955$ (Figure 6.2).

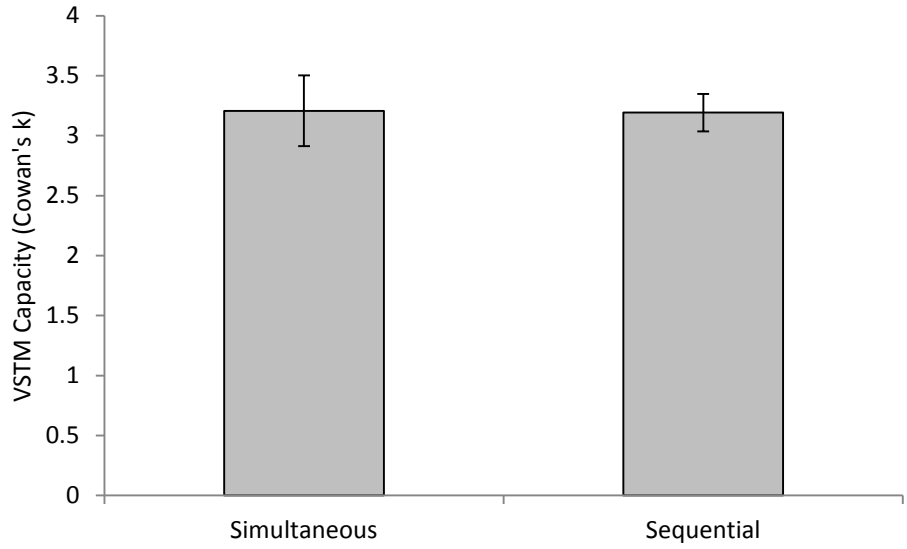


Figure 6.2. Mean VSTM capacity (Cowan's k; Cowan, 2001), for the 8 participants in Pilot 1.

6.1.3 Discussion

We hypothesised that presenting stimuli sequentially should improve VSTM capacity in older adults, by reducing the overall amount of competition present. Inter-stimulus competition is thought to increase in ageing, giving the potential of even greater usefulness of the sequential presentation paradigm than that found previously in younger adults (Ihssen, Linden & Shapiro, 2010). In contrast, there was no difference found between the simultaneous baseline and sequential presentation, although our pilot sample was too small to make solid conclusions.

Another hypothesis concerns Ihssen et al.'s repetition condition. In their study in younger adults, the repetition condition elicited similar performance to the sequential condition. This was hypothesised to be due to offset of the display supporting frontal networks in allowing disengagement of attention. If frontal functioning is impaired in older adults, this condition may not produce the same benefit. Pilot 2 was conducted to test this hypothesis, by assessing the difference between repetition and sequential conditions. A significantly lower performance in the repetition condition would suggest an inability of older adults to use frontal control in conjunction with the repeated displays, to increase performance.

6.2 Pilot 2

6.2.1 Method

6.2.1.1 Participants.

Eight healthy older adults (aged 64-69, mean 66, 5 Females) were recruited through the Bangor University community participant panel. They were compensated £6/hour for the experimental session, which lasted between 60 and 90 minutes. They reported between 11 and 19 years of education (mean 14) and normal or corrected-to-normal vision. The MoCA detected no mild cognitive impairment in any participant. Three of the individuals who participated in the first pilot also participated in Pilot 2, due to recruitment limitations.

6.2.1.2 Stimuli/Design/Procedure

Experiment 2 was conducted in the same manner as Experiment 1, except for the following details. Sequential and repetition display types were tested, to assess participant's ability to improve VSTM performance using repeated displays, thought to require top-down control. The task comprised 32-trial blocks in sequential and repetition conditions. In the sequential condition, each trial comprised two 350 ms sequentially presented 3-item encoding displays, and in the repetition condition, participants were presented with two 350 ms 6-item encoding displays per trial.

As in Pilot 1, participants completed a series of practice phases prior to the task to slowly introduce them to task requirements, before finally performing the task at set size 6. By the end of the experiment, participants completed either three (1 participant) or four (7 participants) 32-trial blocks of each condition. Repetition and sequential blocks were alternated, in a manner counterbalanced between participants. The blocks each lasted approximately 3 minutes (self-paced), and there were short breaks between and during each block. The MoCA was administered, and assessed no participants as having mild cognitive impairment.

6.2.2 Results

Capacity was calculated as for Pilot 1. A paired samples t-test revealed no significant differences between conditions, $t(7)=0.33$, $p=.752$ (Figure 6.3). However, the small sample recruited made it difficult to assess whether the lack of significance was real.

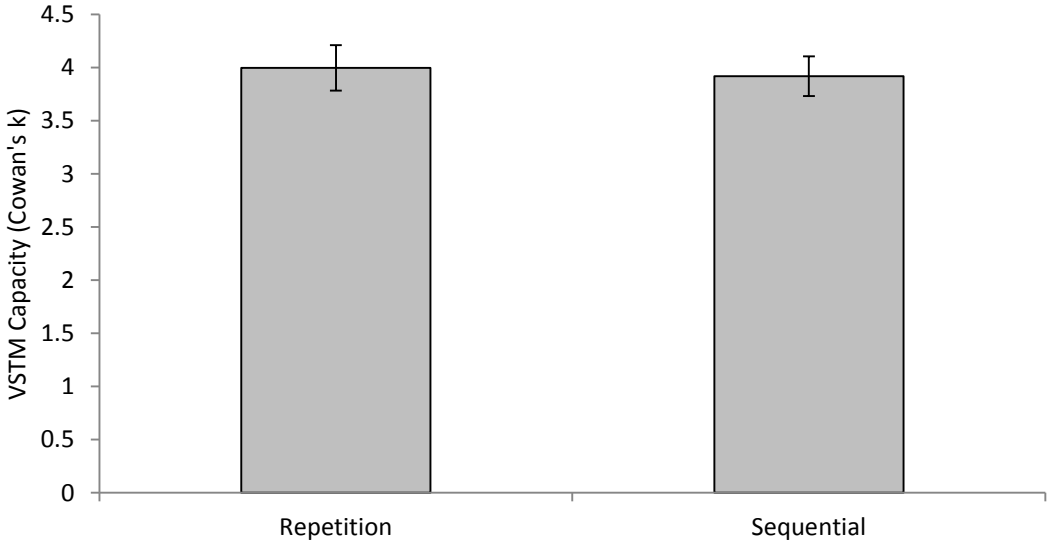


Figure 6.3. Mean VSTM capacity (Cowan's k; Cowan, 2001), for the 8 participants in Pilot 2.

6.2.3 Discussion

We hypothesised that if frontal control was impaired in older adults (Braw, Aviram, Bloch & Levkovitz, 2011), the repetition condition may not improve VSTM capacity in older adults as it did in younger adults (Ihssen, Linden & Shapiro, 2010), resulting in a significant difference between sequential and repetition conditions. Although we found no significant difference found between the repetition and sequential conditions, the small size of our pilot sample was insufficient to make firm conclusions.

In the main experiment (Experiment 1) we increased our sample size, recruiting 18 new participants from the University of Birmingham community panel. By increasing the length of our testing sessions we were able to present all three conditions from Ihssen, Linden and Shapiro's (2010) study in the same testing session, although the number of

blocks per condition was reduced to 3. We presented a set size of 6 items, since the pilot experiments suggested that most of the older adults had sufficiently good performance at this set size, but found set size 8 too challenging. We also decided to recruit older participants (70-80 years), since they were thought more likely to have the memory and frontal deficits reported previously (e.g., Braw, Aviram, Bloch & Levkovitz, 2011; Cabeza & Dennis, 2012)

6.3 Experiment 1

6.3.1 Method

6.3.1.1 Participants.

Eighteen older adults (aged 70-79) were recruited through the University of Birmingham community panel, and were compensated £6/hour for the session, which lasted between 1.5 and 2 hours. Two participants scored below 26 on the MoCA, suggesting possible mild cognitive impairment. The data from these participants were therefore removed prior to analysis, giving a final sample of 16 participants (mean age 74.8, 9 female). They self-reported having between 7 and 19 years of formal education (average 13 years), and all reported normal or corrected-to-normal vision, and normal colour perception.

6.3.1.2 Stimuli/Design/Procedure

Experiment 1 tested sequential, simultaneous and repetition displays. The task comprised 3 blocks per condition, presented in an order fully counterbalanced across participants, and each containing 32 trials. Trials consisted of two 350 ms 3-item sequential encoding displays (whole display: 5.52° x 2.37° visual angle, each stimulus: 1.47° x 1.47°), followed by a test display (Figure 6.1).

6.3.2 Results

Capacity was calculated as previously, using Cowan's k equation (see Ihssen, Linden & Shapiro, 2010). A repeated measured ANOVA was conducted, which established significant differences between conditions, $F(2,30)=6.95$, $p=.003$. Planned, follow-up t-tests were therefore conducted, to compare the sequential condition with both the simultaneous and the repetition conditions in turn. The difference between sequential

and simultaneous conditions was found to be highly significant, $t(15)= 3.93$, $p=.001$, but the sequential and repetition conditions did not differ significantly, $t(15)= 1.07$, $p=.300$ (Figure 6.4).

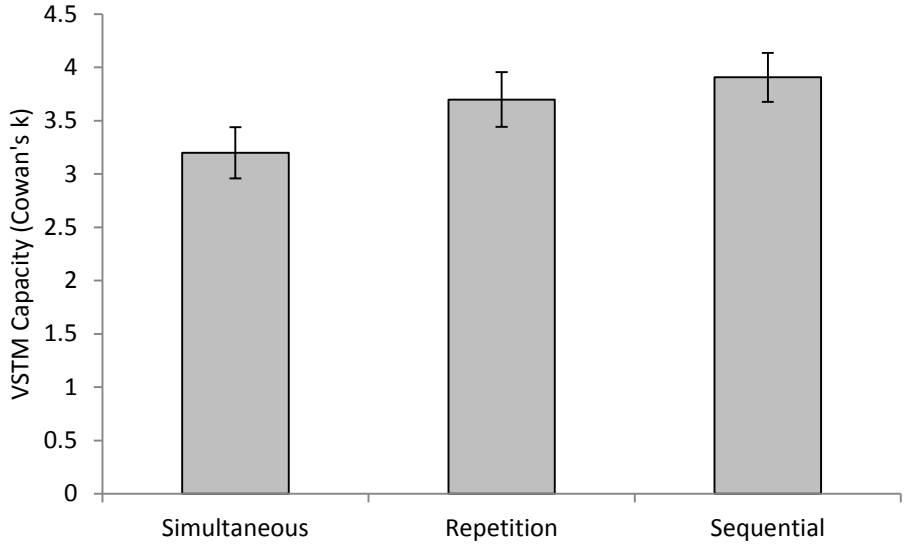


Figure 6.4. Mean VSTM capacity (Cowan's k; Cowan, 2001), for the 16 participants in Experiment 1.

6.3.3 Discussion

This experiment found significantly increased VSTM performance when stimuli were presented sequentially relative to simultaneously, in line with hypotheses based on findings in young adults (Ihssen, Linden & Shapiro, 2010).

Contrastingly, no significant difference was found between the repetition and sequential conditions. Ihssen et al. also found no difference between these conditions in young adults, but we hypothesised that the frontal lobe impairment often seen in ageing (West, 1996) would reduce the repetition benefit relative to the sequential benefit.

6.4 General Discussion

The pilot studies found no significant differences between sequential and simultaneous (baseline) or between sequential and repetition conditions. Their small

sample sizes due to recruitment difficulties likely contributed to the lack of significance. However, they allowed us to define parameters with which to conduct the main experiment, which used a larger sample and found a significant difference between the sequential and simultaneous conditions. This suggests that older adult participants benefit from reducing inter-item competition across a stimulus array, mirroring the benefit previously found in younger adults (Ihssen, Linden & Shapiro, 2010).

We hypothesised that, in contrast, the repetition condition would not elicit the same benefit, due to reduced frontal control in the older participants (e.g., Braw, Aviram, Bloch & Levkovitz, 2011; Cabeza & Dennis, 2012; West, 1996). Contrary to this hypothesis, there was no significant difference between the simultaneous and repetition conditions.

However, these results only consider healthy older adults, whose score on the MoCA suggested little or no mild cognitive impairment. There may be different patterns for older adults with impairments such as Alzheimer's. Future studies should focus more closely on this population, as development of new stimulus presentation strategies has potential to help with such memory impairments. Tasks such as these also have potential to aid with diagnosis of illnesses and impairments which may manifest in similar ways in the early stages, for example, in differentiating between Alzheimer's and mild cognitive impairment. This could lead to earlier treatment, which can make a huge difference in prognosis of dementia, in addition to allowing time for education about the illness and minimising associated risks (Leifer, 2003).

6.5 References

Braw, Y., Aviram, S., Bloch, Y., & Levkovitz, Y. (2011). The effect of age on frontal lobe related cognitive functions of unmedicated depressed patients. *Journal of Affective Disorders, 129*, 342-347.

Buckner, R. L. (2004). Memory and executive function aging and AD: Multiple factors that cause decline and reserve factors that compensate. *Neuron, 44*(1), 195-208.

Cabeza, R., & Dennis, N. A. (2012). Frontal lobes and aging: Deterioration and compensation. In D. T. Stuss & R. T. Knight (eds.) *Principles of Frontal Lobe Function (2nd ed.), New York: Oxford University Press.*

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

De Luca, C. R., Wood, S. J., Anderson, V., Buchanan, J.-A., Proffitt, T. M., Mahony, K., & Pantelis, C. (2003). Normative data from the Cantab. I: Development of

executive function over the lifespan. *Journal of Clinical and Experimental Neuropsychology, 25*(2), 242-254.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8*(10), 1298-1300.

Ihssen, N., Linden, D. E. J., Miller, C. E., & Shapiro, K. L. (2015). Neural mechanisms underlying visual short-term memory gain for temporally distinct objects. *Cerebral Cortex, 25*(8), 2149-2159.Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory capacity by sequencing the stimulus array. *Psychonomic Bulletin & Review*. *17*(5), 680-686.

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex, 21*(5), 1147-1154.

Leifer, B. P. (2003). Early diagnosis of Alzheimer's disease: Clinical and economic benefits. *Journal of the American Geriatrics Society, 51,* s281-s288.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279-281.

McCarley, J. S., Mounts, J. R. W., & Kramer, A. F. (2004). Age-related differences in localized attentional interference. *Psychology and Aging, 19*(1), 203-210.

McCarley, J. S., Yamani, Y., Kramer, A. F., & Mounts, J. R. W. (2012). Age, clutter, and competitive selection. *Psychology and Aging, 27*(3), 616-626.

Myerson, J., Emery, L., White, D. A., & Hale, S. (2003). Effects of age, domain and processing demands on memory span: Evidence for differential decline. *Aging Neuropsychology and Cognition, 10*(1), 20-27.

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I, Cummings, J. L. et al. (2005). The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society, 53*(4), 695-699.

West, R. L. (1996). An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin, 120*(2), 272-292.

7 General Discussion

7.1 Brief overview

The studies in this thesis sought to investigate the effects of inter-stimulus competition, as indexed by visual cortex activity, on VSTM performance. This chapter aims to summarise findings, place them in the context of previous work, and describe implications and areas for future study.

In summary, the ERP experiments in Chapter 3 used a novel paradigm isolating feedforward and feedback competition in V1, in addition to activity in extrastriate cortex. Evidence of competition was found throughout visual cortex, including initial V1 competition for near stimulus pairs (separated by a gap of 0.16° visual angle), and presumed V1 competition after feedback, as indexed by a component we term the 'C2'. This gives new insight into how competition unfolds over time in visual cortex, which has been impossible to study previously using fMRI (e.g., Kastner, De Weerd, Pinsk, Elizondo, Desimone & Ungerleider, 2001).

Chapter 4 extends findings from Ihssen, Linden and Shapiro (2010), investigating the effect of bottom-up inter-stimulus competition on VSTM capacity. Ihssen et al.'s study found increased capacity for sequentially presented half-displays, but also repeated whole displays. They concluded that reduced inter-stimulus competition in the sequential displays allowed increased VSTM performance. However, this study contained a potential confound between number of episodic events and its manipulation of competition. The experiments in Chapter 4 still found differences between conditions in which stimuli were always presented in two episodes but competition was manipulated through varying the ratios of items between the displays, suggesting that there is at least some influence of bottom-up inter-stimulus competition on the VSTM increase observed.

Ihssen Linden and Shapiro's (2010) unexpected finding of increased capacity when presenting all stimuli twice also suggested the influence of top-down factors (see also Ihssen, Linden, Miller & Shapiro, 2015). Chapter 5 explores the ability of participants to manipulate VSTM contents in a top-down fashion, using cues presented at various timepoints during stimulus presentation. These experiments found that performance and ability to manipulate stimuli held in VSTM depends upon the nature of the manipulation. Specifically, participants appeared unable to inhibit the encoding of irrelevant items whilst concurrently maintaining relevant stimuli in VSTM.

Finally, Chapter 6 tested older adults, to determine whether sequential display presentation may compensate for the increased competition associated with the ageing process, perhaps associated with the reduced memory performance often observed in older relative to younger adults (e.g., Jost, Bryck, Vogel & Mayr, 2011).

7.2 Results in context: Links with previous research

Inter-stimulus competition has been widely studied from an attentional selection point of view, and is also hypothesised to play a role in VSTM (Shapiro & Miller, 2011). The intense competition between stimuli in visual cortex must be resolved, in order to allow currently relevant stimuli to be selected, and to avoid overstimulation of visual cortex. In previous studies bottom-up competition was reduced though temporal and spatial stimulus separation. For example, Kastner, De Weerd, Desimone and Ungerleider (1998) found a lower overall BOLD response in visual cortex to stimuli presented in peripheral vision simultaneously, than those presented sequentially. Kastner, De Weerd, Pinsk, Elizondo, Desimone & Ungerleider (2001) also found reduced BOLD when stimuli were close together than further apart.

Although establishing the visual cortical areas in which competition occurred, such fMRI studies were unable to provide evidence about the time course of these competitive interactions due to the low temporal resolution of fMRI. Therefore, although competition was previously identified in V1, fMRI could not determine whether it occurred in a feedforward manner, or required feedback from extrastriate areas. The results from Chapter 3 suggest moderate competition in V1 between stimuli at close proximity, both before and after extrastriate feedback. The spatial range of competition appears to increase between V1 and V4, supporting previous fMRI studies and also single cell research (e.g., Kastner, De Weerd, Desimone & Ungerleider, 1998; Kastner et al., 2001; Luck, Chelazzi, Hillyard & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Chelazzi & Desimone, 1999; Treue & Maunsell, 1996). It is also noteworthy that the EEG method allows measurement of activation in populations of human neurons directly, whereas fMRI is reliant upon the BOLD response, which is constrained by factors such as tissue metabolism and vascular architecture of the head and brain (e.g., Logothetis, 2008). This emphasises that the method presented in Chapter 3 provides a unique and valuable tool for assessing competition throughout human visual cortex at specific timepoints in visual processing and investigating how these competitive interactions vary as stimulus and cognitive factors are manipulated (see Section 7.3).

If bottom-up competition influences VSTM performance, we would expect such manipulations of inter-stimulus competition to affect behavioural measures of VSTM. Indeed, Chapter 4 shows significant improvements in performance on two displays containing similar numbers of items, compared with dissimilar. Findings from previous studies into competition within RFs suggest that the more similar-sized displays are, the less competition will be present. Results from Chapter 4 therefore suggest a relationship between reduced competition during stimulus encoding and increased VSTM task performance.

In Ihssen, Linden and Shapiro's (2010) study, a VSTM performance benefit was found when 8-item displays were either presented twice or split into two 4-item 'sequential' displays, relative to a single 8-item display presented for the same total amount of time (see Section 1.5 for further details). It was hypothesised that improvements in 'repetition' performance relative to the baseline 'simultaneous' condition were influenced by top-down modulation of attention, with display offset allowing disengagement of attention, and re-engagement with a different subset of the stimuli. In the sequential condition this should occur automatically in a bottom-up fashion, through presentation of the stimuli in two subsets. These hypotheses were corroborated in a follow up fMRI study (Ihssen, Linden, Miller & Shapiro, 2015), which in addition to increased BOLD in visual cortex for sequential and repetition conditions, also found increased frontal BOLD in the repetition condition, suggesting greater involvement of top-down mechanisms. Importantly, this study demonstrates the influence of top-down and bottom-up processes within one paradigm, which led to interest in distinguishing between these two factors.

Chapter 4 also addressed a competing explanation of Ihssen, Linden and Shapiro's (2010) increase in VSTM capacity in the sequential and repetition conditions. Other than competition present, these conditions differed from the baseline condition in that stimuli were presented across two episodes. There is potential that this could increase capacity through a mechanism akin to Bowman and Wyble's (2007) STST model. The STST model suggests that a type (instance of a stimulus) and a token (episode containing said type) are bound together in the process of encoding stimuli in working memory (see Section 1.1.3). Although the STST model currently considers attention and working memory in the temporal domain (i.e., across streams of stimuli presented in one spatial location) these principles have the potential to be extended into the spatial domain. The two episodes present in the repetition and sequential conditions of Ihssen et al.'s study would therefore

allow resources to be released after the first episode, ready for encoding of the second, contributing to increased performance relative to the baseline condition. However, Experiment 2 suggests that this is not the whole story; even when two encoding episodes were presented on every trial performance was still significantly increased when inter-stimulus competition was minimised.

Chapter 4 suggests that although top-down control may influence VSTM performance in the repetition condition, there is at least some stimulus driven contribution to the sequential performance benefit. Further, presenting two encoding episodes in the repetition and sequential displays is not the only factor underlying the sequential increase; inter-stimulus competition may play a role. The experiments in this thesis support the biased competition theory (Desimone & Duncan, 1995), suggesting in particular that top-down and bottom-up factors work in conjunction to allow competition to be resolved and relevant stimuli to be attended. For example, resolving competition between to-be-attended stimuli enables representation in VSTM at the highest resolution possible, preserving vital stimulus information.

If top-down competition influences VSTM, orienting attention to a subset of stimuli through cueing should improve VSTM performance. This is the principle behind many retro-cueing studies, which cue participants to which item will be tested after stimulus offset (e.g., Griffin & Nobre, 2003; Landman, Spekreijse & Lamme, 2003; Sligte, Scholte & Lamme, 2008; 2009). In particular, a study by Murray Nobre, Clark, Cravo and Stokes (2013) successfully used cues to increase the probability of successful stimulus recall from VSTM. It was suggested that cueing a stimulus allowed its representation to transition from an inaccessible into an accessible form within VSTM. Murray et al. suggest that directing attention to an item in VSTM may protect it from competition from other items, indicating that control over VSTM contents is still possible after stimulus encoding. Additionally, it is thought that cueing after stimulus offset can increase capacity beyond estimates traditional for VSTM (Sligte, Scholte & Lamme, 2008), likely due to focusing of attention making the memory trace more durable (Makovski, Sussman & Jiang, 2008).

Chapter 5 assesses the extent of participants' top-down control over VSTM storage, using pre- and retro-cues to direct participants' attention to displays of stimuli in a modified change detection task. Previous studies suggest that presenting irrelevant information between to-be-remembered stimuli and a memory test reduces performance relative to presenting only relevant stimuli (e.g., Logie & Marchetti, 1991; Quinn & McConnell, 1996; Woodman & Luck, 2009). However, in these studies participants

always knew which items were irrelevant from the beginning of the trial. The flexibility of top-down control was tested using a new paradigm which assessed ability to inhibit encoding of irrelevant stimuli from the beginning of the trial, inhibit encoding of upcoming stimuli at short notice, and to discard/ignore stimuli previously held in VSTM in order to encode new stimuli. Our primary interest was in comparing participants' performance when they were able to prepare in advance to encode relevant stimuli, relative to their performance when control was required mid-task.

The studies in Chapter 5 suggest that participants can remove old items from and store new items in VSTM relatively easily, but find it harder to inhibit the encoding of new stimuli at short notice. This provides an example of a situation in which retro-cues are ineffective. However, inefficiency in using display 1 retro-cues may also be associated with cueing the entire display, rather than individual items. Makovski and Jiang (2007) suggest that cueing multiple items simultaneously may not elicit the same benefit as single item retro-cueing. In addition, the arrow cues typically used in retro-cueing tasks may be more effective than top-down cues, such as numbers (Berryhill, Richmond, Shay & Olson, 2012). These results emphasise limitations in VSTM control, specifically in inhibiting irrelevant item encoding whilst maintaining relevant stimuli.

Difficulties in inhibiting irrelevant information may be a key factor underpinning VSTM capacity. Low capacity participants tend to have similar CDA amplitude when presented with 2 targets and 2 distractors as with 4 to-be-encoded items (Vogel, McCollough & Machizawa, 2005). However, for high capacity individuals, 2 targets and 2 distractors elicit similar CDA amplitude as 2 target items presented alone, suggesting greater filtering efficiency (see also Zanto & Gazzaley, 2009).

Impaired suppression of irrelevant information may also be involved in the decline in VSTM capacity associated with ageing (Gazzaley, Cooney, Rissman & D'Esposito, 2008). Previous studies suggest that VSTM capacity declines from an average of 2.99 items during young adulthood (19-38 years) to only 2.05 in older adults (aged 64-92; Jost, Bryck, Vogel & Mayr, 2011). More specifically, older adults exhibit difficulties in filtering out irrelevant information, during the early part of the retention interval. The difference in older adults' VSTM performance between sequential and simultaneous presentation methods found in Chapter 6 suggests that this population benefit from reducing inter-item competition in a similar way to younger adults (Ihssen, Linden & Shapiro, 2010).

The close relationship between attention and VSTM, and large overlap between brain areas involved has led some researchers to suggest that they may even be different

terms for the same concept (e.g., Chun, 2011; Oliver, Maijer & Teeuwes, 2006; Rensink, 2002; Shimi, Woolrich, Mantini & Astle, 2015). Attention is a necessity in enabling task-relevant information to be stored in memory, and task irrelevant information to be filtered. For example, conditions such as inattentional amnesia and inattentional blindness emphasise the difficulty of storing items in VSTM when insufficient attention has been allocated to them (e.g., Neisser & Becklen, 1975; Simons & Chabris, 1999; Moore, 2001). The biased competition model is a clear example of this overlap, with items stored in memory able to bias attention within stimulus displays and resulting visual activation. VSTM performance and attention often have a strong relationship (e.g., Pessoa, Gutierrez, Bandettini & Ungerleider, 2002), with other facets shared by working memory and attention, including their capacity of approximately 4 objects (Cavanagh & Alvarez, 2005; Luck & Vogel, 1997; Pylyshyn & Storm, 1988). The research in this thesis supports the idea that attention and VSTM are closely related, and that inter-item competition, a phenomenon traditionally studied with respect to attention, can influence VSTM.

7.3 Future Directions and Implications

Developing presentation strategies to minimise competition should be a priority for future research, with the aim of improving VSTM performance in groups where deficits have been demonstrated (e.g., older adults). The current thesis applies Ihssen, Linden and Shapiro's (2010) method of improving VSTM capacity to older adults, extending previous research into memory in ageing and age-related disorders such as Alzheimer's. Development and refinement of stimulus presentation strategies may help individuals with such memory impairments. In particular, behavioural tasks such as that described in Chapter 6, have potential to aid diagnosis of illnesses and impairments which manifest similarly at early stages, such as Alzheimer's and typical mild cognitive impairment. This could lead to earlier treatment and planning, which is vital in response to illnesses such as dementia. Further studies are needed into the diagnosis and treatment of patient groups with dementia and other populations with memory impairments such as those suffering from dyslexia and schizophrenia.

Further knowledge of the effects of both bottom-up and top-down control during complex stimulus presentations will also support development of new presentation strategies for optimal VSTM storage. This has important applications in vehicular displays and training simulations, in addition to general interface design accessibility. Usefulness in education includes the design of computerised information presentation techniques to

increase effectiveness of displaying information, and allowing efficient attentional focus on the most relevant information.

Future investigations should also address the effect of manipulating competition on the *precision* of VSTM representations. There has been a recent increase in VSTM research involving colour wheel style tasks (see Section 1.3.1), and even while remaining agnostic on the slots vs resources debate, it is clear that this style of investigation provides a useful and different perspective. Increasing competition may affect memory through reducing the precision with which VSTM representation can be stored. Tasks assessing precision directly may therefore be more sensitive to changes than those assessing VSTM contents in a more binary way (i.e., present in memory vs absent from memory).

In terms of ERPs, the study described in Chapter 3 is the first to suggest inter-stimulus competition may begin in the initial feedforward response from area V1. Going forward, studies are needed into the anatomical generator of the C2 wave, and whether it reflects extrastriate feedback into V1, or V2/V3 activation. The possibility that the presence of mirror-image stimuli in Experiment 2 led to the observed difference in P1 results (indexing competition in V4) deserves further exploration. Additional studies could also increase the inter-stimulus distance further, to ascertain whether this reduces competition to a greater degree. The potential of this method to detect small changes in competition which fMRI cannot is also worth further investigation.

As described in Section 7.2, this study supports previous fMRI studies finding competition in V1 and throughout extrastriate cortex, but also extends them by suggesting a method to determine the timings of visual cortical activation. This method provides an independent measure of the degree of competition between stimuli, which could be used in studies investigating the role of such competition on various perceptual and cognitive processes. For example, a planned follow up study will consider how manipulating competition in varying parts of visual cortex influences VSTM. It should also assess at which time points competition occurs between VSTM representations; for example whether competition is stronger during maintenance of stimuli in VSTM than during a passive viewing baseline. In this way, the outlined technique holds potential for isolating competition during cognitive processes such as memory. This may provide further insight into whether the low-level competition seen in Chapter 4 occurs during initial encoding of items, or at later stages such as maintenance or retrieval of stimuli, ultimately providing further insight into the association between attention and VSTM.

As a whole, this work provides a basis for development of future models of VSTM and attention. There is a close bidirectional relationship between memory and attention; the ability to hold stimuli in memory is vital for top-down biasing of attention via prefrontal cortex, and attention is vital in encoding relevant stimuli into VSTM whilst filtering out irrelevant items. Future research should focus on uniting current models of spatial attention and VSTM (e.g., inter-stimulus competition) and also incorporate the temporal domain (e.g., STST) to provide a more comprehensive representation.

7.4 References

Berryhill, M. E., Richmond, L. L., Shay, C. S., & Olson, I. R. (2012). Shifting attention among working memory representations: Testing cue type, awareness, and strategic control. *The Quarterly Journal of Experimental Psychology, 65*(3), 426-438.

Bowman, H., & Wyble, B. (2007). The simultaneous type, serial token model of temporal attention and working memory. *Psychological Review, 114*(1), 38-70.

Cavanagh, P., & Alvarez, G. A. (2005). Tracking multiple targets with multifocal attention. *TRENDS in Cognitive Sciences, 9*(7), 349-354.

Chun, M. M. (2011). Visual working memory as visual attention sustained internally over time. *Neuropsychologia, 49*(6), 1407-1409.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience, 18*, 193-222.

Gattass, R., Sousa, A. P. B., & Gross, C. G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. *The Journal of Neuroscience, 8*(6), 1831-1845.

Gazzaley, A., Cooney, J. W., Rissman, J., & D'Esposito, M. (2005). Top-down suppression deficit underlies working memory impairment in normal aging. *Nature Neuroscience, 8*(10), 1298-1300.

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*(8), 1176-94.

Ihssen, N., Linden, D. E. J., Miller, C. E., & Shapiro, K. L. (2015). Neural mechanisms underlying visual short-term memory gain for temporally distinct objects. *Cerebral Cortex, 25*(8), 2149-2159.

Ihssen, N., Linden, D. E. J., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17*(5), 680-686.

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex, 21,* 1147-1154.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282,* 108-111.

Kastner, S., De Weerd, P., Pinsk, M. A., Elizondo, M. I., Desimone, R., & Ungerleider, L. G. (2001). Modulation of sensory suppression: Implications for receptive field sizes in the human visual cortex. *Journal of Neurophysiology, 86,* 1398-1411.

Landman, R., Spekreijse, H., & Lamme, V. A. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research, 43*(2), 149-164.

Logie, R. H., & Marchetti, C. (1991). Visuo-spatial working memory: Visual, spatial or central executive. In R. H. Logie & M. Denis (Eds.), *Mental Images in Human Cognition* (pp. 105-115). Amsterdam: North Holland Press.

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature, 453,* 869-878.Luck, S. J., Chelazzi, L., Hillyard, S. A., & Desimone, R. (1997). Neural mechanisms of spatial selective attention in areas V1, V2 and V4 of macaque visual cortex. *Journal of Neurophysiology, 77*(1), 24-42.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390,* 279-281.

Makovski, T., & Jiang, Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychonomic Bulletin & Review, 14*(6), 1072-1078.

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology: Learning Memory, and Cognition, 34*(2), 369-380.

Moore, C. M. (2001). Inattentional blindness: Perception or memory and what does it matter? *Psyche,* 7. Retrieved from http://psyche.cs.monash.edu.au/v7/psyche-7–02-moore.html

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229,* 782-784.

Murray, A. M., Nobre, A. C., Clark, I. A., Cravo, A. M., & Stokes, M. G. (2013). Attention restores discrete items to visual short-term memory. *Psychological Science, 24*(4), 550-556.

Neisser, U., & Becklen, R. (1975). Selective looking: Attending to visually specified events. *Cognitive Psychology, 7*, 480-494.

Oliver, C. N. L., Maijer, F., & Teeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology: Human Perception and Performance, 32*(5), 1243-1265.

Pessoa, L., Gutierrez, E., Bandettini, P. A., & Ungerleider, L. G. (2002). Neural correlates of visual working memory: FMRI amplitude predicts task performance. *Neuron, 35*, 975-987.

Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: Evidence for a parallel tracking mechanism. *Spatial Vision, 3*, 179-197.

Quinn, J. G., & McConnell, J. (1996). Irrelevant pictures in visual working memory. Quarterly Journal of Experimental Psychology. *Human Experimental Psychology, 49A*(1), 200-215.

Rensink, R. A. (2002). Change detection. *Annual Review of Psychology, 53*, 245-277.

Reynolds, J. H., Chelazzi, L., & Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *Journal of Neuroscience, 19*(5), 1736-1753.

Shapiro, K. L. & Miller, C. E. (2011). The role of biased competition in visual short-term memory. *Neuropsychologia, 49*, 1506-1517.

Shimi, A., Woolrich, M. W., Mantini, D., & Astle, D. E. (2015). Memory load modulates graded changes in distracter filtering. *Frontiers in Human Neuroscience, 8*, article 1025.

Simons D. J., & Chabris, C. F. (1999). Gorillas in our midst: Sustained inattentional blindness for dynamic events. *Perception, 28*, 1059-1074.

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS-ONE, 3*(2), e1699.

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2009). V4 activity predicts the strength of visual short-term memory representations. *Journal of Neuroscience, 29*(23), 7432-7438.

Treue, S., & Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature, 382*, 539-541.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature, 438*, 500-503.

Woodman, G. F., & Luck, S. J. (2009). Why is information displaced from visual working memory during visual search? *Visual Cognition*, *18*, 275-295.

Zanto, T. P., & Gazzaley, A. (2009). Neural suppression of irrelevant information underlies optimal working memory performance. *Journal of Neuroscience*, *29*(10), 3059-3066.