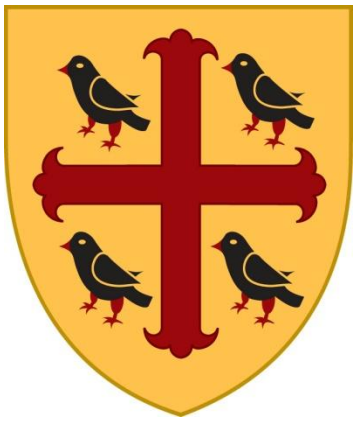
THE CAPACITY AND PRECISION OF VISUAL SHORT-TERM MEMORY

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Doctor of Philosophy Thesis

Michaelmas Term, 2011



St. Edmund Hall, Oxford



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Short Abstract

The Capacity and Precision of Visual Short-Term Memory

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St. Edmund Hall, Michaelmas Term, 2011

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Oxford

Approximate Word Count: 55,000

Despite continued interest in the capacity limitations of Visual Short-Term Memory (VSTM), there is uncertainty as to how these limited resources are distributed: among a limited number of high resolution slots or flexibly according to task demands. This thesis extends current knowledge by exploring how top-down and perceptual mechanisms affect VSTM capacity. The General Introduction describes the current understanding and investigation of capacity limits. This appraisal extends into Chapter 2, which focuses on the specific behavioural, psychometric, and electrophysiological approaches taken in this thesis to estimate effects on the precision and probability of recall of VSTM representations. Most experiments used a change-detection task that parametrically varied the precision of the VSTM representations required for accurate responses. Chapter 3 presents an event-related potential (ERP) study involving a pre-cue, which enabled a shift of spatial attention in anticipation of an upcoming memory array. ERP signatures of anticipatory spatial attention predicted behavioural cueing benefits. As a complement, the study in Chapter 4 involved orienting attention to items already in VSTM. Results from both chapters suggest that attention affects the probability of recall rather than the precision of representations. Chapter 5 describes four experiments exploring the ability to trade the number versus precision of representations in VSTM according to task goals. No flexibility was found in setting this trade-off, suggesting that the balance between number and precision is mainly determined by stimulus driven factors. Experiments in Chapter 6 investigate whether and how competitive dynamics that characterise perceptual processing continue to influence VSTM representations. Competition among item features that were orthogonal to the task relevant features continued to influence performance. Perceptual differences between the conditions cannot account for this effect. Competitive effects were consistent across spatial and non-spatial dimensions. The General Discussion synthesises all results and highlights opportunities for future research.

Acknowledgements

Although it is my name on the title page of this thesis, I am in no doubt that this work would not have been possible without the infinite support of my supervisors, labmates, family and friends.

Firstly, I thank my supervisors and mentors Kia Nobre and Mark Stokes. There is no way I can relate in words how their patience, dedication and insight has been critical in every step in the formation of the work I present here. I marvel at Kia's perspective and seemingly infinite capacity to remember details of countless projects and ideas. This, combined with the insight into how to cope with any situation and the ability to co-ordinate such a wonderful lab is inspirational. As Mark's first student, I have been extremely lucky to have had privileged access to his innovative, creative and insightful ideas. His ability to patiently explain how to dissect problems and approach analyses from multiple angles is amazing. I am honoured to be a student of these two exceptional scientists.

Then of course there is the Brain and Cognition Lab itself. Throughout the years, I have witnessed many flag paintings, viva and paper celebrations which reflect the many special people with whom I have had the pleasure to work. These include: Andre Cravo, Anling Rao, Anna Dalmolin, Bo-Cheng Kuo, George Wallis, Gustavo Rohenkohl, Helena Cousijn, Ian Clark, Kathryn Atherton, Nick Myers, Sonia Doallo, Stephanie Baines, Tzu-Yu Hsu and Valentin Wyart. Of course I must make special mention of my year-mates Zita Patai, Ian Gould and my office buddy Riam Kanso. We have shared scientific anecdotes, music, fun, joy and tears and a special bond which I hope will last many years into the future.

I must thank my friends Maria, Florian, Claudia, Monika, Mary and John who have provided shelter (literally and metaphorically) and happiness during the past years. I am eternally grateful for their support. I also want to thank my Teddy Hall buddies (including Georgi, Martin and Shari) and the Commonwealth Crew. I am so proud to be associated with such remarkable groups of people. I would also like to thank my family and friends in Australia and the UK for their constant encouragement and good wishes.

One special person who deserves particular acknowledgement is Rebecca Kueny. Not only has she witnessed every step of the process (until the very end) but she has provided emotional encouragement and rational insights into problems of every nature. I cannot imagine how I could have finished this thesis without her. I am truly blessed to have her as a friend.

Finally, I must thank my parents. Without their constant support and encouragement I would never have had the courage to even apply for postgraduate study, let alone in such a remarkable place as this. Thank you to my mother for her unending patience, proofreading skills and support and to my father, who always calms me and gives perspective. It is to him that I dedicate this thesis.

Long Abstract

Despite intensive investigation over the past century, there are many open questions regarding the capacity of Visual Short-Term Memory (VSTM). What factors characterise the hallmark VSTM capacity limitation is still being debated. This thesis explores the nature of these limitations using a combination of behavioural, psychometric and neuroimaging approaches. The first chapter will evaluate the current understanding of capacity limits and describe the rationale for the rest of the thesis. Chapter 2 will expand upon the concepts introduced in Chapter 1, but will focus on the methodological and conceptual approaches taken. The experimental chapters (3-6) will describe a series of experiments. Each will provide evidence for and discussion of the behavioural (Chapters 3-6) and neural (Chapter 3) mechanisms underlying the capacity limits of VSTM. These discussions will be synthesised in the final General Discussion and the opportunities for future research will be proposed.

Chapter 1: Introduction

The capacity of and the ability to keep visual information “in mind”, has remained a central topic of investigation for many decades. However, there is still uncertainty as to how VSTM capacity limitations are defined: by the acuity or complexity of the to-be-remembered information or the number of objects.

The remarkable consistency in the estimates of the average maximal number of items that can be retained in VSTM has led to the formation of a “slots”

account of VSTM resource allocation. Proponents of this idea suggest there are a limited number of slots which can represent items in VSTM with high precision; beyond this no further information is retained. An alternative account suggests that the precision and number of representations are determined flexibly according to task demands.

Recent advances in neuroimaging reveal substantial overlap in the neural networks supporting VSTM and perception, suggesting a strong functional correspondence between them. Perception is inherently competitive: items in the visual scene must compete for representation by limited resources. It is still unknown to what extent these competitive interactions extend into VSTM. In a similar way to perception, VSTM can be modulated by top-down signals to improve performance. This can occur by orienting preparatory attention in anticipation of to-be-remembered items or oriented retrospectively to items already in memory. Chapter 1 concludes with the rationale of this thesis and describes how each chapter exploits and builds upon the previous research to gain further insight into the nature of VSTM capacity limits.

Chapter 2: Methodological and Conceptual Approach

The second chapter extends the discussion of the techniques used previously to investigate VSTM capacity limits. Well designed behavioural experiments are critical to advance conceptual and cognitive neuroscientific understanding. Behavioural VSTM performance can be assessed by accuracy and by using measures derived from Signal Detection Theory (SDT). These measures have the advantage of formalising *discriminability* and *bias,* which can give more insight into

the factors driving performance than accuracy alone. This thesis also employed a common metric to calculate the capacity of VSTM: Cowan's k. Questions regarding the precision, not only the number, of representations have prompted the use of psychophysical modelling of behavioural data. Comparing the differences in how the fitted models explain the data can provide quantitative evidence to support different theoretical predictions, beyond what the basic analysis of performance can provide. Importantly, the currently tested models included both a slope parameter to reflect the precision of representations and an asymptote parameter to account for the probability that the probed item was in VSTM.

Another approach taken in this thesis is the use of Event Related Potentials (ERPs). ERPs have very high temporal resolution and provide a rich dependent-variable for investigating the stages of information processing influenced by experimental variables of interest. Four ERPs of particular interest for this thesis are described: three lateralised signatures of preparatory spatial attention (Early Directing Attention Negativity: EDAN; Anterior Directing Attention Negativity: ADAN, and Late Directing Attention Positivity: LDAP) and one lateralised ERP observed during the delay period of VSTM tasks which scales with memory load (Contralateral Delay Activity; CDA). The chapter concludes with a brief introduction to three methodological approaches to extend the scope of the work.

Chapter 3: Effect of Preparatory Attention on the Precision and Probability of VSTM Recall

Due to the limitations in capacity, the role of attention in selecting task-relevant information for storage in VSTM is critical. This first experimental chapter investigated the underlying mechanisms behind increases in VSTM performance afforded by pre-cueing a portion of the to-be-remembered items. Participants performed a variant of a change-detection task, which involved discriminating the direction of angular change of the probe item while ERPs were recorded. Parametric modulation of the magnitude of the angle of change enabled the psychometric modelling of data in accordance with the procedures described in Chapter 2. On half of the trials, a spatial pre-cue was presented to enable the covert orienting of anticipatory attention to one side of the display. The other half of trials presented a neutral spatial cue. Results revealed that, compared to neutral trials, anticipatory attention enhanced performance and the probability of recall rather than the precision of representations. This cueing benefit in the probability of recall and a measure of performance derived from signal detection theory (d') was predicted by the magnitude of the EDAN and ADAN. Such a result suggests that the strength of the preparatory attentional orienting facilitated the selection of task relevant items which ultimately improved performance. LDAP did not predict VSTM performance, whereas increases in the magnitude of CDA tended towards predicting the cueing benefits.

Chapter 4: The Effect of Retrospective Orienting of Attention on the Precision and Capacity of VSTM

As a complement to the study conducted in Chapter 3, the series of experiments in Chapter 4 investigated the effect of retrospective attention rather than prospective attention on the precision of representations and the probability that they were successfully recalled. In this paradigm, participants performed the same VSTM task but all items are equally task-relevant during encoding. Instead of a pre-cue, retrospective attention was oriented to an item during the maintenance period. In the first experiment, performance on retro-cue trials was significantly higher than when a neutral retro-cue or no-cue was presented. Critically, retro-cue performance was higher than when memory was probed at the time of the cue, suggesting that the benefits afforded by the retro-cue are above and beyond those achieved by reducing the delay period. Experiment 2 repeated and extended these results by including a large range of angles of rotation to enable the modelling of individual participant data. Similarly to the effects of Chapter 3, retro-cue benefits were associated with an increase of the probability of recall of the cued item rather than an increase in precision. Four participants completed several sessions of the task to increase the stability of parameter estimates. Individual model comparisons confirmed that the retro-cue benefits were best explained by changes in probability of recall even at a single participant level. The results from this chapter add to the growing consensus that there is much more information coded in the visual system than is consciously accessible. These results, combined with those of Chapter 3, give weight to the idea that VSTM is a highly dynamic system and can be biased at multiple stages of its evolution to maintain the most task-relevant information.

Chapter 5: Fixed Trade-off between the Number and Precision of Items in VSTM

It is now well established in the literature that increases in the number of to-be-remembered items decreases the representational precision of each item; there is a trade-off between the number and quality of representations in VSTM. The extent to which this trade-off is under top down control, however, is unknown. This prompts the question: can participants reduce the upper limit of the number of representations to gain increases in the representational quality? Participants performed a change-detection task in which the likely demands in the number or quality of representations for accurate VSTM performance were cued at either the beginning of trial (Experiment 1) or in a blocked fashion (Experiments 2-4). The expectation of the likely task demands was provided to test whether participants could bias resource allocation to optimise the trade-off. Foreknowledge of the number of items in the upcoming trial(s) (Experiments 1-2) or the precision required to make the correct angular change judgement (Experiment 3) or a combination of these factors (Experiment 4) was provided. The results show a resounding lack of evidence to suggest that participants could use this prior knowledge to optimise the trade-off between the number and precision of items. This suggests that the trade-off is not under top-down, voluntary control and may be determined primarily by stimulus-driven factors at encoding.

Chapter 6: Do Competitive Inter-Item Interactions Extend into VSTM?

As described in Chapter 1, there is converging evidence to suggest that VSTM and perception share common neural resources and can be modulated by top-down signals in similar ways. In perception, there are limited resources to code the entire

visual scene, thus items must compete for representation at the level of the receptive field (RF). Given the overlap between VSTM and perception, these competitive, inter-item dynamics should extend into VSTM maintenance.

In the first experiment, participants completed a change-detection task by comparing the colour of a single probe with the previous presentation in a memory array. Inter-item competition was manipulated by varying the spatial proximity between the memory items. Importantly, this was orthogonal to the task-relevant dimension, in order to reduce confounds related to effects on encoding strategy. The hierarchical organisation of RFs in the visual system means that items with closer spatial proximity (*high competition*) should undergo greater inter-item competition. In accordance with expectations, change-detection performance was lower for closely spaced arrays, suggesting that perceptual competition continued into the VSTM maintenance.

Experiments 2 and 3 were conducted to ensure that perceptual constraints did not impair VSTM encoding in the *high competition* condition. Experiment 2 involved a perceptual search task where participants were required to search for a single target in a subsequent search array. The results of this experiment were inconclusive as there was a trend towards higher performance in the low competition condition, but it was unclear whether additional demands of the perceptual search task may have influenced the results. Experiment 3 was conducted with the same structure as Experiment 1, except the encoding duration was manipulated to test whether the effects may have reflected limitations in encoding time. Critically, competition did not interact with encoding duration, suggesting that the task parameters of Experiment 1 were sufficient.

The final experiment extended the testing of competitive inter-item dynamics into a non-spatial feature dimension. Here, participants performed a similar task to the one described in Chapter 3, except that the items in the arrays were all the same (*high competition*) or different colours (*low competition*). Orientation discrimination was significantly higher for the multi-coloured arrays. This result compliments Experiment 1 and suggests a similarity between the effects of spatial and non-spatial based competition.

Chapter 7: General Discussion

The results of the experiments in Chapters 3-4 show that attention operates upon discrete item representations: increasing the probability of recall rather than increasing the precision of representations. This concurs with previous research suggesting that attention is organised at the object-based level. Although these results do give some credence to the slot-based accounts of VSTM, the use of low set sizes in the presented experiments mean that variability in the precision of representations cannot be excluded. The fact that attention differentially affected the precision and probability of recall of representations gives weight to the recent evidence suggesting that they are separate memory abilities with separate neural support. If so, this could account for some of the inability to trade the precision and number of representations (as per the results of Chapter 5).

Chapter 7 also extends to a discussion of how attention affects the selection and transformation of cued items and the correspondence between VSTM and perception. Capacity limitations of VSTM are complex and defined by many factors, some of which are explored in this thesis: perceptual constraints, task goals,

availability of task-relevant top-down information. By providing clues into the mechanisms that characterise the nature of VSTM capacity, the experiments in this thesis raise many additional questions. Suggestions for future research are provided which will enable the forging of a deeper understanding of the nature, limitations and flexibility of this fundamental cognitive system: VSTM.

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CHAPTER 1

General Introduction

> "…. the span (of visual memory) may be limited by the *capacity* of the visual storage. It may be that, as the number of items put into the storage is increased, resolution of the individual items is destroyed..."
>
> *- Averbach and Coriell (1961, p. 311)*

Fifty years has passed years since Averbach and Coriell (1961) conducted their seminal experiments on visual memory and raised the possibility that capacity limitations of the human visual system may be bounded by the number of items to be remembered, or by the quality with which items are remembered. This thesis will explore this question, and extend upon this issue by determining whether attentional and perceptual manipulations can bias the nature of Visual Short-Term Memory (VSTM) capacity limitations.

The introduction is divided into six main parts. After briefly introducing VSTM, I shall examine the reasons for the severe capacity limitation and review the investigations of the nature of capacity limits to date. The next section will introduce the recent movement from traditional experiments to test capacity limitations using change detection, to tasks which test the resolution of representations in a parametric or continuous fashion. This has led to a debate regarding the flexibility of the distribution of VSTM resources between the number of items and the quality (precision) with which they are remembered. One side argues that there is a strict item-based limit which cannot be alleviated by reducing the precision of individual representations. The other proposes the allocation is infinitely flexible and purely dependent on the task demands.

As an extension of this debate, this thesis will focus on top-down and perceptual influences on VSTM representations. Recent evidence suggests there is a tight correspondence between perception and VSTM. The behavioural and neuroimaging evidence of this overlap will be reviewed. Given the correspondence between VSTM and perception, processes which influence perception are also likely to influence VSTM. One particular phenomenon is biased competition: when items are presented simultaneously, similar stimulus attributes may activate overlapping neuronal ensembles and so items must "compete" for resources. It is unknown to what extent these competitive dynamics extend into other processes, such as VSTM. As an extension, the top-down processes that can modulate perceptual processes can also impact upon VSTM. The influences of anticipatory attention on VSTM encoding and the top-down modulation of maintenance will be of particular importance for the current thesis. The evidence for this will be discussed in light of the debate regarding the distribution of VSTM resources according to the number of representations and the precision with which they are remembered. Finally, the relevant previous work to date will be summarised and the rationale of the current thesis will be described.

1.1 Characteristics of VSTM

VSTM refers to the ability to keep information "in mind" in a temporary, robust, online store. In this way, VSTM can be conceptualised as a "sensory buffer" as part of the overarching models of working memory (WM) (e.g. Baddeley, 2003; Baddeley & Hitch, 1974). Traditional conceptualisations of WM, however, also

include some higher level, ‘executive processes’ such as the manipulation, selection, biasing and planning for the prospective use of information (Hollingworth & Luck, 2008). In the current thesis, however, these higher level mechanisms act upon information stored in VSTM and are, therefore, distinct from the visual store (see also Cowan, 2001). VSTM, however, should not be thought of as a passive or static sensory store; representations are robust, dynamic and actively maintained (Stokes & Nobre, 2012). These characteristics of VSTM are essential for many cognitive processes such as maintaining a stable percept of the world by integrating information across eye movements (e.g. saccades), blinks, and occlusions (Hollingworth & Luck, 2008; Irwin, 1991). Critically, the dynamic ability to bridge gaps in the input of sensory information also allows us to update the contents of VSTM on a moment-by-moment basis according to what is important for the current behavioural goals.

A defining feature of VSTM is its capacity limitation. Unlike either sensory (iconic) (e.g. Phillips, 1974) or long-term memory (e.g. Brady, Konkle, Alvarez, & Oliva, 2008; Standing, 1975), VSTM has a severe capacity limit which restricts the amount of information which can be retained and used for subsequent processes (Cowan, 2001). Individual differences in the capacity estimates have been shown to correlate highly with fluid intelligence (r=0.66; Fukuda, Vogel, Mayr, & Awh, 2010b) and overall cognitive functioning (up to r=0.89; Gold et al., 2010). A greater understanding of the limitations and organising principles of VSTM is also, therefore, critical to the understanding of many basic cognitive processes. The investigation and discussion of capacity limits will be discussed in more detail in Section 1.2 and is a major focus of the current thesis.

Another key feature of VSTM is that it is robust against interference from incoming perceptual stimulation, which differentiates it from the fragile and rapidly decaying iconic sensory trace (Irwin, 1991; Luck, 2008; Neisser, 1967). For example, Averbach and Coriell (1961) presented arrays of letters and, after a variable delay, asked participants to report the identity of the letter at the cued location. They found that presenting a circle after the presentation of the array at the same spatial location could effectively "erase" the sensory representation of the target letter. This effect, known as "masking", does not impact upon VSTM in the same way. As the time between the target and the mask increased from more than 100ms, the decrement in performance from the erasure of the sensory information increased, but only up to a certain point. From their measurements, delays greater than 200ms between the array and the onset of the masking circle, allowed the information in the sensory store to transferred to a "more permanent memory" now known as VSTM (Averbach & Coriell, 1961, p. 315). Furthermore, Phillips (1974) found that representations formed when a memory and test array were separated by 300ms were relatively impervious to masking and changes in the spatial location of the test array (from the memory array) (for more on the relational information in VSTM see also Jiang, Olson, & Chun, 2000). In contrast, iconic representations were highly disrupted by masks and changes in spatial locations.

These experiments clarified the distinction between a 'maskable', rapidly decaying store, which is inextricably linked to the retinal spatial position and a longer lasting, robust but temporary store (Irwin, 1991). The iconic trace can last in the order of hundreds of milliseconds before information is transferred to VSTM (e.g. Phillips, 1974). Estimates of the time to "consolidate" representations into

VSTM suggest this process is quite rapid, ranging between 50-100ms per item (see Bays, Gorgoraptis, Wee, Marshall, & Husain, 2011; Gegenfurtner & Sperling, 1993; Vogel, Woodman, & Luck, 2006; Woodman & Vogel, 2005).

Currently, attention is considered to be critical to the selection and encoding of sensory information into stable VSTM (e.g. Vandenbroucke, Sligte, & Lamme, 2011; Zanto, Rubens, Thangavel, & Gazzaley, 2011). Though models of VSTM are subtly different, they propose that representations which are present in VSTM reflect what is being attended to and is relevant to the current behavioural goals (Hollingworth & Luck, 2008; Stokes & Nobre, 2012). VSTM representations are robust enough to enable participants to introspect about them, make decisions and respond deliberately.

Recently, a tripartite subdivision in VSTM processes has been proposed (Coltheart, Laming, Routh, & Broadbent, 1983; Landman, Spekreijsea, & Lamme, 2003; Sligte, Scholte, & Lamme, 2008). The model differentiates among iconic memory, a high-capacity but fragile VSTM store, and a low-capacity but robust form of VSTM. Like the iconic trace, fragile VSTM is disrupted by pattern masks but, unlike the icon, the contents of this store are relatively unaffected by light masks. Critically, the capacity of fragile VSTM is proposed to be far greater than typical capacity estimates of VSTM (see Section 1.2). The transfer of information to robust VSTM is analogous to what Sperling (1967) describes as “scanning”. After this process (through the orienting of attention or otherwise), scanned representations are available for conscious report and information which was not transferred to the more permanent memory is lost.

Once information has entered strong VSTM, representations are actively maintained across time and interference. Neural activity related to the maintenance of items in VSTM is distributed throughout prefrontal, parietal, temporal and sensory areas (see Chafee & Goldman-Rakic, 1998; Cohen et al., 1997; Curtis & D'Esposito, 2003; Harrison & Tong, 2009; Lepsien, Thornton, & Nobre, 2011b; Linden et al., 2003; Pasternak & Greenlee, 2005; Serences, Ester, Vogel, & Awh, 2009). Foremost, the involvement of Prefrontal Cortex (PFC) in visual memory tasks has been well established (see Deco & Rolls, 2008; Gazzaley, Rissman, & D'Esposito, 2004; Goldman-Rakic, 1987; Goldman-Rakic, 1995). Studies using single-unit recordings of monkeys performing WM tasks have shown that activity of neurons in the dorsolateral PFC (dlPFC) is specifically associated with the delay period in a delayed reaching task (Fuster & Alexander, 1971; Kubota & Niki, 1971). Using a visual delayed match-to-sample task, Miller, Erickson and Desimone (1996) found sample-selective activity throughout the delay period in both prefrontal and inferior temporal (IT) cortices. Critically, however, the activity in PFC was sustained throughout the presentation of intervening (distractor) stimuli, whereas activity in IT was not. Human neuroimaging studies confirm that PFC activity is associated with the sustained, robust maintenance of visual representations (Cohen et al., 1997; Courtney, Ungerleider, Keil, & Haxby, 1997; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002).

1.2 Capacity Limitation – the Hallmark of Visual Short Term Memory

1.2.1 Investigation of Capacity Limits

The severe capacity limitation of VSTM has been of interest to researchers for many decades (see Blankenship, 1938). In a seminal series of experiments, Sperling (1960) presented participants with arrays of letters of various sizes for brief periods of time (50ms). Then, participants attempted to report as many letters as possible. When the array had 4 – 5 letters, participants performed almost perfectly. As the number of letters increased (to 9 or 12 letters), however, participants were still only able to report, on average, 4.5 letters. Critically, if cued to report only a particular portion of the array (for example, the middle three letters in a 3x3 array), participants could easily perform the task. It was clear, therefore, that participants had a large store of information. The *accessible* representations (which presumably were in VSTM), however, were strictly limited in number.

This dissociation between the sensory store and VSTM was unequivocally confirmed by Phillips (1974). He showed that the capacity of VSTM is much lower than the iconic trace[1] by testing participants' ability to detect changes between two random dot patterns, separated in time. When the time between the two presentations was short (e.g. 20 ms), performance was almost perfect, regardless of the complexity[2] of the array. As the interval between the two presentations increased, performance decreased. Performance also depended on the complexity of the array: performance at longer delays was disproportionately lower when the arrays were complex. Performance was still above chance, however, when the

[1] For the purposes of this thesis, however, discussion will focus on the capacity and precision of VSTM rather than the limitations of the iconic trace.
[2] As defined by the number of dots presented.

memory and test arrays were separated by nine seconds. In summary, these classic experiments showed that VSTM is limited in capacity but can last over several seconds.

Since this early work, studies estimating VSTM capacity have focussed on the *number* of items that can be successfully maintained. Estimates are in the range of 3-5 items for simple stimuli, and have been remarkably consistent across paradigms and research groups (e.g. Alvarez & Cavanagh, 2004; Averbach & Coriell, 1961; Cowan, 2001; Eng, Chen, & Jiang, 2005; Luck & Vogel, 1997; Pashler, 1988; Sperling, 1960; Todd & Marois, 2004; Vogel, Woodman, & Luck, 2001). Typically, these studies have used variants of the Change-Detection (CD) task. Participants are briefly (in the order of 200ms) presented with an array of to-be-remembered objects, letters or abstract items. After a variable delay, a probe array is presented and participants must compare this to their mnemonic representation to decide whether any of the items has changed. By varying the number of items in the array, it is possible to calculate the maximal number of items that participants can recall on average (for more discussion, see Section 2.2.4).

Evidence for the limitation of VSTM capacity to be defined in an item based fashion has come from studies which have shown that performance for integrated objects (e.g. 4 items with 4 features) is equivalent to memory for individual features (Luck & Vogel, 1997; Vogel et al., 2001)[3]. This was not due to separate storage units for each feature: performance was unaffected when objects combined two of the same feature (e.g. a smaller square inside a larger one of a different colour).

[3] Foungie, Asplund and Marois (2010), however, suggest that integrated features do still incur some cost, although this is observed in a reduction in estimates of precision rather than the capacity of VSTM.

This result dovetails with object-based theories of attention which suggest that attentional mechanisms also operate upon integrated objects rather than upon spatial locations or particular stimulus features or attributes (Duncan, 1984; Lee & Chun, 2001)[4]. Together, these results raise the question of whether limitations in attentional mechanisms in integrating representations of objects create the item-defined capacity limits of VSTM (see Wheeler & Treisman, 2002). Or, more generally, attention may be required to protect representations before they decay. As such, limitations in the ability to attend to multiple stimuli concurrently may be the cause of item-based capacity limitations (Cowan, 1988, 2001).

Variability in estimates from the typical 3-5 items that can be simultaneously held in VSTM has only recently become the subject of great interest among researchers. It is now well established that estimates of capacity vary greatly depending on the experimental parameters such as the complexity (Alvarez & Cavanagh, 2004; Eng et al., 2005; Phillips, 1974) and similarity (Lin & Luck, 2009; Olsson & Poom, 2005) of stimuli. Capacity estimates also differ according to many individual differences such as intelligence (Fukuda et al., 2010b), encoding strategy (Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011), and the presence of psychiatric disorders (Gold et al., 2010), just to name a few. In addition to capacity estimates varying among individuals, recent evidence suggests that WM capacity and performance more generally can change due to experimental and strategic factors such as participants having extensive cognitive training schedules (Klingberg, 2010), or segmenting the display into different arrays (Ihssen, Linden & Shapiro, 2010). Irrespective of differences in crowding and perceptual load, Ihssen

[4] But see Vecera and Farah (1994), as attention may also be allocated according to spatial location.

and colleagues (2010) showed a significant increase in VSTM capacity when items in a memory array were split across the presentation of two arrays separated in time. Moreover, estimates of capacity may change across the lifespan and are modulated by different developmental factors (see Astle & Scerif, 2011; Gazzaley, Cooney, Rissman, & D'Esposito, 2005b). Together, these ideas suggest that a fixed conceptualisation of the maximal number of possible representations is too rigid to capture experimental and individual variability. As such, a more flexible consideration of what defines VSTM capacity may be required.

1.2.2 Neuroimaging of Capacity Limits

Electrophysiological studies using similar tasks have found a lateralised Event-Related Potential (ERP) which tracks the number of items currently being maintained in VSTM (Vogel & Machizawa, 2004). Typically, this Contralateral Delay Activity (CDA; also known as Sustained Posterior Contralateral Negativity (SPCN)) is concentrated over posterior sites during the delay period, starting approximately 300ms after the onset of a memory array (Jolicœur, Brisson, & Robitaille, 2008; Vogel & Machizawa, 2004). The CDA is established by requiring participants to encode only items on one side of space, and is characterised by an enhanced negativity over electrode sites contralateral to the maintained items. This signature of VSTM maintenance has been likened to the sustained delay activity found in single-unit recordings of non-human primates (see Kuo, Stokes, & Nobre, 2012; McCollough, Machizawa, & Vogel, 2007). Critically, the magnitude of the CDA has been shown to increase in accordance with the number of to-be-remembered items

(Ikkai, McCollough, & Vogel, 2010; Jolicœur et al., 2008), to correlate with measures of VSTM capacity within individual participants (Anderson, Vogel, & Awh, 2011; Kuo et al., 2012; McCollough et al., 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), and to be sensitive to whether a trial is correct or incorrect (e.g. McCollough et al., 2007).

Measures of oscillatory neural activity have also been associated with VSTM maintenance and capacity limits. Alpha-band activity has long been shown to increase with increases in VSTM load (e.g. Grimault et al., 2009; Jensen, Gelfand, Kounios, & Lisman, 2002). Specifically, alpha activity is thought to aid in the suppression of distracting information at encoding and/or during maintenance (Sauseng et al., 2009; Zanto et al., 2011). Dijk and colleagues (2010) have further highlighted the link between alpha and VSTM by showing that hemispheric asymmetries in alpha power may underlie lateralised ERPs reflecting VSTM maintenance, such as the CDA. Neural activity in other frequency bands has also been associated with VSTM capacity. Sauseng et. al (2009) found that the extent of lateralised synchronisation of gamma phase to the negative peak of theta oscillations was enhanced as memory load increased and this synchronisation could predict VSTM capacity. Recent studies, furthermore, have extended the imaging of VSTM capacity limitations to Magnetoencephalography (MEG), reporting the Event-Related Field (ERF) counterpart to the CDA (e.g. Mitchell & Cusack, 2011; Robitaille, Grimault, & Jolicoeur, 2009). Capitalising on the superior spatial resolution of MEG, Robitaille and colleagues (2009) were able to localise the sources of this load-dependant activity to be in posterior parietal cortex (probably intra-parietal/intra-occipital cortex).

Using fMRI regression analysis to isolate regions which reflected the number of to-be-remembered items in VSTM, Todd and Marois (2004) found another neural correlate of the capacity of VSTM in posterior parietal/occipital cortex (IPS/IOS). Furthermore, the BOLD response in posterior parietal cortex could be used to predict individual VSTM capacity estimates (Todd & Marois, 2005). Edin et. al (2009) suggest that the role of the prefrontal cortex in VSTM maintenance is to boost the capacity of capacity-limited posterior areas in situations requiring numbers of representations above capacity (see also Linden et al., 2003). Moreover, sustained delay activity in parietal areas measured by fMRI is sensitive to correct VSTM performance (Pessoa et al., 2002).

1.2.3 Moving from Basic Change Detection to Psychophysical Modelling

Accompanying the call for a more flexible conceptualisation of VSTM capacity, there has been an increased appreciation of the limitations of change-detection tasks (e.g. Bays & Husain, 2008). It has been noted that some types of stimulus arrays that are typically used may enable reliance on long-term memory associations to aid performance and inflate capacity measures (e.g. Olsson & Poom, 2005). Furthermore, the use of whole stimulus arrays to probe VSTM can encourage the use of configural cues to aid change detection (see Jiang et al., 2000). These methodological issues are described in greater detail in Section 2.2.5.

One fundamental conceptual problem with a typical change-detection measure of VSTM performance is the underlying assumption that all changes are the same. Such an approach is insensitive to subtle changes in the *quality* of

representations (Wilken & Ma, 2004). By parametrically manipulating the precision of representation required to make a choice about whether or how an item has changed, it becomes possible to measure effects on the quality of VSTM representations. Without any consideration of quality of VSTM representations, the field is biased to observe discrete effects couched in terms of changes in the numbers of items in VSTM. Consideration of precision variables in VSTM has led to a debate in the literature that is of particular relevance to the current thesis.

1.3 Nature of Resource Allocation – The Capacity and Precision of VSTM

There has been a recent debate in the VSTM literature concerning whether the allocation of resources is (1) constrained according to a limited number of integrated objects that can be stored or (2) can be allocated flexibly so that the trade-off between the number and quality of item representations depends upon the task demands. Those on the former side of the debate assert that items are stored in discrete 'slots' which are stored in an 'all-or-nothing' way. The account asserts that if items are represented in VSTM, there should be no difference in the quality of the representations: items are either remembered (with high resolution) or they are not. Alternatively, proponents of flexible models suggest that resources are divided flexibly between the items that need to be recalled. The quality of the representations will vary systematically with the number of items maintained in VSTM and will also depend on task demands.

Although the ideas raised by both sides have been considered more than fifty years ago (Averbach & Coriell, 1961) and investigated more than twenty years

ago (e.g. Palmer, 1990), the debate has re-entered the focus of the contemporary VSTM literature (e.g. Bays & Husain, 2008; Gorgoraptis, Catalao, Bays, & Husain, 2011; Zhang & Luck, 2008). In this section of the thesis, both sides of the debate will be outlined and the evidence for each account will be discussed.

1.3.1 No Flexibility, Slots are "All or None"

The traditional view of VSTM resource distribution is that there is a small and discrete number of "slots" or ways to represent a limited amount of items concurrently (e.g. Luck, 2008; Miller, 1956). Proponents of the slots model suggest that there is an item limit which, when exceeded, prevents more information from being stored (Anderson et al., 2011; Awh, Barton, & Vogel, 2007; Buschman, Siegel, Roy, & Miller, 2011; Luck & Vogel, 1997; Zhang & Luck, 2008).

The slots are "all or none": representations are either stored with high quality or, once the limit is exceeded, not at all. The representation in each slot is relatively invariant to the amount of information stored, i.e. each slot can store a given representation with a constant resolution (Luck, 2008). Early evidence for this account came from studies which showed that the limits of VSTM resources were defined at the integrated object level, rather than by features across different stimulus dimensions (e.g. Luck & Vogel, 1997; Vogel et al., 2001). Such claims were then substantiated by evidence that the capacity estimates varied according to the number of items rather than the complexity of the information contained in each item once sample-test similarity is taken into account (Awh et al., 2007).

Recently, proponents of this side of the debate have made two amendments to the strict, high threshold, fixed resolution hypothesis. Firstly, it should be noted

that capacity estimates may vary from trial-to-trial according to the amount of noise in the system which would account for variability of within-participant estimates of capacity (Luck, 2008). Secondly, in order to account for results showing co-variation of precision with the number of items below VSTM capacity (e.g. Bays & Husain, 2008), Zhang and Luck (2008) proposed a "slots + averaging resource" model. When arrays are below VSTM capacity, participants can devote more than one slot to represent task-relevant items which increases the precision of their representations (Zhang & Luck, 2008). Such an amendment, however, does lose some of the elegance and parsimony of the original model. In addition, it is difficult to conceptualise the neuronal basis of a "double" slot and what mechanism controls the application of a "double slot" (see Bays & Husain, 2009). Nonetheless, further studies have found that the quality of VSTM representations varies with the complexity of items while still showing discrete object based effects up to the typical 3-4 item capacity limit (e.g. Barton, Ester, & Awh, 2009).

Measures of VSTM representations over time have recently extended this side of the debate. Research suggests that memory representations decay deterministically: representations of items in the original memory array are either available for report or are lost catastrophically (Gold, Murray, Sekuler, Bennett, & Sekuler, 2005; Zhang & Luck, 2009).

In many ways, having discrete memory representations of whole items makes ecological sense. We interact with objects or beings, as such, having discrete item 'slots' allows us to maintain integrated representations of what is important in our environment. Having strict 'slot' limitations does, however, raise doubts as to the flexibility of our mnemonic system, some of which are discussed in the following section.

1.3.2 Infinite Flexibility, Resources are Divided According to Task Demands

The alternative to the fixed slots hypothesis is a flexible resource account. According to this side of the debate, the limited VSTM resources are divided among items in the visual scene according to task demands. There is no upper limit to the number of representations that can be held in VSTM. This account complements previous models of VSTM which suggest that representations are inherently noisy and degrade in a gradual, rather than discrete way (see related Bays et al., 2011; Kinchla, Chen, & Evert, 1995; Wilken & Ma, 2004). Critically, studies supporting this side of the debate have shown that performance may not only depend on the number of items, but also on the information load, the complexity of individual items, and the quality with which items need to be maintained (Alvarez & Cavanagh, 2004; Bays, Catalao, & Husain, 2009; Bays & Husain, 2008; Eng et al., 2005; Wilken & Ma, 2004).

According to Wilken and Ma (2004), VSTM is based on inherently noisy, imperfect representations of the world. Increases in complexity or the number of memoranda simply add more noise to the system, which may obscure the 'signal' for later processing. This account is founded on the tenets of signal-detection theory (for more details see Section 2.2.2), and suggests that during encoding, the visual system establishes some type of cognitive 'filter' based upon the to-be-remembered items. Upon presentation of the probe, this 'filter' is used to gauge the strength of similarity (or match) between the memory and test array. Ideally, the strength of the signal of a "match" between the memory array and probe is normally distributed with the width of the distribution reflecting the amount of noise in the system (see Verghese, 2001). This is considered a "low contrast" approach which

has also been applied to visual search and other attentive processes (Palmer, Verghese, & Pavel, 2000; Verghese, 2001). Such a notion contrasts with the "high-threshold" accounts, which assert that a representation is either stored almost perfectly or not at all (see Section 1.3.1). The maintenance of noisy, internal representations is somewhat consistent with models of the central nervous system that argue that noise is unavoidable in the communication of information between neurons (e.g. Faisal, Selen, & Wolpert, 2008). Errors may, therefore, be due to a combination of noise in the target dimension (e.g. colour), as well as in a task-irrelevant dimension (e.g. location) which helps to individuate items (Bays et al., 2009). From this account, changes in the quality of the representation, either via a reduction in the amount of noise (in task-relevant or task-irrelevant dimensions), or an increase in the signal, are fundamental to the understanding of VSTM representations and are closer to mimicking the behaviour of neural patterns (Bays & Husain, 2009).

Recently, Bays and Husain (2008) proposed a shared resource account, based on these ideas. They proposed that VSTM is a limited but flexible resource, which must be divided between to-be-maintained items; increasing the number of items simply reduces the quality of each item's representation. Bays and Husain (2008) found evidence that the precision of representations declined in an exponential fashion as set size increased[5]. Critically, in contrast to the prediction of a fixed-slots account, there was no evidence of constant, high-resolution estimates of representations below the 3-4 item capacity limit followed by a sudden drop-off in precision as capacity limits were exceeded. Instead, the precision of

[5] Interestingly, the exponential decline in sensitivity (d', see Section 2.2.2) as set size increases has also been observed in macaques (Elmore et al., 2011).

representations appeared to vary according to task demands. This notion was extended by a second experiment, which investigated the allocation of resources according to eye-movements. Here, Bays and Husain (2008) showed increased representational precision for items which were the target of an upcoming saccade, meaning that VSTM resources had already been allocated in anticipation of the behavioural goals. Results of this study, and others since, have shown that the allocation of VSTM resources is dynamic and highly flexible according to task demands (Bays et al., 2011; Bays & Husain, 2008; Gorgoraptis et al., 2011).

Despite the appeal of an infinitely flexible system, the flexible resource hypothesis has come under scrutiny (e.g. Cowan & Rouder, 2009; Zhang & Luck, 2008, for a greater discussion of the models see section 2.3.2). Infinite flexibility may not result in the most adaptive outcome. Stokes and Nobre (2012) argue that sub-dividing the resources *ad infinitum* may result in large numbers of representations that are too coarse to be useful for further processing. Ultimately, we are anatomically constrained to interact with a small number of objects in our environment. Perhaps these behaviourally relevant constraints should also be reflected in our mnemonic representations of the world.

1.3.3 New Insights into the Debate

One possibility, which is not clearly addressed by either side of the debate, is the notion that the precision and the probability of recall of mnemonic items are distinct features of VSTM and can operate independently. For example, expertise in perceptual judgements results in an increase in precision of representation but the maximal number of representations (or slots) remains relatively unchanged (Scolari,

Vogel, & Awh, 2008). In contrast, psychiatric disorders, such as schizophrenia, appear to manifest in a reduction of the number of representations while sparing precision (Gold et al., 2010). Latent variable analyses of IQ data also suggest that orthogonal factors for both resolution and number can best describe VSTM representations (see Fukuda et al., 2010b). Similarly, Awh and colleagues (2007) found no relationship between the number and resolution of VSTM representations. This is in line with recent fMRI evidence that shows distinct regions specifically sensitive to the complexity (superior intraparietal sulcus and LOC) and number (inferior intraparietal sulcus) of representations (Xu & Chun, 2006).

The possible dissociation between the number and quality of representations is also evident in Electroencephalographic (EEG) studies. The investigation of the electrophysiological signature of VSTM maintenance, the CDA (see Section 1.2.2 for more detail), for example, has led to mixed evidence for both sides of the debate. Typically, the CDA is considered to track the number of items being actively maintained in VSTM (e.g. Anderson et al., 2011; Gao et al., 2011a; Kuo et al., 2012; Vogel & Machizawa, 2004) and is taken to reflect a discrete distribution of resources (Fukuda, Awh, & Vogel, 2010a). Perceptually challenging stimuli, for example, which clearly impact upon behavioural performance do not affect CDA amplitude (Ikkai et al., 2010). In contrast, evidence also suggests that the CDA is affected by the complexity of remembered information (Gao et al., 2009; Gao, Yin, Xu, Shui, & Shen, 2011b; Luria, Sessa, Gotler, Jolicoeur, & Dell'Acqua, 2010). Luria and colleagues (2010) found that CDA amplitude is larger for complex, random polygons compared to simple coloured squares. This, in combination with the

results of Xu and Chun (2006), suggests that VSTM maintenance is affected by both the number and the complexity of to-be-remembered items[6].

Recently, there has been a proposal to combine elements from the “slots” and the “flexible resources” camps of the debate (e.g. Barton et al., 2009). This suggests that resources are allocated in both a discrete, object-based fashion and are bounded by an upper limit; variations in the resolution within each representation, however, can vary according to task demands. This concurs with recent evidence from single-unit recordings in macaques showing independent resources in the two hemispheres, akin to “slots”, but limited resources within each hemifield that are allocated in more a gradual fashion until an upper bound is reached (Buschman et al., 2011). It may be the case that the decline in resolution accompanying increases in set-size may be due to a limit in the co-ordination between regions associated with limits in the number of representations (such as the inferior IPS) and visual regions presumably coding the perceptual content, and hence quality, of representations (such as LOC) (Anderson et al., 2011). When the number of items increases, it may be the case that ‘quality’ information from sensory areas cannot be sufficiently integrated into the representations of items which results in a reduction in the precision of representations. As such, VSTM may be defined by both the number of items and the quality or amount of information stored (Alvarez & Cavanagh, 2004; Chun, 2011).

For the purposes of this thesis, the distinction between the quality and number of representations in VSTM may suggest that other cognitive processes may differentially affect or interact with these factors. For example, it may be

[6] Notably, however, this is distinct from perceptual effects on VSTM, therefore, care must be taken to ensure that the encoding time is sufficient so that differences in perceptual analysis are not falsely attributed to differences in VSTM (see Bays et al., 2011; Eng et al., 2005).

reasonable to expect that anticipatory attention (i.e. before the memory array) may help to encode only the task-relevant items, which could, in principle, increase the probability of their successful recall *as well as* the quality of their representations. Orienting attention to items during the maintenance period of VSTM, however, may only be able to improve the probability that task-relevant representations are not forgotten, but may not be able to restore any quality that was not encoded in the first place (see Matsukura, Luck, & Vecera, 2007).

The independence between the number and quality of items, furthermore, would have implications for the ability to control the allocation of VSTM resources flexibly. If there were a central "pool" of VSTM resources which could be used to code a variable number items with a flexible degree of precision, it is conceivable that one could adapt the allocation of resources according to task demands (akin to the flexible resource hypothesis, see Bays & Husain, 2008; Wilken & Ma, 2004). However, if separate mechanisms underlie the number and quality of items in VSTM, then it may not be possible to "trade" a smaller number of representations for higher quality representations. In this case, the ability to bias the trade-off between the number and quality of representations would not be under flexible control. A "slots" account would also suggest that the resolution and number of representations is fixed and thus cannot be 'traded'.

1.4 Intersection between VSTM and Perception

When considering the number and quality of internal representations in VSTM, it is important to consider how information entered VSTM in the first place:

through perceptual analysis of the visual scene. The notion that perceptual representations eventually evolve into the representations in VSTM suggests that there is a great deal of commonality between the two processes.

1.4.1 Evidence for Overlap between VSTM and Perception

Two key arguments give weight to the notion that VSTM and perception are highly overlapping mechanisms. Firstly, recent neuroimaging studies show that specialised sensory processing areas are involved in both the perception and the continued maintenance of representations in VSTM. Secondly, both perception and VSTM appear to be spatiotopically organised, suggesting that the spatial organisation evident in perception continues through VSTM.

This supposed overlap between VSTM and perception has led to the idea of a "sensory recruitment hypothesis" which suggests that the areas involved in the initial perceptual analysis of information are also involved in the on-going maintenance of information (e.g. Ester, Serences, & Awh, 2009; Serences et al., 2009). The proposal is intuitively sensible: if early sensory areas are tuned to specific stimulus attributes then, they should be best suited to representing this information, even in the absence of physical stimuli. The evidence for the sensory recruitment hypothesis, however, has not always been forthcoming (see Magnussen & Greenlee, 1999; Offen, Schluppeck, & Heeger, 2009; Pasternak & Greenlee, 2005). Conventional analysis of fMRI BOLD data does not reliably reveal significant activation in early visual areas during the maintenance period (Dumoulin & Wandell, 2008; Serences et al., 2009; Stokes & Nobre, 2012). Recent

developments in analysis, however, have led to researchers finding key evidence that neural populations involved in forming perceptual representations also contribute to their continued maintenance in VSTM (e.g. Silvanto & Cattaneo, 2010). For example, in a seminal study, Harrison and Tong (2009), showed that the orientation of a stimulus maintained in VSTM could be decoded in areas V1-V4 by using multivariate pattern analyses, even in the absence of significant modulation of BOLD activity. In addition, decoding accuracy was better in areas with greater orientation selectivity (areas V1 and V2 compared to V4); which provided yet further evidence in favour of an overlap between VSTM and perception. Serences, Ester, Vogel and Awh (2009) found analogous effects in V1 for maintenance of both orientation and colour features. Using single-unit recordings, Woloszyn and Sheinberg (2009) also showed that neuronal groups clearly implicated in encoding also demonstrated stimulus-specific activity during a delay period. The implication of these results is that early visual areas involved in perceptual processing of memoranda still play a role in the on-going maintenance of items in memory.

In addition to the overlap in activity in early visual areas between perception and VSTM, there is evidence that some of the spatially-based organisation of perception is preserved in VSTM (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Eimer & Kiss, 2010; see also Jiang, Olson and Chun (2000) for more on space as an important organising principle in VSTM). Using event-related potentials, for example, Kuo, Rao, Lepsien and Nobre (2009) found a spatially specific marker for identifying a target within a VSTM array that was analogous to the spatially specific marker for identifying a target within a perceptual search task: the N2PC. The similarity in this lateralised component suggests that at least basic

information about the spatial layout of the items in a perceptual array is carried into VSTM. This, combined with the recruitment of early sensory areas for the maintenance of VSTM representations, suggests that there is considerable overlap between VSTM and perception.

1.4.2 Perception is Competitive, is VSTM Competitive too?

Given the high degree of overlap between VSTM and perception, it is reasonable to suggest that some of the dynamics associated with perception may continue into VSTM. When activated by sensory input, neurons that are selective for a particular stimulus attribute also inhibit nearby neurons which code for other attributes. It is well established that competition occurs at the level of the Receptive Field (RF). When two or more stimuli are presented in the same RF, the neuronal response is suppressed compared to if a stimulus is presented alone (e.g. Kastner, De Weerd, Desimone, & Ungerleider, 1998; Luck, Chelazzi, Hillyard, & Desimone, 1997). Perceptual processing is, therefore, inherently competitive when multiple stimuli are presented simultaneously and in close proximity (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Reynolds, Chelazzi, & Desimone, 1999; Stokes & Nobre, 2012). Representations which “win” the competitive interplay between neuronal ensembles then remain active and available for further processing.

Most of the competitive mechanisms investigated are based on spatial properties of receptive fields. Spatial competition is due in part to the retinotopic (e.g. Engel, Glover, & Wandell, 1997) organisation of visual cortex, which means that items arranged closely in space are processed by neighbouring neuronal

groups. Importantly, receptive field size increases as more information is integrated higher up in the visual processing hierarchy. For example, estimates of the receptive field sizes in V1 are less than 2° whereas they are thought to be between 4° and 6° in V4 (e.g. Kastner et al., 2001). As the proximity among stimuli increases, items become subject to competitive dynamics progressively earlier in the processing stream.

Increased spatial proximity ultimately impairs the resolution of competition between items and leads to confusion because there is ambiguity about which stimulus is coded within any given receptive field (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000). For example, during perceptual search, the identification of a target became increasingly difficult as the distance between four potential target items decreased (Müller-Plath & Elsner, 2007). Analogous results have been shown in attentive tracking paradigms; multiple object tracking performance decreased as the target-target distance was reduced (Shim, Alvarez, & Jiang, 2008).

Though seldom considered, it is also possible to conceive of competitive mechanisms based on non-spatial features of stimuli. Other stimulus dimensions may be subject to similar competitive dynamics. Increasing the number of similar features (e.g. similar colours) presented simultaneously could, in principle, reduce the neural resources available to code each specific feature. The result can be conceptualised as a reduction of the precision with which each feature can be perceived and stored, which would ultimately reduce performance. Effects of this nature have been observed in visual search paradigms. In a seminal study, Duncan and Humphreys (1989) showed that the similarity between targets and distracters decreases search efficiency. The results can be interpreted in the framework of

non-spatial competitive interactions. When targets and non-targets are similar, they both compete for representation until the competition is resolved and the target is identified. Reducing this similarity, improves the ability to select target items because there is less overlap in the processing of the objects/features and thus the inter-item competition is lower.

Ultimately, competitive dynamics in visual cortex underlie a limitation in our ability to perceive and encode items from our rich visual environment. Like perception, VSTM is also severely capacity limited. Given the high degree of functional overlap between VSTM and perception (see Section 1.4), competitive interactions in perception may, therefore, extend into VSTM and contribute to the continued maintenance of representations.

1.4.3 Perception and VSTM – Where to next?

As further evidence of a correspondence between VSTM and perception, it appears that attention can affect these two processes in a similar way (see also Awh & Jonides, 2001). Information regarding the relevance of items has been shown to improve the probability of "survival" of task-relevant items in the inter-item competition during perception and encoding for subsequent behaviour (Desimone & Duncan, 1995; Kastner & Beck, 2005; Kastner & Ungerleider, 2001).

Similar to perception, representations of items entering or being maintained in VSTM can be biased and enhanced through top-down attentional processes (Gazzaley & Nobre, in press; Griffin & Nobre, 2003; Stokes & Nobre, 2012). Given the overlap between the mechanisms supporting perception and VSTM maintenance, it is reasonable to assume that some of the factors that affect the

perception of items would also continue to influence their maintenance. If successful VSTM maintenance depends on activity in early visual areas, then the competitive limitations of what can be perceived simultaneously are likely to affect items stored simultaneously in VSTM (Edin et al., 2009). Experiments in this thesis will investigate the extent to which these competitive dynamics continue into VSTM maintenance.

In light of all this evidence, the notion that emerges is that VSTM and perception are not anatomically or functionally decoupled; but instead that VSTM is a natural extension of the perceptual process. Furthermore, VSTM is not a static storage unit but a dynamic representation that may, like perception, continue to be shaped by competitive inter-item interactions and top-down influences (Edin et al., 2009; Stokes & Nobre, 2012). The effect of attention on VSTM performance is another important focus for the current thesis.

1.5 Interaction of VSTM and Attention

Top-down modulation of visual processing is critical to focus on task-relevant information and to suppress irrelevant distraction. Given the limited capacity of VSTM, the role of selective attention in protecting or prioritising task-relevant information is critical (e.g. Matsukura et al., 2007). Selective attention mechanisms can modulate every stage of processing implicated in VSTM (Gazzaley & Nobre, in press): expectation of an upcoming array to be remembered, perceptual processing and encoding of relevant array items (Rutman, Clapp, Chadick, & Gazzaley, 2010), maintenance (Griffin & Nobre, 2003), and retrieval (Theeuwes, Kramer, & Irwin, 2011). The interaction between VSTM and attention is so widespread that some

researchers believe that they are essentially the same phenomena, with the same control processes and representational content (see Sergent & Dehaene, 2004). Furthermore, there is a suggestion that VSTM capacity limits are due to the limits in directing attention to protect task relevant representations from decay, interference or other such processes (e.g. Cowan, 2001; Mayer et al., 2007). As such, it is thought that VSTM can act as the intermediary through which attention selects and maintains task-relevant representations for subsequent, higher-level processing (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993; Chun, 2011; Chun, Golomb, & Turk-Browne, 2011; Desimone & Duncan, 1995).

This section of the thesis will review the literature to date regarding the interaction between VSTM and attention but it will focus on only two main effects: the effect of selective attention in anticipation of to-be-remembered array and the effect of orienting selective attention during VSTM maintenance.

1.5.1 The Effect of Attention before and during VSTM Encoding

Early attentional influences on VSTM can be divided into two main effects. The spatial anticipation of a task-relevant stimulus elicited by a pre-cue is thought to result in greater cortical excitability toward the expected stimulus, which can enhance processing in that location (Kastner et al., 1999; Luck et al., 1997). Ultimately, these attended stimuli are processed more thoroughly and are more likely to be successfully maintained (see Gazzaley, 2011). Secondly, pre-cuing can influence the selection of task relevant stimuli and the suppression of distracters,

which has not only been linked to successful recall but also to individual estimates of VSTM capacity (e.g. Vogel et al., 2005).

In the absence of physical stimuli, studies have shown that preparatory attention to a particular location in space can excite corresponding areas of visual cortex (Kastner et al., 1999; Luck et al., 1997). These anticipatory effects can ultimately result in the enhanced processing of stimuli presented in the cued location (Posner, 1980). Top-down influences, however, are not unique to spatial cueing (e.g. Bollinger, Rubens, Zanto, & Gazzaley, 2010; Rutman et al., 2010). Gazzaley, Cooney, McEvoy, Knight and D'Esposito, (2005b) showed that anticipatory attention can also modulate processing in category-specific sensory cortices. In this fMRI task, participants were instructed to encode either upcoming face or scene stimuli. Importantly, activity in occipitotemporal areas functionally specialised for processing face and scene stimuli was significantly elevated when cues indicated that the preferred stimulus type had to be remembered compared to a neutral passive viewing condition, and was significantly suppressed when cues indicated that the preferred stimulus type was to be ignored. These results suggest that top-down effects can dynamically modulate the processing of information according to task demands. Critically, these data link the top-down enhancement of task-relevant information at encoding with subsequent VSTM performance. This result concurs with research which shows the extent of functional connectivity between frontal areas and early visual areas, and the strength of top-down modulation has been linked to higher memory performance (Kuo, Yeh, Chen, & D'Esposito, 2011; Sergent, Ruff, Barbot, Driver, & Rees, 2011).

For the purposes of the current thesis, however, it is important not only to consider the effects that anticipatory attention has on perception and visual processing generally, but how these effects ultimately affect VSTM. It is now well established that attention can gate access into VSTM (e.g. Bundesen, 1990; Duncan & Humphreys, 1989). The presentation of an exogenous cue, for example, 50msec before the presentation of a memory array could assist in the transfer of the item in the cued location to VSTM. This effect was apparent even when the cue did not predict the location of the upcoming probe (Schmidt, Vogel, Woodman, & Luck, 2002)[7].

Endogenous cues can also modulate visual processing to prioritise task-relevant information. For example, in a study conducted by Rutman et al. (2010), participants were instructed to orient attention to the face or scene contained within a composite stimulus. The strength of the attentional enhancement of an ERP component reflecting perceptual processing predicted VSTM performance. Specifically, the enhancement of the P100 (97-129msec after the onset of the stimulus) reflected a greater processing of the anticipated stimulus category and resulted in a higher recall. In this way, endogenous anticipatory attention can prepare early visual areas for up-coming task relevant stimuli. These top-down effects can occur through the enhancement of task-relevant items (as demonstrated by Rutman et al., 2010) and/or the suppression of distracters (Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005a).

The idea that the ability to suppress distracting information is an important factor in determining VSTM performance is well established. In a trial-by-trial

[7] For more on the distinction between endogenous and exogenous effects of attention on VSTM, see Botta, Santangelo, Raffone, Lupianez and Belardinelli (2010).

analysis of a task requiring participants to attend to the colour or the motion of random dot displays, Zanto and Gazzaley (2009) suggest that it is the protection of task-relevant information from distraction which underlies successful VSTM maintenance (see also Clapp, Rubens, & Gazzaley, 2010; Fukuda & Vogel, 2009). It is thought that PFC, as part of a highly flexible fronto-parietal network (Duncan, 2010), is a critical region involved in the protection of representations from distraction. In an fMRI-guided Transcranial Magnetic Stimulation (TMS) study, Zanto, Rubens, Thangavel and Gazzaley (2011) confirm that PFC plays a causal role in top-down modulation of VSTM performance by suppressing task-irrelevant information. Using a feature delayed-response task McNab and Klingberg (2008) also show that PFC and structures in the Basal Ganglia are critical in filtering what information enters VSTM. Activity in these regions, during a pre-encoding period, reflected the expectation of distracters to be present in the upcoming memory array. Furthermore, this activity could predict individual VSTM-capacity estimates, suggesting preparing an efficient filter can effectively channel limited resources to the most task relevant information.

In a similar way, using an ERP experiment, Vogel and colleagues (2005) show that VSTM capacity can predict individual differences in the ability to filter task relevant information. The CDA magnitude of participants with high VSTM capacity suggested that they were able to filter task-relevant information efficiently and thus only maintained cued items. Given that preparatory attention can aid in the suppression of distracters and the enhancement of task-relevant information (e.g. Gazzaley et al., 2005b), it would be reasonable to expect that the extent of these

attentional shifts can also predict the ability to *select* task-relevant information and ultimately affect VSTM performance.

It is possible to track the shifts in spatial attention with high temporal resolution by using a number of event-related electrophysiological signatures. No studies, to my knowledge, have directly investigated the effect of spatial attentional shifts on VSTM performance. It may be the case that individual differences in the strength of attentional preparation can predict the benefit in cueing in VSTM performance.

1.5.2 Electrophysiological Signatures of Spatial Attention

There is a typical sequence of three lateralised ERP signatures of spatial attention which can be used to track the degree and evolution of attentional orienting in anticipation of an upcoming stimulus. ERPs are especially well suited for tracking the effects of these attentional shifts due to their high temporal resolution (see Section 2.4). Two early markers: the Early Directing Attention Negativity (EDAN) and the Anterior Directing Attention Negativity (ADAN) have been linked to the processing of directional cues and the initiation of shifting anticipatory spatial attention (Harter, Mille, Price, LaLonde, & Keyes, 1989; Jongen, Smulders, & Van Der Heiden, 2007; Nobre, Sebestyen, & Miniussi, 2000).

First reported by Harter et al. (1989), the EDAN is an enhanced negativity in posterior sites contralateral to the cued side of space between 200 and 400ms after cue onset (e.g. Hopf & Mangun, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994). Van Velzen and Eimer (2003), however, suggest that the EDAN is very sensitive to

the physical shape of the directional cue and may not, therefore, be directly linked to the control of covert attention (cf. Nobre et al., 2000). Praamstra and Kourtis (2010) applied a dipole source reconstruction analysis and showed the EDAN is functionally related to attentional orienting and possibly reflective of the parietal activity as part of the fronto-parietal network. In addition, their data suggest that the EDAN is the posterior precedent to the ADAN (Jongen et al., 2007; Praamstra, Boutsen, & Humphreys, 2005; Seiss, Driver, & Eimer, 2009; Van Der Lubbe, Neggers, Verleger, & Kenemans, 2006). Like the EDAN, ADAN is an enhanced negativity contralateral to the cued hemifield but is concentrated in anterior areas approximately 300-500ms after the onset of a cue (Jongen et al., 2007). The ADAN is thought to reflect the anterior part of fronto-parietal activity involved in controlling the allocation of spatial attention. This marker of anticipatory attention has been linked to the interpretation of cue meaning and is reflective of a supramodal control of attention (Seiss et al., 2009).

The third component, the Late Directing Attention Positivity (LDAP; Harter et al., 1989; Yamaguchi et al., 1994), is a later and sustained posterior ERP marker, reflecting an enhancement in cortical excitability in anticipation of upcoming stimuli. Consequently, the LDAP has been linked to enhancements in perceptual processing (Jongen et al., 2007), perhaps by enhancing the cortical excitability cortex in cued locations. In contrast to the earlier components, the LDAP is an enhanced positivity contralateral to the cued hemifield and is typically observed upwards of 500ms, often until the cued stimuli are presented (McDonald & Green, 2008).

Given the influence that preparatory attention can have on perception

(Hillyard, Vogel, & Luck, 1998; Rutman et al., 2010) and higher-level processes such as motor response planning (Praamstra & Kourtis, 2010; Seiss et al., 2009), this top-down mechanism may also play a critical role in encoding stimuli to be remembered. By tracking the shifts of preparatory attention, using event-related potentials, it would be possible to gain insight into how the system governs access to resource limited VSTM. It may become possible to determine, for example, whether selective attention affects the precision or the probability that task-relevant representations are recalled.

1.5.3 Retrospective Orienting of Attention can also Modulate VSTM representations

In addition to preparing the visual system to encode task-relevant information, there is a growing consensus in the literature that attention can also enhance VSTM performance retroactively: that is, after information is already in VSTM (Delvenne, Cleeremans, & Laloyaux, 2010; Landman et al., 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Lepsien & Nobre, 2007; Makovski, Sussman, & Jiang, 2008; Nobre et al., 2004; Sligte et al., 2008). These studies give further weight to the notion that VSTM is dynamic and is constantly under top-down control (Stokes & Nobre, 2012).

For example, in a paradigm developed by Griffin and Nobre (2003), participants were presented with a retrospective cue (i.e. retro-cue) 1500-2500msec *after* the memory array presentation but 500-1000msec before probe presentation. These retro-cues retrospectively predicted, in 80% of cases, which item was going to be probed at the end of the trial. It is important to note that the time of the

presentation of the cue is well after the decay of the iconic trace (Averbach & Coriell, 1961; Sperling, 1960). Even though all stimuli were relevant during encoding, the behavioural benefit of the retro-cues was equivalent to the benefit found on the pre-cuing trials. Like the benefits for pre-cues, on trials where attention was oriented to an item in memory, participants responded more accurately and quickly about this item, compared to if the item was not cued (see also Landman et al., 2003). Similarity in the neural traces of orienting attention to perceptual arrays and arrays already in memory was also found (Griffin & Nobre, 2003) and replicated (Nobre et al., 2004). In addition to the similarities between the two neural mechanisms, retro-cues also elicited an enhanced early (120-200msec) response in anterior regions, which is thought to be unique to orienting attention to internal representations (Griffin & Nobre, 2003).

The source of retrospective top-down modulations of VSTM maintenance is considered to be the “control regions” within prefrontal and parietal cortices. The direct comparison of activity reflecting the orienting of retrospective attention reveals enhanced prefrontal activity when compared to prospective attentional orienting (Nobre et al., 2004). Griffin and Nobre (2003) also provide converging evidence of the comparatively enhanced frontal activity in the retrospective orienting of attention in an EEG study. A meta-analysis of 5 retro-cueing experiments participants (Lepsien et al., 2005; Lepsien & Nobre, 2007; Lepsien et al., 2011b; Nobre et al., 2004; Yeh, Kuo, & Liu, 2007) using an activation likelihood estimation (ALE) software package GingerALE (The BrainMap Project, San Antonio, USA), revealed seven significant clusters which reflect the orienting of retrospective attention (for more details see Appendix A). These include posterior

parietal (precuneus, superior parietal lobule, inferior parietal lobule), prefrontal (middle frontal gyrus), and occipital (superior occipital gyrus) regions (see Figure 1.1).

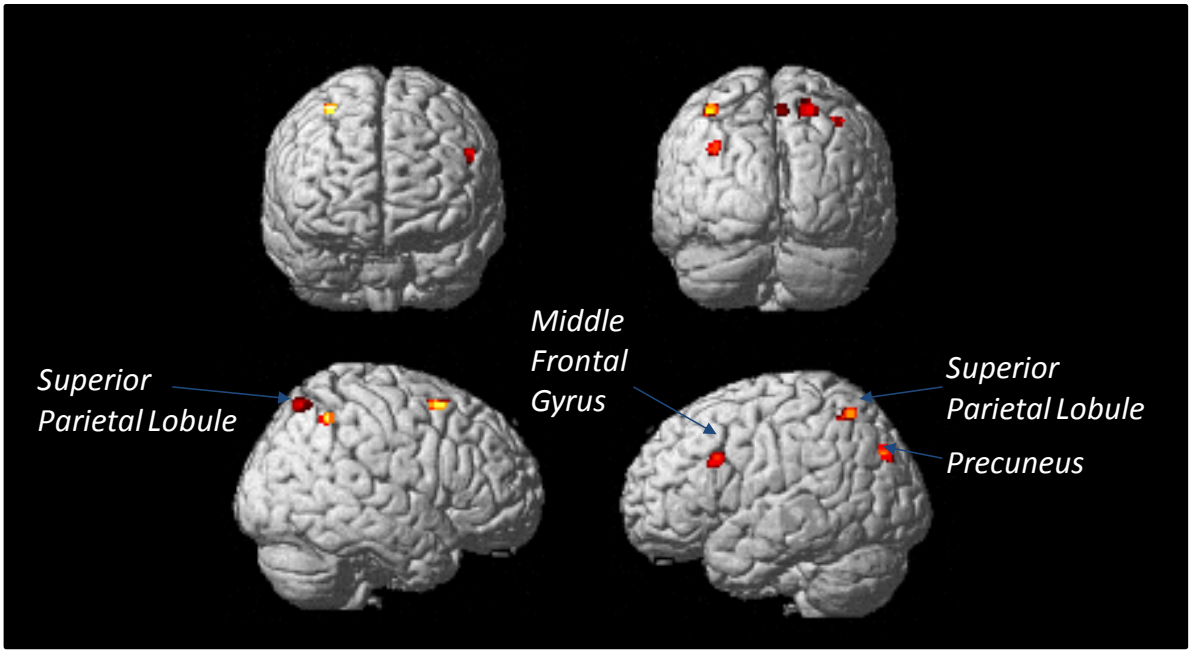


Figure 1.1: Control regions associated with the orienting of retrospective attention. Activations were based upon results of a meta-analysis of five retro-cueing studies calculated using the GingerALE procedure (Lepsien et al., 2005; Lepsien & Nobre, 2007; Lepsien et al., 2011b; Nobre et al., 2004; Yeh et al., 2007).

Depending upon the particular task demands, signals from these areas can modulate maintenance activity in stimulus specific cortex (Stokes, 2011). The studies from Nobre's laboratory (e.g. Lepsien & Nobre, 2007; Lepsien et al., 2011b), for example, show that presentation of a symbol cueing attention to houses or faces could enhance activity in PPA or FFA respectively. Similarly, Sligte, Scholte and Lamme (2009) show evidence that spatially specific retro-cues can

modulate the corresponding retinotopic areas in V4 and this activity could predict the accessibility of that information to VSTM. The strength of the connectivity from control regions and posterior, visual associative cortex, furthermore, can predict VSTM performance (Gazzaley et al., 2004; Kuo et al., 2011). As further evidence that retro-cueing can modulate maintenance activity, in an ERP study, Kuo and colleagues (2012) show that a spatial retro-cue could reduce the CDA, probably reflecting the reduction of the effective memory load to only the cued item.

Despite the well established retro-cueing benefits in VSTM performance, the underlying mechanisms are still poorly understood. As previously discussed, Sligte and colleagues (2008) propose a tripartite system involving a limited-capacity strong VSTM that is resistant to interference, a high-capacity but fragile store, and an earlier iconic trace (see also Sligte et al., 2008; Sligte, Vandenbroucke, Scholte, & Lamme, 2009; Sligte, Wokke, Tesselaar, Steven Scholte, & Lamme, 2011). In their view, selective attention acts to consolidate and transfer items in fragile VSTM to the more robust form of strong VSTM. In this limited capacity, highly robust form, representations are supra “probe-threshold” and thus, are not overwritten by the probe. A corollary implication of such a model is that much more information may be coded in the visual system than is normally revealed through traditional probing procedures (see also Astle, Nobre, & Scerif, 2010b).

The role of attention may be to determine which low-level, perceptual information is transformed into the robust, but limited-capacity form of VSTM (Bundesen, 1990; Stokes & Nobre, 2012; Vandenbroucke et al., 2011). For limited resource systems like VSTM, this is especially important to ensure that only the most task-relevant information is maintained and available for subsequent processing (for a review see Lepsien & Nobre, 2006; Stokes & Nobre, 2012). The

question remains, however, how retroactive attention assists in biasing the competitive interactions between items for representation in VSTM. In line with the evidence that preparatory attention can suppress distracting information (see Section 1.5.1), one could consider the role of retrospective attention being one (or both) of two possibilities: attention may suppress un-cued or enhance cued items in memory. Within capacity limits, VSTM performance for invalidly cued items has been shown to be equivalent to performance for neutrally cued items, suggesting that attention is not used to suppress uncued items from further processing (Astle, Summerfield, Griffin, & Nobre, 2011; Landman et al., 2003). Instead, it appears attention is involved in the transformation of representations into a format which is robust to the degrading processing during the delay interval and comparatively immune to interference from the probe (Makovski & Jiang, 2007; Makovski et al., 2008). Importantly, this benefit is above and beyond simply reducing the effective memory load to one item, because performance on retro-cue trials was higher than when memory was probed at the time when the retro-cue was presented (Makovski et al., 2008).

Matsukura and colleagues (2007) show that retro-cueing does not simply prioritise the retrieval of cued items. In a double-cueing paradigm, performance for uncued items, which were then later cued, was significantly worse. This suggests that somehow task-irrelevant information was degraded because there was ample opportunity to switch the priority of items for retrieval to the second set of cued items (cf. Landman et al., 2003). This concurs with another study which suggests that, in supra-capacity situations, the retro-cue is used to ensure task-relevant information is maintained while uncued information is lost (Astle et al., 2011). Together, these studies show that uncued items are likely to be lost to VSTM,

rather than actively suppressed, and cued items are protected by transforming these representations into a robust, “probeable” format.

Despite the recent explosion of studies which have investigated the effect of top-down modulations on VSTM performance, at the time I was conducting research for this thesis, there had been no studies regarding the question of whether retrospective attention affects the quality and/or number of items in memory. One series of experiments examined this question directly (see Chapter 4). Very recently, however, one study has been published in this area, during the final write-up stages of the thesis. Bays and colleagues (2011) found evidence exogenous retro-cueing benefits in a delayed orientation-match VSTM task are attributed to a decrease in the variability (or increase in the precision) of representations. Similarly, when the distracter item was invalidly cued, the decrease in performance for targets was attributed to differences in the precision (or variability in the response distribution) rather than probability of recall. This result would suggest that attentional cueing can trigger a dynamic reallocation of resources to the cued item. The use of item numbers (2 items) well below conventional item-number capacity limits, however, may have made the task especially sensitive to changes in the precision, rather than probability of recall. Specifically, attention may have had no benefit in increasing the probability of recall because there were already sufficient resources to code and maintain both items. The current thesis will also investigate the effect attention has on the representational quality and number of items in VSTM, in situations approaching or at capacity limits.

1.6 The Precision and Capacity of VSTM – Work of the Current Thesis

This final section of the introduction will summarise the main issues just raised and then present the rationale for the upcoming chapters. Finally, the introduction will conclude with a preview of the results of each chapter in the thesis and the main implications for discussion.

1.6.1 Summary of Previous Work

In summary, the introduction reviews the evidence which suggests that VSTM is a highly flexible and dynamic system and under the influence of top-down control during each major stage of evolution of VSTM. The hallmark of VSTM is the severe capacity limitation, typically defined as being 3-5 items presented simultaneously. What characterises this capacity limitation is still being debated. Are VSTM resources allocated according to a limited number of items with high precision or are they distributed flexibly to the requirements of the quality and number of representations that the task demands? Evidence suggests that the precision and number of representations may be separate characteristics to describe VSTM performance.

Like perceptual representations, internal mnemonic representations are modulated by top-down mechanisms to select task relevant information and maintain it in a form which can be utilised by subsequent processes. In addition to both perception and VSTM being under flexible control, there are other similarities which have important implications for the current thesis. For example, there is a

high degree of overlap in neural activity reflecting the processing of perceptual and mnemonic representations e.g. delay activity in early visual cortex. The limited neural populations to encode and maintain visual information means that visual processing is inherently competitive. The inter-item dynamics that underlie competition for perception is well established in the literature. There has been very little investigation, however, to determine whether these competitive dynamics extend into another resource-limited system: VSTM.

Due to the limitations in capacity, the role of attention in selecting task-relevant information for storage in VSTM is critical. There is evidence to suggest that attention can modulate activity in every stage of the evolution of VSTM representations: expectation, encoding, maintenance and retrieval. Of particular importance, attention can modulate anticipatory activity in visual cortex, either by cueing a spatial location or cueing categorical information. This modulation can result in enhanced processing of cued items. The extent of this modulation, furthermore, can predict VSTM performance. In a similar way, attention can also be applied retrospectively, that is, to items already in memory. Results suggest that attention can modulate maintenance activity and transform representations into a more robust format. Together, previous research suggests that top-down and competitive mechanisms contribute to VSTM being a dynamic reflection of what is currently relevant for task goals.

1.6.2 Rationale and Questions to be Addressed

Despite the continued interest in the limitations in VSTM throughout the past century (see Blankenship, 1938), there are a number of open questions and unexplored issues. This thesis explores the mechanisms underlying the attentional benefits afforded by anticipatory and retrospective cues. Does attention affect the precision of representations and the probability of recall differentially? Or, does that depend upon the task requirements? One could consider that when anticipatory attention is already oriented to preferentially select task-relevant items, there may be an enhancement of both the probability that it is successfully maintained and the quality with which it is maintained. This is because the limited capacity is used to encode and maintain only task relevant information, which may result in higher representational quality as well as improved probability of recall. Furthermore, what are the brain mechanisms underlying this attentional shift? Can electrophysiological signatures of anticipatory spatial attention predict the benefits in VSTM performance gained from the cue?

In the case of retrospective attention, however, there is no indication from the beginning of the trial which item may be task relevant. The system should then code as much information as possible, which may result in lower representational quality per item. Attention may not, therefore, be able to restore the loss of “quality” of representations due to decay or inter-item competition before the cue onset. As such, attention may serve to protect and consolidate the cued item into a robust from and improve the probability that it is recalled.

As an extension of this concept, it is clear that there is a trade-off between the number of items and the quality with which they are maintained. Given the vast

literature suggesting that VSTM is under flexible control, one might expect that the top-down control may also be able to bias the trade-off between the quantity and quality of representations. In situations where, on average, it would be optimal to represent fewer items with higher precision, participants should be able to trade the number of items for an increase in the quality of representations.

Finally, there is evidence to suggest that perception and VSTM are based on the same underlying mechanisms. Because both systems depend on similar neural structures, they should be subject to similar pressures due to the limited resources to encode and maintain representations. This thesis will examine the extent to which the competitive dynamics which are present in perceptual processing extend into VSTM. It is expected that under conditions of higher competition, be that spatial proximity or other feature dimensions (e.g. colour), there will be greater inter-item interference and consequently lower VSTM performance.

1.6.3 Overview of Chapters

Before the experimental chapters, Chapter 2 describes the methodological approach undertaken in the current thesis. In particular, this chapter will include a discussion of the main experimental paradigms employed in the thesis and the psychophysical model used to estimate the precision of representations and the probability of recall. An introduction to EEG will also be provided. Chapter 3 then introduces the first experiments of the thesis. The study uses behavioural and ERP methods to test the extent to which anticipatory attention can modulate the precision and the probability of recall of items. This study also tracks the brain

mechanisms that mediate attentional selection for VSTM and attempts to use electrophysiological signatures of anticipatory attention to predict VSTM performance. As an extension of this idea, the aim of the series of experiments in Chapter 4 is to determine whether retrospective attention enhances the precision (quality) of VSTM or the probability that items are maintained in memory. The experiments in Chapter 5 then test the extent to which the trade-off between the quality and number of items in VSTM can be flexibly controlled. Given the correspondence between perception and VSTM, the experiments in Chapter 6 investigate whether the phenomena that constrain perception continue to constrain representations in VSTM. Finally, the discussion (Chapter 7) will draw upon the main concepts introduced throughout the thesis and will conclude with possibilities for future research.

CHAPTER 2
Methodological and Conceptual Approach

This chapter provides an overview of the basic methodological approaches used in data collection and analysis of the experiments in the thesis. There are three main sections which introduce methods used in the current thesis including behavioural testing, psychophysical modelling of VSTM, and electroencephalography. The final section will briefly introduce some methodological approaches to extend the work of the thesis. This chapter is not intended as a comprehensive guide to these methodologies, but instead as a discussion of the relative contributions and limitations and of these techniques in light of the ideas presented in this thesis.

2.1 Overview to Behavioural Testing

Well designed and controlled experimental paradigms are the basis for any well founded cognitive neuroscientific research to investigate the contributions and interactions of cognitive processes on behaviour. Behavioural testing can give an insight into the foundation of the interaction between cognitive mechanisms of interest and can assist in arbitrating between competing theoretical debates. Other pragmatic advantages of behavioural testing are that it is useful for getting the right experimental manipulations to combine with neural measures as well as being relatively inexpensive to run and non-invasive. Analysis of behavioural experiments is not just limited to accuracy and reaction time. This section will discuss a range of

analysis methods including approaches from Signal Detection Theory (Green & Swets, 1966), and psychophysics.

The aim of the current thesis is to be able to gain an insight into the number and quality of available VSTM representations. The effects of other manipulations, such as attention and context on either the precision and/or number of representations are of central interest. As such, techniques are needed to determine whether attentional (Chapters 3, 4, 5) or perceptual (Chapter 6) manipulations are reflected in changes in accuracy (see Section 2.2.1), sensitivity, or bias in the decision-making process (see Section 2.2.2). Critically, however, there is a need to extend the dependent measures to get some type of metric of the precision and number of representations. Capacity estimates (see Section 2.2.4) can be calculated and compared among conditions. Capacity estimates alone, however, do not give any insight into whether the limits are dictated by the number of items or the quality of representations.

By parametrically modulating the degree of precision that is required to make correct discriminations based on VSTM representations, however, one can observe under which conditions the precision and number of items in VSTM can be modulated. For example, one could vary the degree of rotation of a probe compared to a memory array so that small rotation changes would require relatively precise representations whereas large rotation changes would not. Using a repeated-measures design, it is possible to estimate the average proportion of times participants can correctly discriminate each angle of rotation condition. Such an approach then allows us to model the precision and number of representations

simultaneously (see Section 2.3). Comparisons of these estimates should ultimately yield a greater insight into the very nature of VSTM.

2.2 Dependent Variables used in the Current Thesis

2.2.1 Accuracy

The average accuracy of participants in the different experimental conditions provides a simple but informative dependent variable. It may seem obvious, but if a participant has a VSTM representation or trace of the probed item, they will on average, perform better in a discrimination or judgement task than would be predicted by chance. The approach taken in this thesis is fairly representative. Experimental factors of interest were manipulated within participants using factorial designs. Participants performed one or multiple (Chapter 4) sessions of the task. Analysis of Variance (ANOVA) tested for main effects of and interactions among the experimental factors on the behavioural measures of interest.

2.2.2 Variables from Signal Detection Theory (SDT)

As an extension of the analysis of accuracy, Signal Detection Theory (SDT) was developed in an attempt to characterise or model the decision-making process. In this way, it is thought that SDT was the first formalisation of estimating "discriminability": the ability to distinguish signal from noise and "bias": the tendency

to value one outcome of a decision more than another (Busemeyer & Diederich, 2010). According to SDT, with every decision made, there are four possible outcomes or ways to describe this decision (see Table 2.1). Say one rejects a (null) hypothesis. This could have been the correct decision (called a hit) or the incorrect decision (called a false alarm). Alternatively, one might accept the null hypothesis. If the null hypothesis was true, this would be a correct rejection or, if the null hypothesis was false, it would be a miss.

Table 2.1: A decision matrix according to Signal Detection Theory. The four outcomes according to the decision made and the actual state of the world: Hit, False Alarm, Miss and Correct Rejection (adapted from Macmillan & Creelman, 2005; WISE Project, 2010).

		State of the World	
		H_o False	**H_o True**
Decision	**Reject H_o**	Hit	False Alarm Type I Error (α)
	Fail to Reject H_o	Miss Type II Error (1-β)	Correct Rejection

Theoretically, if decisions were made a large number of times, the distribution of the outcomes may be something similar to what is presented in Figure 2.1. The black distribution represents a case where, along different values of the stimulus intensity (x-axis), there is no signal present. The red distribution, however, represents cases where there is a signal present. Both signal-present and signal-absent states have a Gaussian distribution because there is noise in the

environment, which may obscure the true state of the world. The distance between the means of the “signal-absent” and “signal-present” distributions is known as *d’* or the sensitivity to the signal. Given the information that is available, the observer must make a decision which is based on the criterion “c” which characterises the propensity to respond “signal present” or “signal absent” (Green & Swets, 1966; Macmillan & Creelman, 2005). Often, this is used when hits and false alarms are valued differently, for example, in a medical diagnosis. In this case, the decision to perform a biopsy may result in a potential diagnosis (hit) compared to the expense and inconvenience of an unnecessary procedure (false alarm). The relative importance of the possible outcomes of the decision is reflected in the criterion of the individual doctor and/or professional guidelines (Macmillan & Creelman, 2005).

As can be seen in Figure 2.1, there is an overlap of the “signal absent” and “signal present” distributions. By moving the criterion along the x-axis, there will be a different weighting or proportion of “hits” to “false alarms”. If observers, for example, only decide a signal is present at very high stimulus intensities then, on average, there will be very few false alarms but many signals would be missed.

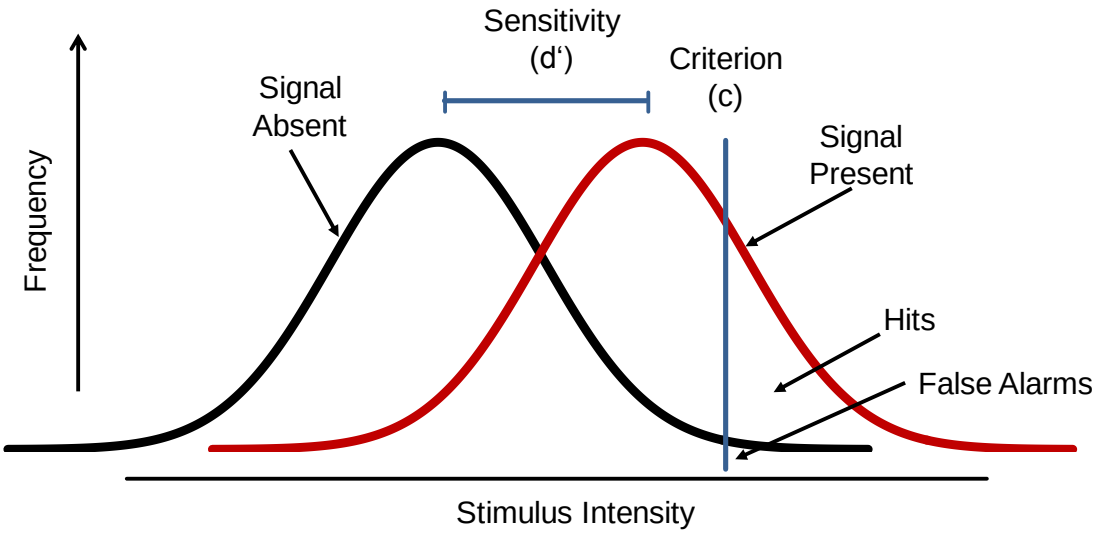


Figure 2.1: A schematic of the components of Signal Detection Theory. The two probability-distribution functions reflect different states of the world: either where the signal is absent (left) or present (right). The difference in means between the two distributions is d'. The response criterion c, is the point which determines relative proportion of hits and false alarms of the decision (adapted from Macmillan & Creelman, 2005; Simak, 2011).

The SDT approach has been used to model the decision-making processes in range of age groups or clinical populations. SDT can also be applied to VSTM experimental situations. In the current thesis, for example, elements of SDT are used to test how factors linked to attention influenced the quality or the number of items in VSTM representations. Analyses of sensitivity and criterion can provide insight into two important aspects of processing: discriminability and bias. Neither of these can readily be derived from a basic analysis of accuracy. In addition, the

distribution of d' and c is closer to normal than that of a bounded accuracy measure, such as proportion correct.

This could be applied, for example, in a VSTM paradigm where a memory probe is compared to the mnemonic representation of a previously presented item. This is similar to the approach used in Chapter 6 of the current thesis, where the proportion of the participant's "match" responses on *match* (hits) compared to *no-match* trials (false alarms) is compared using the following formula (see Figure 2.1, Green & Swets, 1966):

$$d' = z(hit) - z(false\ alarm)$$

Where d' is the sensitivity to change or the difference in the means of the theoretical distributions reflecting occasions where the "match" signal is absent (*no-match* trials) and the other reflecting situations when the "match" signal is present (*match* trials) (see Figure 2.1).

The SDT analysis can also be applied to other types of correct versus incorrect decisions about the relationship between a probe item and a VSTM representation. For example, SDT was used in Chapter 3 to describe how participants judged whether a probe item had been rotated clockwise or anti-clockwise relative to the corresponding item in the previous array. In this case, a "clockwise" judgement on a clockwise-change trial can be conceptualised as a hit, and as a false alarm on an anti-clockwise-change trial.

In VSTM change-detection tasks (for example see Chapter 6), the criterion may also be used to measure how different perceptual conditions influence the

decision-making process and biases. In this way, the *c* scores can be calculated with respect to the standardised proportion of trials in which the participant responded “match” on *match* (hits) versus *no-match* trials (false alarms):

$$c = -0.5 * (z(hits) + z(false\ alarms))$$

As such, a higher criterion score represents a more conservative attitude – a propensity to respond “no match”, which would result in fewer false alarms. A negative criterion score, therefore, represents a heightened propensity to respond “match” which may result in more hits but an increased false alarm rate (see Figure 2.1).

2.2.3 Reaction Time (RT)

In most VSTM experiments, the interpretation of differences in Reaction Time (RT) is dependent upon the type of experimental question. If the focus of the experiment was on whether an item was readily available to retrieval processes, for example, RT would be an important dependent variable. For the specific questions regarding the precision and capacity of VSTM used in the current thesis, however, differences in RT are not readily interpretable. It is not necessarily the case that a memory that is maintained more precisely in VSTM is retrieved more quickly. Differences in RT due to an experimental manipulation may be due to differences in encoding, maintenance, the final probe comparison process, or response generation. Although analyses based on accuracy are still subject to some of these issues, a memory is either available or it is not. Gradual variations in RT, however, cannot directly inform us of differences in the quality or nature of the mnemonic

representation. As such, analyses in the current thesis focus on accuracy, SDT and the outcome of psychophysical modelling.

2.2.4 Calculating a Metric of Capacity

As has been discussed in the introduction of this thesis, the limited nature of VTSM capacity has been a central point in Experimental Psychology for many decades (Cowan, 2001; Luck, 2008). Probably the most widely used metrics to calculate the average number[8] of items being maintained is Cowan's *k*. This metric is part of a "high threshold" approach meaning that participants are expected to have either a perfect representation or none at all (Luck, 2008). Estimates of *k*, therefore, will increase as the number of to-be-remembered items increases until the average capacity reaches its maximal point and no additional items can be maintained. It is important, therefore, that arrays are large enough to observe the maximal performance. Cowan's *k* is calculated according to the following formula (Cowan, 2001; Cowan et al., 2005; Pashler, 1988):

$$k = (H + CR - 1)N$$

where k is the capacity score, H is the hit rate (e.g. proportion of changes detected when a change occurs), CR is the correct-rejection rate (proportion of matches judged when no change occurs) and N is the number of items in the array. The measure of k can never exceed the total number of items being displayed.

[8] Although these Capacity scores are usually non-integer values.

Cowan's k, however, is not the only metric for calculating capacity. Other research groups have formed their own conceptualisation of capacity. For example, according to the Theory of Visual Attention (TVA; Bundesen, 1990), stimuli "race" towards representation. A simplified metric to calculate the TVA capacity (*K'*) is as follows (taken from Peers et al., 2005):

$$K' = \left(m \times \frac{T_m}{T_m + T_{m-1}}\right) + \left((m-1) \times \frac{T_{m-1}}{T_m + T_{m-1}}\right)$$

Where K' is maximum number of items that can be reported (capacity), m is the maximum number of items ever reported by a participant and T_m is the proportion of trials with m number of items reported.

The "race" for representation continues until (1) capacity is exceeded, (2) perceptual processing is stopped (by a backwards mask or similar) or (3) items decay before entering VSTM (Bundesen, 1990; Peers et al., 2005). Although the theoretical suppositions which underpin this theory may differ from other VSTM conceptualisations, differences in capacity metrics often arise because of differences in the designs of experimental tasks. Tasks used to calculate capacity according to TVA often require participants to report as many items (usually letters) as they can remember (known as a "whole report"). In contrast, tasks used to calculate Cowan's *k* are typically based on the ability to detect a change between memory and probe arrays.

In the current thesis (Chapter 6), the traditional Cowan's *k* was used to aid comparability with other groups and because the paradigm required a variant on Change-Detection tasks (see Section 2.2.5) rather than a whole-report approach.

2.2.5 Moving from Change Detection to a Parametric Modulation of Precision

As previously discussed in the introduction, it is important to use a method of probing VSTM that minimises interference with the memory itself (Luck, 2008; Stokes & Nobre, 2012). For example, the processes involved in having to report a string of numbers in a backwards digit-span task may interfere with the rehearsal mechanisms of the remaining mnemonic representations (Luck, 2008). A popular approach to overcome some of these problems is the use of change-detection (CD) tasks. Here, simple, non-verbalisable stimuli are used, and a simple forced-choice response is required. Performance, therefore, relies on the visual memory, rather than long-term traces, and errors due to difficult response mappings are minimised. Typically, participants respond whether a probe array "matches" (in terms of the colour of items, locations etc.) the mnemonic representation of a previously presented array or not. Common variants on this idea, however, may only include a single probe, such that participants must respond whether the probe item matches the corresponding item in the full memory array. This partial report approach has the advantage of reducing the reliance on configural cues and thus encourages the encoding of the individual items themselves (e.g. Jiang et al., 2000; Olsson & Poom, 2005).

Recent approaches have been developed, which enable testing not only the presence of a memory item, but its quality. Participants are presented with an array and, after a short delay, have to make a *discrimination* about colour (Zhang & Luck, 2008), line length (Palmer, 1990), location or orientation (e.g. Bays & Husain, 2008) of the probe stimulus. This involves parametrically manipulating the degree of

change that is introduced between the memory array and a probe item (e.g. Bays & Husain, 2008; Gorgoraptis et al., 2011; Zhang & Luck, 2008). Because this task requires a different process than a "match" versus "no match" judgement, it is important to simplify the response mapping. In the current thesis (Chapters 3-6) participants judged whether a probe had rotated "clockwise" or "anti-clockwise" from the initial presentation in the memory array. To make the clockwise or anti-clockwise response mapping more intuitive a modified mouse was used as the response input device, which required turning a lever in the direction of the angular change.

The parametric modulation of the mnemonic precision required to discriminate between the memory and probe item had the major advantage of enabling modelling of the data to gain further insight into the quality and or absolute presence of representations. As will be discussed in Section 2.3.2, cognitive models can be formulated, applied and tested in order to generalise about the nature of VSTM representations and distinguish between theoretical viewpoints and to understand the influence of other processes (like attention) on the precision and number of representations. Such data are very rich; however, large numbers of trials are required to get stable model fitting estimates which may limit the number of other possible manipulations. The current thesis, therefore, takes a combined approach of both traditional CD and parametric modulations of a CD task. This was done to provide some insight into the nature of representations and the attentional effects on the quality and presence of representations using a psychophysics approach (Chapters 3, 4). To increase power[9], however, non-parametric, single-

[9] For a demonstration of a power calculation, see Appendix B.4.

probe CD approaches to VSTM were taken in Chapter 6. This allowed the examination of other cognitive phenomena like the effect of perceptual competition on VSTM performance to be examined.

2.3 Psychophysical Modelling of VSTM

Systematic attempts to measure the relation between the effect of the parametric modulation of one variable on a behavioural outcome (such as VSTM accuracy, d' or k) can allow us to attempt to model that relationship to generalise it to other, untested situations. More generally, this is considered to be a psychophysical approach: the study of the relationship between physical stimuli and sensation (Fechner, 1860 | 1966; Gescheider, 1997). Fechner, building on seminal work by Weber, is considered to have founded psychophysics[10]. His work influenced that of other pioneers such as Peirce and Jastrow (1885) and Stevens (1957), leading to our contemporary methods. Classical psychophysics focussed on changes to sensation and perception according to small variations in stimulus properties (Gescheider, 1997). Using this approach, however, it is also possible to quantify how changes to stimulus properties influence other cognitive processes, like VSTM. Experiments in this thesis take a psychophysical approach to build a model of how manipulations of the experimental factors of interest affect VSTM performance.

[10] Although this has been questioned (see Khaleefa, 1999).

2.3.1 Overview of Psychophysical Modelling

According to the to-be-tested theory, models of the data are constructed to include parameters to explain particular constraints on behaviour. For example, in VSTM, variability in performance may be captured by a parameter explaining a capacity limitation (see Section 2.3.3). The stance of two theories may differ in the need to have such a limit. By modelling the data, the effect of including or excluding that parameter can be quantitatively assessed. The fit of various candidate models, with different parameters to explain the relationship between behaviour and the manipulated dimension can then be compared. This comparison is based on the likelihood that each model could fit the data (or similar approach, see Section 2.3.7). If the models do adequately fit the data, the implications of the necessity and estimated values of the parameters can extend beyond the scope current experiment. For example, the inclusion of a parameter to explain the precision of representations from different conditions cannot be ascertained directly from an analysis of the accuracy. An entire distribution of responses with varying stimulus intensities is needed. Other cognitive phenomena such as a guess rate may not have any important theoretical implications but need to be considered to fit the data adequately.

Typically, the outcome or response is plotted on the y-axis and the manipulated stimulus dimension (e.g. contrast, colour etc.) is plotted on the x axis. This results in a plot in an ogave fashion (“s” shaped), typically resembling the cumulative counterpart of a probability density function (Gescheider, 1997). The data are then modelled using one of the common psychophysics sigmoidal

functions such the Weibull, Logistic, Gumbel, cumulative von Mises, or Cumulative Normal (Gaussian) (Wichmann & Hill, 2001a). Examples of some cumulative normal distributions are shown in Figure 2.2).

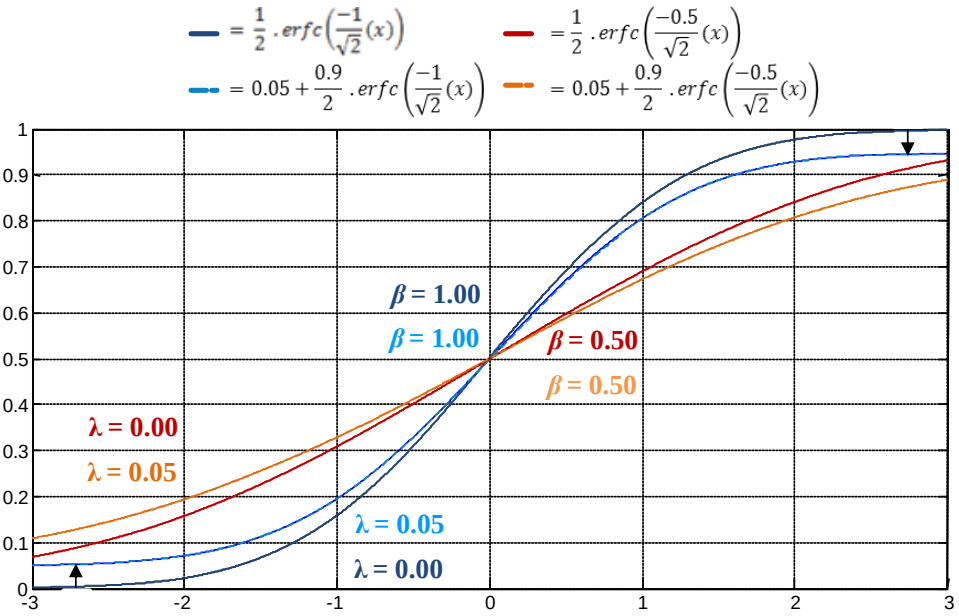


Figure 2.2: Four cumulative normal distributions, which differ in slope (β) and/or asymptote (λ). The equations for each function are given above the plot and the parameter values are listed next to the corresponding functions. The blue functions have a higher slope (β) than the red and orange functions and so the rate of increase in y is greater. The darker (dark blue and red) functions, however, have an asymptote (λ) of zero, whereas the lighter (light blue and orange) have an asymptote of 0.05 so the bounds of those functions are 0.05 to 0.95. The black arrows represent the asymptotes (λ).

For this thesis, the cumulative normal distribution was chosen because the Gaussian distribution is well documented and has been studied in the VSTM

literature, especially when a two-alternative forced-choice task is employed (e.g. Bays & Husain, 2008). Studies which have employed a continuous response, however, typically use a von Mises distribution to model error responses, that is, distance the response was from the original memory array in colour space or orientation (Bays et al., 2009; Zhang & Luck, 2008; Zhang & Luck, 2009). The von Mises (or Tikhonov) distribution is considered to be the circular analogue to the normal distribution. This is used in situations when the manipulated stimulus dimension "wraps around", that is, extremely large values on the x-axis eventually become very small values (or vice-versa). The cumulative normal distribution is most appropriate for the current forced-choice task, especially since the stimulus parameters used are within the maximal range of the distribution. Specifically, rotation judgements are maximal at ±45° so there is no issue of response confusion due to the stimulus values "wrapping around"[11].

2.3.2 The Model Used VSTM in the current thesis

In Chapters 3-5, the fit of cumulative normal models was tested in order to get an insight into the precision and number of items in VSTM under various conditions. Using a single probe variant of the CD task, the effect of the degree of change of the rotation angle on VSTM performance was assessed. By transforming the data into proportion of responses judged "clockwise" (e.g. see Figure 2.1), it became possible to plot the data in the typical ogave shape and to estimate two parameters

[11] Results from a pilot experiment confirmed that ±45° was indeed the rotation angle associated with the highest performance for the stimuli used in the current thesis. This suggests that a range of -45° to 45° is the optimal range for estimating the slope and asymptotes using a cumulative normal function

of primary interest: the asymptote (λ), which reflects the probability that items were maintained in VSTM (Zhang & Luck, 2008), and the slope (β), which represents the precision of the memory representation (Bays & Husain, 2008). The following equation was used to model the response function:

$$y = \lambda + \frac{(1 - 2\lambda)}{2} \cdot erfc\left(\frac{-\beta}{\sqrt{2}}(x)\right)$$

where y is the proportion of "clockwise" responses, x is the angle of rotation, *erfc* is the complementary error function (see Spanier & Oldham, 1987), (λ) is the asymptote, and (β) is the slope.

When estimating the two parameters of interest: slope and asymptote, they were not fixed[12] and not constrained to be the same for each condition. When attempting to arbitrate between changes in performance attributable to difference in the number versus the quality of representations in VSTM, it is important to enable asymptote and slope variables to vary in an independent fashion. The curve, however, was forced to be symmetrical, meaning that subtle differences between clockwise and anti-clockwise judgements were eliminated in the model. Further detail is given in the following sections. In previous research, functions have assumed fixed asymptotes (Bays & Husain, 2008) at zero and one. But, as noted by Cowan and Rouder (2009, see also Wichmann & Hill (2001a)), this can distort the shape of the function and force differences in performance to be explained by differences in the slope. Modelling in this thesis, therefore, used parameters to enable the asymptote parameter to vary to assess the effect this had on the estimates of precision and the overall model fits (see Section 2.3.7).

[12] Except the asymptote limits were set to be between 0 and 0.5.

2.3.3 Asymptote: Guess Rates and Lapse Rates

A line that continually approaches a curve but does not reach it[13] is defined as an asymptote (see the black arrows in Figure 2.2). For a standard psychometric curve, the values of the y axis are bounded between zero and one (i.e. it is not possible to have a proportion of clockwise responses greater than one or less than zero). In the psychophysics literature, the upper and lower bounds (asymptotes) are commonly referred to as the lapse or miss rate (γ) and guess rate (λ). Specifically, the guess rate is the minimum distance from zero that reflects a certain proportion of correct responses independent of the stimulus intensity, due to guessing, response error or other phenomena (Wichmann & Hill, 2001a, 2001b). Similarly, the lapse rate reflects the upper bound estimate for performance due to similar factors (manual response errors etc.).

The inclusion of an asymptote which is not fixed to be zero or one has recently been controversial in the VSTM literature (see Cowan & Rouder, 2009). Failure to include estimates of λ and γ (i.e. when they are forced to be zero and one) can distort the fitted functions because changes in performance have to be accounted for by changes in slope (see Wichmann & Hill, 2001a). Ultimately this can lead to interpretation of results as being evidence for no set capacity limit. In the current thesis, it was important to include a non-fixed asymptote parameter to test whether the addition of such a parameter could result in a better fit of the data.

[13] At arbitrarily ($\approx \pm \infty$) large values of x, however, there is still discussion whether the asymptote touches the curve, is tangential to or neither (see Giblin, 1972).

I interpreted the estimate of the asymptote to be an index of the maximum number of items that are available in VSTM at the time of the test probe (as per Zhang & Luck, 2008). If there is a limit in the number of items that can be stored, independently of any variation in their precision, there would be a proportion of trials in which participants would fail to represent items from large arrays, even when the decision required was infinitely easy. For example, assume that a putative capacity limit of four items is true and anything beyond this cannot be represented. If five items are presented then, on 1/5 of the times the probed stimulus would not be represented in VSTM so the average maximal performance on this (infinitely easy) discrimination would be approximately 80%[14]. To translate this to an asymptote estimate in the current thesis, the distance between the curve describing the proportion judged clockwise would always be at least 0.2 from zero and one. This estimate should be far higher than any inattention or response-related mistakes (which should be less than 0.06 for trained observers (Wichmann & Hill, 2001a)). It is then possible to test whether the addition of an asymptote parameter results in a significantly better fit; if so, then one can conclude that there is an additional constraint on the system which affects VSTM performance.

Only the single parameter, λ, was included to model both the guess and lapse rates to capture the performance asymptote (analogous to Zhang & Luck, 2008). The alternative was to include a separate parameter (γ) to explain the distance from the x-axis separately. If the estimation of this parameter did differ from the estimate of (λ), this difference would not be immediately interpretable in terms of VSTM performance because the differences in performance between

[14] This example does not take into account guessing or other factors, it is just an illustration.

clockwise and anti-clockwise changes are not relevant to the current experimental questions (for more details, see Section 2.3.5). As such, the model was constrained to estimate a single guess and lapse rate to explain the upper and lower bounds in the same way.

2.3.4 Slope

The slope (β) can be characterised as the rate with which the performance level changes with adjustments along one stimulus dimension (Wichmann & Hill, 2001a, 2001b). A larger value for β reflects a steeper slope, meaning that performance is more sensitive to comparatively smaller changes in the stimulus. In the current thesis, the slope can be interpreted to reflect the precision with which a representation is stored in VSTM (see Bays & Husain, 2008; Zhang & Luck, 2008). Specifically, when participants have a more precise representation, the degree of stimulus change required to make a correct response is comparatively smaller than when the representation is coarse.

2.3.5 Threshold

As defined by Wichmann and Hill (2001a, 2001b), a response threshold is the intensity or value of a stimulus that is needed to elicit a given response or level of performance. It can be conceptualised as the left/right displacement of the psychometric curve on the x-axis. Thresholds are important in the mapping of various stimulus intensities to sensation (for example, loudness, brightness, pain)

(Gescheider, 1997). For the current thesis, however, the actual values of the proportion according to particular angles of rotation are not of particular importance. The absolute difference between clockwise and anti-clockwise judgements does not give any particular insight into the nature of VSTM, although it was important to eliminate the possibility of large biases affecting the results. This was checked for the paradigms in each chapter and then data were collapsed across the direction of angular change for analyses of accuracy. The threshold parameter was, therefore, not included, but instead fixed at zero (see also Section 2.3.3 for more on this issue).

2.3.6 Estimation Method

This section will focus on Maximal Likelihood Estimation (MLE) methods, which are used for finding the optimal set of parameters for a given model. MLE approaches attempt to maximise the likelihood that the function (with the estimated parameters) can explain the current data. Modelling in the current thesis was conducted using the Matlab toolbox Palamedes (Prins & Kingdom, USA). This toolbox utilises the Nelder-Mead simplex direct search algorithm for objective function (or tested model) minimisation (Nelder & Mead, 1965). The Nelder-Mead simplex algorithm is the most commonly used in the field, and can overcome problems when there are discontinuities or jumps in the data unlike other derivative-based approaches (Busemeyer & Diederich, 2010). Basically, this algorithm starts by taking three sets of possible parameters (called a simplex) and estimating the resulting fit of the objective function to the current data. Then, a fourth set of

parameters is generated close to the other three points in “parameter space”. This set of parameters is then compared to the others. Only the best three sets of parameters are retained, and the process begins again (Busemeyer & Diederich, 2010). Constraints regarding the number of times the algorithm searches for a new set, and how far it can jump to generate new sets are under the control of the experimenter.

Bayesian constraints were applied to the parameter values to ensure realistic estimates for the paradigm. For example, the asymptote (λ) parameter could only take values of between 0 and 0.5, which represent the boundary conditions for perfect versus chance performance respectively. If participants performed worse than chance, then the algorithm would not converge. In the current thesis, participants who performed worse than chance were excluded from all analyses and results were only reported for participants’ data which converged.

2.3.7 Statistical Comparisons of Models

When arbitrating among alternative theoretical proposals captured by different models, it is critical to have objective means for comparing models and selecting the optimal one to explain the data. In addition to a visual inspection of the data, a number of quantitative approaches can be employed in the process of model selection (Akaike, 1974). There is a trade-off between increasing the number of parameters to increase the explained variance in the data and creating a parsimonious model which is theoretically meaningful (Busemeyer & Diederich, 2010). When comparing models difficulties arise when the alternatives differ in the

number of parameters. Most model-comparison approaches, therefore, include a penalty for the number of included parameters. The penalty also reduces the possibility of over-fitting the data, which can lead to overcomplicated models which are overly sensitive to small fluctuations in the data which may capture local peculiarities in the modelled data (Vermorei, 2009). This can limit the generalisability of the model to new situations (Busemeyer & Diederich, 2010).

One tool for comparing two models quantitatively is the Chi-Squared test. The Chi-squared test can give an estimate of whether the "cost" of additional parameters results in a significantly higher likelihood in fitting the data (Busemeyer & Diederich, 2010). The assumption of this test, however, is that one model is "nested" in the other. The "nested model" and "full model" have the same parameters except the "fuller" model has some additional parameters. The utility of the additional parameters, in comparison to the likelihood of the "nested" model explaining the data will be determined by the outcome of the test. The test statistic is calculated as follows:

$$G^2_{difference} = -2(LL_1 - LL_2)$$

Where $G^2_{difference}$ is the value of the Chi-squared test statistic, LL_1 is the log likelihood of the reduced, less complex or "null" model, and LL_2 is the log likelihood of the more complex or "full" model (with a higher number of free parameters) fitting the data (Claessens & Wagemans, 2008; Kroese & Rubinstein, 2004).

The difference in the number of parameters between the two models is then taken as the degrees of freedom of the Chi-squared test. If the test statistic exceeds the critical value (according to a pre-determined α) of the Chi-Squared distribution,

given the degrees of freedom, then it can be concluded that the full model results in a significantly higher likelihood in fitting the data.

In some cases, it may be desirable to compare different types of models with the same number of parameters. This could occur when comparing whether the addition of a threshold versus an asymptote parameter results in a significantly better fit of the data. In these cases, alternative approaches to the chi-squared tests are needed to compare and select models.

One useful metric is Akaike's Information Criterion (AIC), which can be used to compare the goodness of fit of models even when the number of parameters is the same. It was first developed Hirotugu Akaike (Akaike, 1973, 1974) in an attempt to improve the classic Neyman-Pearson type of statistical hypothesis testing which assumes the null distribution should, by default, adequately fit the data. The AIC also removes the need for a, somewhat arbitrary, criterion (α) and is based on the estimation of maximal likelihood of the data, given the model. AIC is not used statistically to test the fit of a model against a null hypothesis, but to give a sense of the fit of the data and to rank models to select the best model from the available candidates. In addition, AIC reduces the possibility of over-fitting by penalising models with larger number of parameters. Like the Chi-squared test, it attempts to balance the trade-off between accuracy and complexity of the model (Busemeyer & Diederich, 2010). Unlike the Chi-squared test, however, AIC does not require the models to be nested.

AIC is calculated according to the following equation (adapted from Akaike, 1974):

$$AIC = 2k - 2\ln(L)$$

where k is the number of parameters used in the model and L is the maximum likelihood value for the given function. Note that a lowest AIC score indicates the preferred model.

There are other alternatives to AIC and Chi-squared testing to compare models. The choice of which approach to use to compare models is still under debate in the psychophysical literature (see Burnham & Anderson, 2004). The most popular alternative is the Bayesian Information Criterion (BIC; Schwarz, 1978). Often BIC is considered preferable to AIC because it is thought to be founded in Bayesian Theory. Burnham and Anderson (2004), however, argue that AIC also has a foundation in Bayes Theory and is preferable to BIC because, in their simulations, the AIC selected model always resulted in an equivalent or higher goodness of fit to the data in realistic sample sizes. Given these advantages, AIC was used in Chapter 4 of this thesis. Other computational methods to compare models have been developed, however, are still less well documented and understood (e.g. Bozdogan, 2000).

2.4 Electroencephalography (EEG) and Event Related Potentials (ERPs)

In addition to characterising the psychological parameters, the experiment presented in Chapter 3 also investigates the neural processes underlying the interaction between VSTM and attention. The aim of this study was to investigate whether the neural signatures of anticipatory attention and VSTM maintenance could be related to VSTM performance: more specifically, the precision and number

of VSTM representations. The nature of the task was rapid and thus, to track the various stages in the allocation of attention and maintenance, a methodology with high temporal resolution such as EEG was needed. This part is divided into three main sections: first the underlying physiology which results in the EEG signal will be described, then how the information is recorded, referenced and processed, finally the section will conclude with how the signals are averaged into Event-Related Potentials (ERPs).

EEG measures the ongoing electrical potential generated by the brain and measured by electrodes on the scalp (Nunez & Srinivasan, 2006). EEG is a non-invasive method to measure neural activity with real-time resolution. It is possible to measure this activity at the scalp because brain tissue and skull act as volume conductors (Fabiani, Gratton, & Coles, 2000). For over more than one hundred years, researchers have been investigating how changes in EEG signals are associated with cognitive and behavioural processes (Adrian & Matthews, 1934; Berger, 1929; Caton, 1875). The continued refinement of tools derived from EEG, like Event-Related Potentials (ERPs) and time-frequency analysis (see Section 2.5.2), and a greater understanding of the neural systems and mechanisms generating these has led to a great boost in popularity of EEG in the past 20 years (Handy, 2005; Luck, 2005a). In addition to behavioural-only studies, EEG can provide a complementary measure for understanding psychological factors at play as well as direct measures of the neural systems and dynamics involved.

2.4.1 Underlying Physiology

The information exchange between and within neurons can be described by two main types of transmembrane electrical currents. Firstly, the transmission of current from the cell body, down the axon to the terminals is known as an “action potential”. The recording of the action potential is tri-phasic, meaning, that while measuring the potential across the cell membrane with an electrode in extracellular space ahead of the action potential there is a: (1) positive phase which reflects the compensatory outward flow of capacitive current immediately before the depolarisation reaches the electrode (2) negative phase reflecting inward current flow during the depolarisation at the place of the electrode and (3) positive phase returns to reflect the outward current flow after depolarisation has passed (Allison, Wood, & McCarthy, 1986; Lorente de Nó, 1947; Offner, 1954).

The second type of electrical signal reflects transmission of current between cells due to the release of neurotransmitters into the synapse by one cell triggering the opening of ionic channels in the receiving cells. In contrast to action potentials, post-synaptic potentials (PSPs) are graded and much slower (tens to hundreds of milliseconds). They can be either excitatory (EPSP) or inhibitory (IPSP) (Allison et al., 1986). When an EPSP occurs, the excitatory synaptic input opens ion channels which results in an increase in the flow of positive ions into the cell which results in a negative potential in the nearby extra-cellular space called a “sink”. Then, the current will flow through to a more distant part of the cell and flow back out into extracellular space to complete a closed ionic pathway. This will result in an overall positive potential in extracellular space near to the outflow called a “source” (Nunez,

1990). As such, local synaptic sinks are compensated for by distant sources (Nunez, 1990). This can explain the differences in ionic flow (and potential differences) between the apical dendrites and soma or basal dendrites of a neuron. The ionic flow between the sinks and sources makes what is known as a “dipole” (Luck, 2005a). The opposite pattern of current flow occurs when an IPSP is present: inhibitory input creates a local source at the synapse and a sink at a distant location of the cell (Nunez, 1990).

The small individual fluctuations in current coming from a single neuron are too small to be measured directly at the scalp. Two conditions must be satisfied in order for the electrical signals of a local population of neurons to be integrated and measured in the EEG signal. Firstly, a group of neurons must be active synchronously so the signal can summate and be detected. As such, it is usually the longer-lasting PSP which is recorded with EEG because the currents are mutually reinforcing. Typically, action potentials (spikes) are moving too rapidly down the axons for an ensemble to be synchronous for the signal to summate (Fabiani et al., 2000). The sinks and sources caused by the dynamic changing currents in the action potential do not always align so much of the signal fails to integrate and is lost. Secondly, the arrangement of a neuronal ensemble must be in an arrangement that allow the inward and outward extracellular currents to be mutually reinforcing so the individual signals can summate (Allison et al., 1986; Fabiani et al., 2000). This was what Lorente de Nó (1947) described as an “open field” (see Figure 2.3). Here, all the dendrites, axons and soma with common input are aligned in parallel so the generated current flows can summate and be measured at the scalp. The strength of the recorded current flow, furthermore,

exponentially decreases as the distance from the cell increases meaning that the resultant signal is biased towards sources of activity close to the scalp. Most of the EEG signal, therefore, reflects PSPs of well aligned pyramidal neurons (Nunez, 1990).

Alternatively, neurons can be arranged in a “closed field” where the dendrites and soma are arranged in an orthogonal fashion so that the signals cannot summate and thus cannot be measured at the scalp (e.g. neurons from midbrain structures). Dipoles with opposite polarities (e.g. by an EPSP nearby an IPSP) can cancel each other out (Luck, 2005a). Complex anatomical folding (e.g. the cerebellum) can also affect how the dipoles are summated. This, combined with the need for signal summation, and the sharp reduction in signal as a function of distance means that the EEG is only reflective of a proportion of total neural activity (Rugg & Coles, 1995).

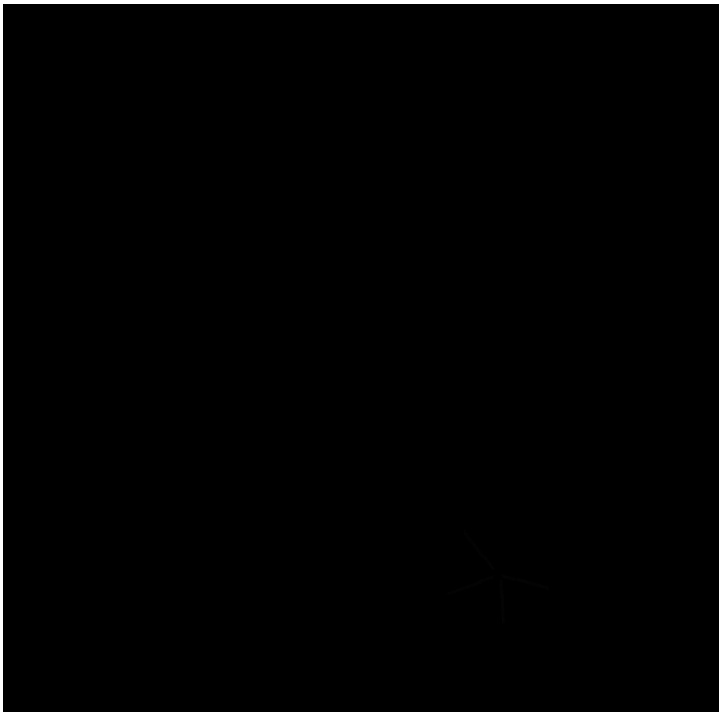


Figure 2.3: A theoretical example of two ways that neuronal ensembles can be arranged. On the left, an “open field” may result in the summation of the signal of the individual neurons so current flows can be measured at large distances (e.g. pyramidal cells of the hippocampus or cortex). The right hand panel shows the opposite “closed field” where the dendrites and soma are arranged in a way that is not conducive toward signal summation. Adapted from (Allison et al., 1986; Lorente de Nó, 1947).

Source localisation in EEG is difficult for two reasons. Firstly, a major factor which affects the EEG signal is volume conduction through the head. The different tissues and skull have differing conduction properties which affect how the electrical activity is propagated from the generators through to the scalp. Given that electrical activity follows the path of least resistance, potentials may be smeared laterally and

distorted due to the high resistance of the skull (Fabiani et al., 2000). “Spatial summation” may occur when the EEG signals interact during the propagation through the brain, signals may be detectable at different locations over the scalp. Also, “temporal summation” may occur when the signals interact over time. The timing of EEG deflections, therefore, does not necessarily directly correspond with the timing of the neural generators which created them. Secondly, the complex pattern of signal reflecting simultaneously active neural ensembles makes it impossible to trace the source of activity with 100% certainty. If there was knowledge of the exact generators of the electrical currents (their alignment, timing and so forth) as well as the shape and conductive patterns of the brain, skull and scalp then it would be possible to construct a topographic map of the observable signals at the scalp. This would be a solution to what is known as the “forward problem”. In contrast, what researchers would need to solve is the “inverse problem” which would localise the set of brain areas generating the activity which is observed at the scalp. Given a distribution of activity at the scalp, however, there is an infinite combination of generators in three-dimensional space that could in principle generate the particular map. This is an unsolvable (underdetermined) mathematical problem, because it is impossible to pinpoint the unique combination of sources that are active at specific times (Fabiani et al., 2000; Luck, 2005a).

2.4.2 Recording, Referencing and Processing

Before recording, electrodes are usually arranged according to the 10-20 system (see AEEGS, 1991) which involves placing electrodes at 10 percent and 20 percent points along lines of latitude and longitude across the scalp. A standardised layout helps to improve the comparability of results across individual participants and with other research groups. In order to record the EEG signal, each electrode of interest should be connected to a "reference electrode" so the difference in voltage can be calculated (Rugg & Coles, 1995). This also removes any common background noise and residual electrical signals from the recording.

There are a number of options in choosing a reference. A common reference is an electrode(s) placed at a site where the experimental manipulation should not affect the neural activity e.g. the nose or earlobe, or bias activity towards one hemisphere (Rugg & Coles, 1995). There is, however, no perfect reference site, and the resultant EEG signal will always contain some trace of activity from the reference electrode (Luck, 2005a). A popular choice of a common reference which was used in the current thesis is an average mastoid reference. This is performed by using an electrode at one mastoid (the flat bone behind the ears) as the reference during recording. Then, offline, the average activity from both mastoids is calculated and the data are re-referenced to the average activity from the two mastoids. The average mastoid reference was used in the current thesis because it has the advantage of being distant from the brain while recording relatively muscle artefact-free activity and not being biased towards one hemisphere (Luck, 2005a).

Another reference option is an “average reference” which involves the subtraction of the average activity from all electrodes from the electrode of interest. This approach is thought to accentuate regional differences. Alternatively, activity between pairs of electrodes (using bipolar references) can be compared (Rugg & Coles, 1995). In the current thesis, an electro-oculogram (EOG) was also recorded by using references electrodes left, right, above and below one eye. The signal was, thus derived using bipolar derivations between left and right (for horizontal movements) and above and below (for vertical movements).

From the scalp, the electrodes are attached to a differential amplifier[15] which then outputs data to an acquisition computer. Here, the computer registers traces of voltage fluctuations over time, with very high temporal resolution. During recording, data should be digitally sampled according to the Nyquist rule: at a frequency more than twice any frequency of experimental interest (for more details see Edgar, Stewart, & Miller, 2005). In the experiment in this thesis, EEG data were recorded continuously. Residual electrical activity (e.g. using a “line filter” for a specific frequency of 50 Hz or 60 Hz) or high frequency muscle-related artefacts can be filtered out digitally (Luck, 2005a). The choice of what filter to use, whether it be low-pass (e.g. a low pass filter of 50hz would attenuate data of frequencies above 50 Hz), high-pass (which would attenuate data below a certain frequency) or band-pass (which would attenuate data above or below a given frequency range) should be performed in a way to reduce the distortion of the ERP (e.g. a bandpass of 0.01 to 40 Hz might be appropriate). Filtering can help eliminate drifts in the data due to

[15] Differential amplifiers amplify the differences in electrical signals but not amplifying common signals (noise) (for further details and simulations see eCircuit Center, 2004; Luck, 2005a).

movements of the participants or changes in the impedance of the skin (e.g. due to sweating).

When recording EEG it is critical to minimise sources of noise and artefacts in order to increase the signal-to-noise ratio (Luck, 2005a). For example, EEG recordings should take place in an electrically shielded room and with an electrically shielded monitor (in a Faraday cage or similar) to reduce the distortion of the EEG signal by background or mains-related electrical noise (Luck, 2005a). In addition, it is important to reduce the impedance of the skin before EEG recording (ideally below 5KΩ). To this end, electro-conductive gels and/or alcohol pads are used to gently abrade the skin and increase conduction between the electrode and the scalp.

After recording, the EEG signal time-locked to the stimulus-related events of interest can be extracted and “epochs” of activity associated with the processing of the stimulus can be examined. In addition to filtering, epochs with excessive voltage fluctuations can be automatically excluded from any further analysis by setting a threshold at, for example, ±100µV. Moreover, eye movements can contaminate the EEG recording because the eye-ball acts as an effective dipole, and movements create a current which propagates through the head and overshadows the smaller potentials of interest (Rugg & Coles, 1995). For this reason, participants are asked to avoid blinking or moving their eyes during critical periods of the trial, and to fixate their gaze on a central position. By recording an electro-oculogram (EOG) during EEG recording and a visual inspection of the EOG channels can help identify eye-movement related artefacts during particular epochs. For EOG channels, setting a threshold at ±50µV may be more appropriate to eliminate blinks, and other large

eye-movements. A visual inspection of each epoch is recommended to identify eye-movements below this threshold (e.g. saccades) and to check that all trials are otherwise artefact free. Alternative approaches for removing artefacts from data include algorithms such as Principle Component Analysis (PCA) and Independent Components Analysis (ICA), which can automatically detect artefacts such as background noise, eye movements and blinks (Luck, 2005b). Such approaches should, however, be used with caution and a manual inspection of the data is useful to ensure that erroneous artefacts have not been removed and all other artefacts have, in fact, been rejected.

2.4.3 Event-Related Potentials (ERPs), Interpretation and Statistical Analysis

On each trial, it may be difficult to identify the EEG signal which is relevant to the particular perceptual or mnemonic activity triggered by single events. By averaging many repetitions of trials in equivalent task conditions, however, ratio of signal-to-noise can be improved. Basically, this process maintains the task-relevant signal, time-locked to the event of interest while averaging out the background noise of EEG recording. This averaging process results in an Event-Related Potential (ERP). Parts of the ERP waveform are usually called “components” or “potentials” and are typically described by their amplitude, latency, polarity, and scalp distribution (Rugg & Coles, 1995). A component, therefore, is the observed potential at the scalp which is generated by a neuronal ensemble when a computational operation is performed (Luck, 2005a; see section 2.4.1).

Components, therefore, may occur at different times, under different conditions, and may have different topographies depending on the particular stimulus or operation in question (e.g. the component reflecting the encoding of an item in a memory array may result in a slightly different scalp topography depending on the spatial location of the item).

The common ERP nomenclature includes a letter to denote the polarity and a number to describe the approximate latency or order (e.g. P300 (or P3) describes a positive peak at approximately 300ms after the presentation of a stimulus). Alternatively, the name can allude to the polarity and the cognitive phenomenon the potential may reflect, for example the ADAN is an Anterior Attention Directing Negativity. Potentials like the ADAN are "lateralised" meaning that data are transformed and compared, not in left or right space but whether the stimulus event or cue occurs in a location ipsilateral or contralateral to the electrode(s) of interest[16]. In both lateralised and non-lateralised components, mean amplitude (in μV) or latency values of peaks and troughs in the ERP (in ms) over specific time periods at electrode sites of interest of each experimental condition can be extracted and compared quantitatively. Typically, statistical comparisons are done using ANOVAs including factors related to experimental manipulations and electrode sites.

Caution in the interpretation of ERPs, however, must be taken. There need be no "one-to-one" relationship between potentials generated by the brain and what is observed at the scalp. For example, the modulation of a particular component

[16] This can be achieved by taking all the trials where the stimulus occurs on the right, "flipping the data" so that the data from the corresponding left and right electrode pairs is swapped. This data is then averaged with the "left" trials. Now, the data is in left, "ipsilateral space". This data set is then taken, and data from corresponding left and right electrode pairs is swapped again and now, this dataset is in "contralateral space". These two data sets can now be compared to investigate any lateralised effects of interest.

according to an experimental manipulation may suggest that the manipulation differentially affected the underlying processing. Due to the principles of temporal and spatial summation, however, the EEG trace may be the result of the aggregate of many underlying generators performing different stages of processing (Allison et al., 1986). Combinations of potentials in the brain summate giving rise to topographical patterns that cannot be directly mapped back onto the brain (the inverse problem). Patterns at the macroscopic level, on the scalp surface, may differ a lot from internal potentials. Peaks and troughs on the scalp, for example, may have no corresponding peaks or troughs of activity in the brain, but may simply emerge through summation. Luck (2005a, 2005b) refers to the ERP signatures of single generators as “latent components” about which we can only speculate and not directly observe.

As previously described, ERPs are very sensitive to fluctuations in activity due to many factors such as noise (e.g. mains power), the choice of reference, and the orientation of the underlying neuronal field. If no significant difference is found between the conditions of interest, however, it does not necessarily suggest that the manipulation did not elicit differential processes. In some cases, real differences in neural processing may just not be detectable (Handy, 2005). In addition, the overall polarity of an ERP does not indicate whether the underlying circuitry is inhibitory or excitatory. The polarity of the ERP is dependent upon the relative positioning of the current electrode of interest in comparison to the reference electrode (for more information, see Section 2.4.2; Allison et al. (1986)). For this reason, the electrode montage and reference must be taken into consideration when comparing results with other research groups (Rugg & Coles, 1995). Although advantageous for

increasing the signal-to-noise ratio, averaging eliminates trial-by-trial variability, which can restrict the type of analyses conducted. Furthermore, grand-averaged (across all participants) waveforms are often smaller due to individual differences in the shape and latency of potentials. In addition, this averaging across participants may obscure or confound overall latency differences due to different experimental manipulations (Luck, 2005a, 2005b; Rugg & Coles, 1995).

When comparing ERPs from different experimental conditions it is necessary to be able to compare the absolute voltage of activity for each epoch with respect to a cognitively "neutral" baseline. Usually, when ERPs are time-locked to the presentation of a stimulus event, the data are normalised to a baseline period by subtracting the average activity from preceding 200ms (e.g. at rest while fixating in the centre). Given the case of a cued VSTM task, like the one presented in Chapter 3, there were two particular epochs that were potentially of interest: the lateralised activity time-locked to the pre-cue and during the delay period, time-locked to the memory array. Firstly, there are a series of well-established potentials linked to the orientation of preparatory spatial attention: the Early Direction Attention Negativity (EDAN), ADAN and the Late Directing Attention Positivity (LDAP) (Harter et al., 1989; Jongen et al., 2007; Yamaguchi et al., 1994). In this case, the -200ms baseline is valid, when examining activity time locked to the cue because during this time there was only fixation and there should be no lateralised differences.

A lateralised potential has been described as reflecting VSTM maintenance-related activity, known as Contralateral Delay Activity (CDA) (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005) or the Sustained Posterior Contralateral Negativity (SPCN) (e.g. Jolicœur, Brisson, & Robitaille, 2008). The

CDA is elicited by selectively encoding and maintaining stimuli from only one visual hemisphere. Interestingly, the CDA is load dependent, meaning that its magnitude increases as the number of to-be-remembered items increases (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). What is not acknowledged in the literature, however, is that, by definition, the CDA potential follows a state of anticipatory spatial attention. Long-lasting lateralised potentials reflecting the orientation of spatial attention to either side of space (such as the LDAP) are likely to persist at the time immediately before the CDA. Importantly, these two potentials have opposite polarities so using the time period immediately before the onset of the memory array as a baseline for calculating the CDA may exaggerate the apparent delay activity. In the current thesis, the possibility of any lateralised pre-stimulus activity (from the LDAP or otherwise) potentially contaminating the CDA was eliminated by taking the baseline from the pre-cue period, as opposed to the period preceding the memory array.

Finally, it is important to note that analyses relating the ERPs and the manipulations of experimental variables are purely correlational (Allison et al., 1986; Rugg & Coles, 1995). Just because an ERP signature predicts an improvement in performance, for example, does not necessarily mean that the underlying process is *causing* the change in performance. Only interference methods such as transcranial magnetic stimulation (TMS), lesion, or pharmacological interventions are able to invite causal inferences between certain cognitive processes and behaviour (Handy, 2005).

2.5 Methodologies to Extend the Work of the Thesis

This section will briefly introduce three approaches to extend the work of the thesis. Three techniques will be outlined: two imaging methods: Magnetoencephalography (MEG), and functional Magnetic Resonance Imaging (fMRI) and a separate analysis technique: time frequency analysis of EEG (or MEG) data. Specifically, this section will focus on the relative advantages and contributions of each technique with respect to future research to extend the ideas discussed in the thesis.

2.5.1 Magnetoencephalography

Magnetoencephalography (MEG) can be thought of as the magnetic complement to EEG. It is a non-invasive neuroimaging technique which records the magnetic fields generated by the electrical activity of the brain (Hansen, Kringelbach, & Salmelin, 2010). Because the magnetic fields are so small, magnetic sensors using superconductor technology are used for recording (Superconducting Quantum Interference Devices, i.e. SQID). These sensors primarily measure neuronal activity from tangentially oriented sources. As such, MEG signal mainly originates from the sulci of the cortex (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Unlike electric potentials, magnetic fields are relatively unimpeded by the skull and scalp tissues. This, in combination with the knowledge of the possible orientations of sources to produce such a magnetic field and the large number of sensors makes source localisation easier than EEG (Fabiani et al.,

2000; Hansen et al., 2010). Depending on the configuration of generators involved, the spatial resolution of MEG may be as be as good as 2-3 mm (Hansen et al., 2010). This spatial resolution when combined with the high temporal resolution, makes MEG a powerful imaging tool. Like EEG, MEG is still correlational in nature.

2.5.2 functional Magnetic Resonance Imaging MRI

In the past 20 years, the advent of functional MRI has had a great impact on the cognitive neuroscientific community (Huettel, Song, & McCarthy, 2009). By measuring the changes in the relative blood flow, researchers have had a unique, non-invasive "window" into the function of the brain at very high spatial resolution (usually $3mm^3$). In comparison to EEG and MEG, however, fMRI has poor temporal resolution. The hemodynamic response function (HRF), which characterises the increased blood flow to a region, is many orders of magnitude slower (seconds) than the neural events that trigger it (milliseconds) (Mangun & Hillyard, 1995). Typically, the HRF provides a measure of the population of activated neurons at the level of functional brain areas. From this measurement, one can compare the modulation of the activity of individual brain areas with experimental parameters but also the modulation of correlations among brain regions. Like EEG and MEG, this method is, however, still correlational in nature.

2.5.3 Time Frequency Analysis of MEG and EEG data

The oscillatory nature of the electrical activity of the brain has been investigated since the development of the EEG methods in the early 20th Century (Berger, 1929; Herrmann, Grigutsch, & Busch, 2005). In recent years, however, the improvements in digital processing power have increased the ability to process and analyse these signals (Basar, Basar-Eroglu, Karakas, & Schurmann, 1999). To date, it is thought changes in oscillatory responses may reflect the co-ordination of activity of different distributed cortical and sub-cortical networks (Basar et al., 1999). Furthermore, neural oscillations are fundamental to co-ordinated activity across networks of neural ensembles, which is central to many processes such as VSTM and attention (Klimesch, 1999; Uhlhaas & Singer, 2010).

Time frequency analysis is based on the result of a Fourier Transform, which decomposes the EEG or MEG trace into the amplitude and phase of the signal at every frequency of interest, between particular time periods of interest. Phase synchronisation, for example, has been proposed to be critical in controlling the relative timing of different networks in the co-ordination of VSTM, and to be involved in the communication between regions, and long term plasticity (Fell & Axmacher, 2011). Unlike ERPs or ERFs, the analysis of time-frequency information can reveal modulation in “induced” oscillatory phenomena as well as changes in the amplitude of time-locked, stimulus “evoked” activity (Herrmann et al., 2005). Such analysis can give insight into a range of cognitive processes and states including attention, motor planning and memory (e.g. Gould, Rushworth, & Nobre, 2011; Klimesch, 1999). Effects are typically investigated at particular frequency bands and are

categorised in terms of power in comparison to a baseline, for example, alpha desynchronisation (compared to baseline) at posterior sites contralateral to a pre-cue has been associated with the deployment of anticipatory spatial attention (e.g. Worden, Foxe, Wang, & Simpson, 2000).

CHAPTER 3

Effect of Preparatory Attention on the Precision and Probability of VSTM Recall

VSTM is limited in capacity. Therefore, it is important to encode only visual information that is most likely to be relevant to behaviour. Here I asked which aspects of selective biasing of VSTM encoding predict subsequent memory-based performance. I measured EEG during a selective VSTM encoding task, in which the memory load and the precision of recall required to compare a remembered item to a subsequent probe item were parametrically varied. On half the trials, a spatial cue indicated that participants only needed to encode items from one hemifield. The typical sequence of markers of anticipatory spatial attention: Early Attention Directing Negativity (EDAN), Anterior Attention Directing Negativity (ADAN), Late Directing Attention Positivity (LDAP); as well as of VSTM maintenance: Contralateral Delay Activity (CDA) was observed. Individual differences in preparatory brain activity (EDAN/ ADAN) predicted cue-related changes in recall accuracy, indexed by memory-probe discrimination sensitivity (d'). Importantly, the parametric manipulation of memory-probe similarity also allowed us to model the behavioural data for each participant, providing estimates for the quality of the memory representation and the probability that an item could be retrieved. Selective encoding primarily increased the probability of accurate memory recall; and that ERP markers of preparatory attention predicted the cue-related changes in recall probability.

3.1 Introduction

The ability to hold in mind images of objects that are no longer physically present is critical for many higher-level cognitive processes. This type of 'visual short-term memory', however, is severely limited in its capacity (Phillips, 1974), and therefore only the most behaviourally relevant information should be encoded and maintained. Consequently, mechanisms of attention are likely to be important for selective encoding of behaviourally relevant information (Bundesen, 1990; Schmidt et al., 2002). Extensive research demonstrates how preparatory attention directed to task-relevant attributes can facilitate sensory processing (Hopfinger, Buonocore, & Mangun, 2000; Luck et al., 1997; Nobre et al., 2000; Posner, 1980). In this

experiment, the question of whether and how preparatory attention may also optimise VSTM is explored.

Surprisingly little empirical research has focused on the attentional gating into VSTM and the consequences on subsequent performance. Behavioural evidence demonstrates how a preparatory attention cue biases VSTM encoding in favour of cued items (Schmidt, Vogel, Woodman, & Luck, 2002), however, previous neural studies have focused on the attentional modulations of perceptual processing in VSTM tasks rather than the preparatory state per se. For example, in a series of ERP experiments, Gazzaley and colleagues have shown that attention directed to specific memory items in a VSTM task modulates neural processing of a composite memory array when part of the array was previously cued (for a review see Gazzaley, 2011). Recently, Rutman, Clapp, Chadick and Gazzaley (2010), further demonstrated that the magnitude of the attentional modulation of activity reflecting the perceptual processing of the array predicts VSTM performance. However, these studies did not examine the role of preparatory neural activity in anticipation of the array. Studies with a spatial manipulation of attention can, in principle, be used to examine specific anticipatory states (e.g. left vs. right). Despite this, previous studies of spatially selective VSTM do not typically report cue-related activity (Vogel & Machizawa, 2004; Vogel et al., 2005) or use it to predict behaviour (Griffin & Nobre, 2003). In this study, the effect that preparatory spatial attention has on VSTM encoding and performance is directly examined. Additionally, manipulations of load and precision will be included to determine which aspects of VSTM representations are facilitated by attention.

In order to investigate the influence of preparatory attention on neural markers of VSTM maintenance and subsequent behavioural performance, lateralised ERP signatures of anticipatory attention and of VSTM maintenance were measured. The Early Direction Attention Negativity (EDAN) and the Anterior Attention Directing Negativity (ADAN) have been linked to the processing of directional cues and initiation of anticipatory shifts in spatial attention (Harter et al., 1989; Jongen et al., 2007; Nobre et al., 2000). Recently, Praamstra and Kourtis (2010) have suggested that the EDAN reflects visual processing in occipital cortex which precedes activations in fronto-parietal cortices manifested by the ADAN. The Late Directing Attention Positivity (LDAP; Harter et al., 1989; Yamaguchi et al., 1994), is a late and tonic posterior marker, thought to reflect an enhancement of visual cortical excitability in anticipation of upcoming stimuli (e.g. Jongen et al., 2007).

CDA (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), also known as SPCN (e.g. Jolicœur, Brisson, & Robitaille, 2008), serves as a marker of selective maintenance in VSTM. This sustained negative potential over posterior electrodes contralateral to the selectively remembered items has been shown to scale with memory load until the capacity limit is reached (Vogel & Machizawa, 2004; Vogel et al., 2005). The relationship between the necessary preparatory attentional precedent to the CDA and VSTM performance, however, has been largely overlooked.

In this study, the specific behavioural consequence of selective VSTM encoding, and related these to neural markers of selective attention and VSTM maintenance was examined. Using a novel behavioural paradigm, preparatory

spatial attention was manipulated and both the memory load and the precision of recall required to perform the task were parametrically varied. This enabled the separation of the behavioural advantage of preparatory attention in terms of the quality versus probability with which selected items are maintained in VSTM (cf. Bays & Husain, 2008; Zhang & Luck, 2008). Selective attention optimised VSTM encoding primarily by biasing the probability that task-relevant items will be represented, but not necessarily their representational precision. Critically, the neural markers for selection – EDAN and ADAN – predicted this behavioural cueing advantage.

3.2. Material and Methods

3.2.1. Participants

Sixteen right-handed volunteers with normal, or corrected-to-normal, vision were recruited for the study. One participant was excluded owing to noisy electroencephalographic activity (± 2 standard deviations from the mean). The remaining 15 participants (age range=22 to 33 years, *M*=26.87, 8 female) were used for all behavioural and neural analyses. All participants provided informed written consent, and were reimbursed £17 for their time. To maintain motivation throughout the experiment, participants were informed that they would receive a small financial bonus (£3) for good behavioural performance, which all participants received. The experimental protocol received approval from the Central University Research Ethics Committee of Oxford.

3.2.2 Task Design and Procedure

Adapting a task originally developed by Bays and Husain (2008), arrays of arrows were presented and then participants were asked to compare their memory representation with a probe arrow which rotated clock-wise or anti-clockwise. A schematic of the task is presented in Figure 3.1. Each trial began with a centrally presented fixation cross (0.86° by 0.86°) for 200ms, followed by a spatial selection cue lasting 800-1200ms. The temporal variability in cue duration was included to reduce temporal expectation (see Griffin & Nobre, 2005). The cue was either a semi-circle presented around the fixation cross (valid cue), or a full circle (neutral cue). On validly cued trials, half the participants (randomly selected) were instructed to direct covert attention toward the hemifield indicated by the “closed” side of the cue, whereas the other half of participants were instructed to attend to the hemifield indicated by the “open” side. This manipulation ensured that cues signalling spatial attention to the left versus the right visual field were physically equated across participants. Immediately after the offset of the cue, a memory array was presented for 200ms. The memory array consisted of two, four or eight coloured arrows, distributed across both sides of the visual display. On neutral trials, participants were instructed to encode into memory the orientation of as many arrow stimuli as possible across both visual fields. On cued trials, participants were instructed to encode only the orientation of arrows presented on the cued side. After a variable delay period (between 800-1200ms), memory was probed for an item selected at random from the set of stimuli to be remembered. The probe stimulus was always an arrow presented at the same location, and with the same colour, as an item from

the memory array. However, its orientation varied parametrically across trials, being rotated 5°, 20° or 45° clockwise or anti-clockwise relative to the orientation of the memoranda. Participants were instructed to indicate the direction of rotation via a key press: the right CRTL button (with right hand) for clockwise and the left CTRL button (with left hand) for anti-clockwise rotations. Visual feedback was provided after each response: stimuli for correct (centrally presented '£') or incorrect ('X') responses were presented immediately after the response was made. Finally, after feedback, the fixation cross was presented again throughout a variable inter-trial-interval (1300-1800ms).

Participants were given both verbal and written task instructions before the task began. The task was completed in a quiet, dimly illuminated, and electrically shielded room. Head position was stabilised using a chin rest positioned 100cm from a computer monitor. Eye position was monitored throughout the experiment using a remote infrared eye tracker (ISCAN Inc., Woburn, USA). Participants were asked to refrain from blinking during the active portions of the task and, if necessary, to blink just after responding to the probe stimulus. Participants completed one block of twenty practice trials to become familiar with the task; followed by ten experimental blocks of 72 trials (720 trials in total). Breaks between blocks were self-paced. The order of trials with each cue type, set size and rotation change conditions was randomised across the entire experiment

3.2.3 Stimuli

The stimuli were constructed using Presentation (Neurobehavioral Systems, Albany CA, USA) software on a trial-by-trial basis, and presented against a black background. The fixation cross and cue stimuli were light grey and subtended 0.86° by 0.86° of visual angle. The cues were formed by adding either one (cued trials) or two (neutral trials) semi-circles to the fixation cross. Memory items were arrows (subtending 1.43° from base to tip) presented at a randomly selected orientation (angles equally distributed between 0 and 2π). Memory stimuli were presented at randomised locations within 2 bounding boxes, 23.44° (vertical) by 13.67° (horizontal), centred at 6.8° to the left and right of fixation. Each arrow was separated by a minimum distance of 2.39° to reduce perceptual effects of crowding. The colour of each memory item was chosen at random, and without replacement, from a selection of easily discriminable colours (Red, Blue, Green, Cyan, Yellow, Magenta, Orange or White). Behavioural feedback, presented directly after the response, was a light grey "£" for correct, and an "X" for incorrect (in Arial, 28pt font, approximately 0.86° by 0.86°).

3.2.4 Behavioural Analysis: d', recall probability and precision

Behavioural analyses were conducted on estimates of sensitivity (d') for change discrimination (Green & Swets, 1966). The d' scores were calculated with respect to the standardised proportion of trials in which participants responded clockwise on clockwise (hits) versus anti-clockwise change trials (false alarms):

$$d' = z(hit) - z(false\ alarm)$$

Behavioural data were also modelled to estimate two parameters: λ (asymptotic performance: the probability that items were maintained in VSTM; Zhang & Luck, 2008) and β (slope or precision of the memory representation; Bays & Husain, 2008) according to the following equation:

$$y = \lambda + \frac{(1 - 2\lambda)}{2} . erfc\left(\frac{-\beta}{\sqrt{2}}(x)\right)$$

where *erfc* is the complementary Gaussian error function. These estimates were modelled using the Matlab toolbox Palamedes (Prins & Kingdom). Estimates for both slope and asymptote were unconstrained across the cue conditions and, because differences in performance between clockwise and anti-clockwise were not important in this experiment, a parameter for the threshold was not included. Similarly, only the single parameter, λ, was included for both the guess and lapse to capture the performance asymptote (analogous to Zhang & Luck, 2008).

A larger value for β reflects a steeper slope, which can be interpreted as a more precise representation stored in VSTM (see Bays & Husain, 2008; Zhang & Luck, 2008). Specifically, when participants have a more precise representation, the degree of change required to make a correct response is comparatively smaller than when the representation is coarse. Estimates of λ, on the other hand, can be interpreted as an index of the maximum number of items that are available in VSTM at the time of the test probe (Zhang & Luck, 2008). More specifically, λ reflects the upper bound estimate for recall accuracy if the change discrimination were infinitely easy.

3.2.5 Electroencephalography Recording

The EEG was recorded continuously using NuAmp amplifiers (Neuroscan Inc., Albany, USA) from 40 silver/silver chloride electrodes positioned according to the 10-20 international system (AEEGS, 1991). Recordings were taken from electrodes: Fz, FCz, Cz, CPz, Pz, POz, Oz, FP1/2, F3/4, F7/8, FT7/8, T7/8, TP7/8, FC3/4, C3/4, CP3/4, P3/4, P7/8, PO3/4, PO7/8, and O1/2. Blinks and eye movements were monitored by deriving bipolar recordings from an electrode placed below the right eye and FP2 (VEOG) and from electrodes placed to the left and right of the right eye (HEOG). The electrode placed at AFz served as the ground, and the left mastoid served as the active reference. Electrical impedances were kept below 5kΩ and activity was filtered with a low-pass filter of 300Hz. The analogue-to-digital sampling rate of brain activity was set at 1000Hz and data were recorded continuously for the entire experiment. Digital codes were also sent via the parallel port by the stimulus presentation computer to mark the moments of various stimuli onset for each trial.

3.2.6 EEG Processing

All further processing and analyses were done offline. Firstly, the EEG was re-referenced to the average of the left and right mastoids. The two bipolar electro-oculogram (EOG) signals were derived by calculating the difference between the upper and lower HEOG electrodes and between the left and right VEOG electrodes.

Data were then cut into separate cue-locked and memory array-locked epochs (-200 to 1000ms) for each trial.

Pre-processing algorithms removed epochs with excessive noise or drift (exceeding ±100 μV at any electrode) from subsequent analysis. In addition, epochs containing blinks or eye movements (exceeding ±50 μV from the EOG channels) were excluded. All epochs were then visually inspected, and any epochs with detectable smaller eye movements were removed manually. Error trials were also rejected. After pre-processing, cue-related ERPs were derived by averaging cue-locked epochs according to the two cue directions. Memory-array ERPs were derived according to cue direction and memory load. Only neural activity that was lateralised with respect to the attention cue, and correspondingly, the spatial location of items in VSTM was of interest. To increase trial numbers, data from left- and right-cue trials were combined in a way that preserved the spatial positioning of the electrodes relative to the side indicated by the cue (i.e., ipsilateral and contralateral). To ensure quality of the ERP data, a minimum criterion of 25 epochs per condition was set. Because of low performance accuracy, combined with the usual EEG artefacts, the experimental conditions including 8-item arrays failed to reach this criterion in a large proportion of the participants and could not be included in the analyses. The ERP analysis, therefore, focused on the conditions with 2- and 4-item arrays only.

Data were then imported into Matlab (MathWorks, Natick, USA) and baseline-corrected. The 200ms period before cue onset was used as the baseline for both cue-locked and memory-array-locked ERPs. This is important to eliminate the possibility of any lateralised activity occurring as a result of anticipatory spatial

attention before appearance of the memory array (e.g. tonic effects related to the cue-related LDAP) potentially contaminating the lateralised VSTM maintenance-related activity (CDA). This is especially important in the current experiment because the LDAP (related to lateralisation of pre-stimulus visual excitability) and the CDA (related to lateralisation of VSTM maintenance) are modulated in opposite directions (enhanced contralateral positivity and negativity, respectively). Using the time period immediately before the onset of the memory array as a baseline would conflate sustained measures of lateralisation related to anticipatory spatial attention and VSTM maintenance, and thereby exaggerate the magnitude of delay activity reflected in the CDA.

3.2.7 ERP Analysis

To investigate the neural underpinnings of cue-related processing, and their relationship to behaviour, the mean voltage amplitudes of lateralised ERPs previously associated with preparatory spatial biases of attention (EDAN, ADAN, LDAP, CDA) was quantified. Repeated-measures Analyses of Variance (ANOVAs) were used to compare neural activity across the conditions of interest. EDAN was quantified as the mean voltage difference between contralateral and ipsilateral sites over P7/8 and O1/2 at 250-400ms after cue onset (Jongen et al., 2007; Praamstra & Kourtis, 2010); ADAN was quantified as the mean amplitudes in the anterior electrodes sets (FC3/4, C3/4) averaged over the period 350-500ms after cue onset (Jongen et al., 2007); LDAP was quantified as the mean amplitude over electrodes

(PO3/4) averaged over 550-800ms after cue onset (McDonald & Green, 2008; Van Velzen & Eimer, 2003). The CDA was quantified using mean amplitudes (between 450-800ms) at PO7/8 post memory array onset (Vogel & Machizawa, 2004).

Where appropriate, the Greenhouse-Geisser correction was used to control for effects of non-sphericity. The extent to which the magnitude of anticipatory markers of spatial attention (EDAN, ADAN and LDAP) and maintenance activity (CDA) could predict behavioural cueing effects was also tested. Measurements of d' were averaged across set sizes. Model parameter estimates, however, were only stable for set size 2 so these correlation analyses focused on data from the smaller set size. The functional link between these ERPs and behavioural measures was assessed using split-half independent t-tests and Pearson's correlations (one-tailed).

3.3 Results

3.3.1 Behavioural Results

The behavioural results are shown in Figure 3.1. Note that each condition was named according to the total number of items that were presented despite the fact that participants were required to only maintain half the number of items on cued trials. As expected, accuracy decreased for trials with smaller changes in rotation and for the larger set sizes, and performance was better for cued, relative to neutral, trials. Statistical effects were assessed via a 2 (Cue type: valid and neutral) x 2 (Set size: 2 or 4 items) x 3 (Angle of rotation: 5°, 20°, 45°) repeated-

measures ANOVA. Sensitivity (d') was significantly higher in trials with spatial cues compared to neutral cues (cued>neutral: $F(1,14) = 27.61$, $p<0.001$). There were also significant main effects for set-size (2 item>4 items: $F(1,14) =145.64$, $p<0.001$) and change magnitude (linear trend, $F(1,14)=208.64$, $p<0.001$). Finally, there was a significant interaction between set size and rotation change ($F(2,28)=8.22$, $p=0.002$), due to a significantly smaller difference between set sizes at the small (5°) compared to the medium (20°; $p=0.014$), and large rotation change (45°; $p=0.015$). No other terms reached significance (ps>0.3).

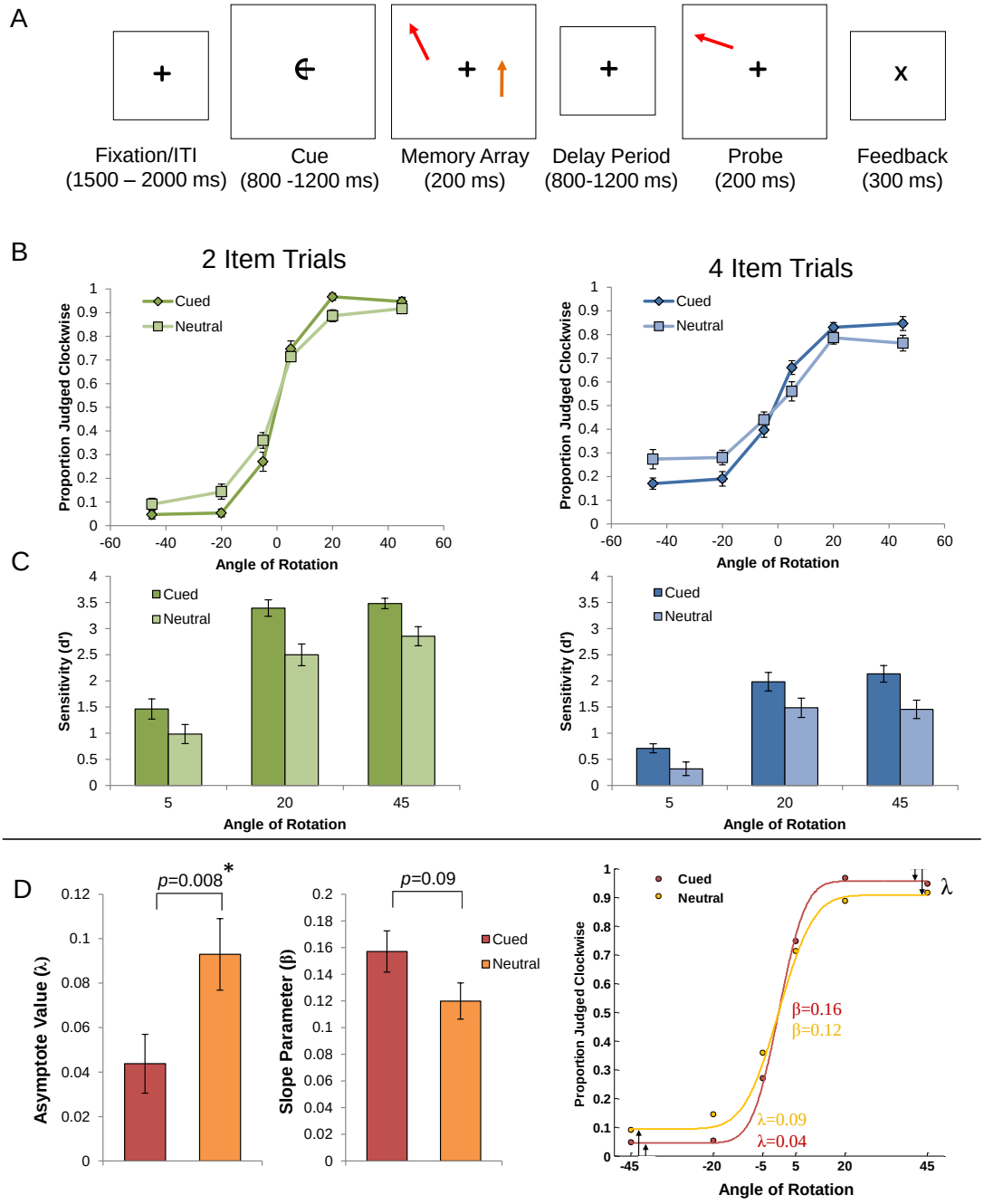


Figure 3.1: Task schematic and behavioural results. [A] On cued trials, a spatial selection cue (800-1200ms) indicated which items to encode from a subsequent memory array. After the variable delay period (800-1200ms), memory was assessed via a test probe. The probe appeared in the same location of a randomly selected item from the cued side of the memory array, with the important exception that it was

rotated about its central axis. Participants judged whether the change was clockwise or anti-clockwise. Neutral trials were the same, except the cue provided no predictive information regarding the side from which items could be probed. [B] The proportion of probe stimuli judged clockwise as a function of the rotation angle for both cued and neutral trials and set-size (set-size 2: left; set-size 4: right). [C] Sensitivity for change discrimination is shown as a function of rotation angle (averaged across direction), cue-type and set-size. [D] The average parameter estimates across subjects for set size 2, showing asymptote (λ) and slope (β) parameters respectively. On the right, the psychometric function generated by these average parameters is plotted against the corresponding average data points. Error bars represent ±1 s.e.m.

3.3.2 Modelling Results

Model parameters for slope (β) and asymptote (λ) were estimated for all set sizes, however, only data from set size 2 yielded stable results. Consistent with the results described above for d', a paired-samples t-test revealed that there were significantly lower asymptote estimates for cued compared to neutral trials ($t(14)=3.09$, $p=0.008$, see Figure 3.1). This effect suggests that preparatory attention can increase the probability that items are maintained in VSTM. There was also a trend for higher slope estimates for cued relative to neutral trials (trend: $t(14)=1.81$, $p=0.092$, see Figure 3.1). Together, these results are consistent with evidence that attentional orienting effectively reduces the encoding set size, which in turn increases the probability that items are maintained in VSTM and may also

increase the precision with which they are maintained (Bays & Husain, 2008), at least when the total number of items is relatively low (Zhang & Luck, 2008).

3.3.3 Cue-Related ERPs

As shown in Figure 3.2, the lateralised markers of anticipatory attention (EDAN, ADAN and LDAP) during the cue period were observed, before the memory array was presented. To test for the presence of these markers, repeated-measures ANOVAs tested for the effect of relative hemisphere (ipsi vs. contra) as well as electrode pair where relevant. Significant differences in mean voltages were observed in each case: EDAN (contra<ipsi: $F(1,14) = 5.89$, $p=0.029$); ADAN (contra<ipsi: $F(1,14) =6.57$, $p=0.023$); LDAP (contra>ipsi, $F(1,14) = 5.01$, $p=0.021$; No other significant terms were observed ($ps>0.17$).

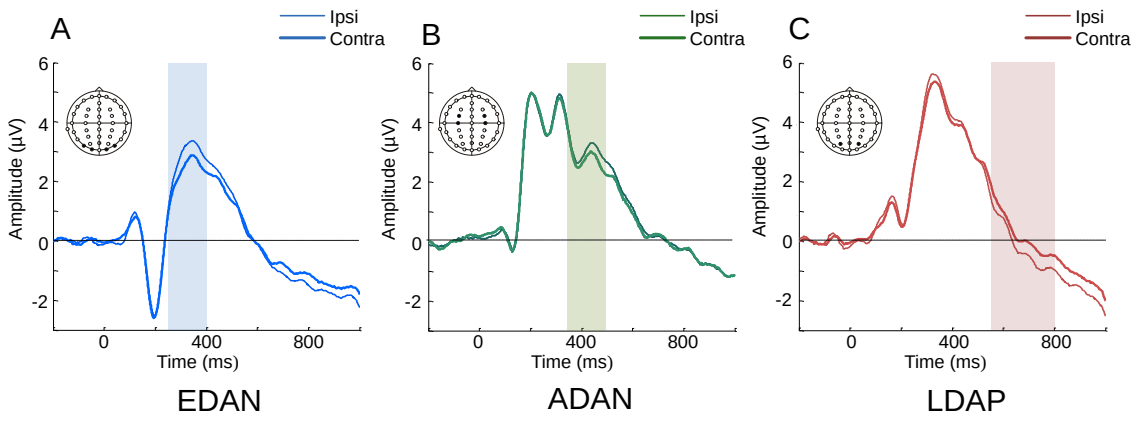


Figure 3.2: Grand-averaged ERPs time-locked to the cue. Thick lines indicate activity from contralateral sites whereas thinner lines indicate activity from ipsilateral sites. Shading highlights the time period of interest, during which ipsilateral and

contralateral activity differed significantly. [A] EDAN – activity for ipsilateral and contralateral sites for electrodes P7/8 and O1/2 from 250-400ms, [B] ADAN – activity for ipsilateral and contralateral sites for electrodes FC3/4, C3/4 from 350-500ms, [C] LDAP – activity for ipsilateral and contralateral electrode sites for PO3/4 from 550-800ms.

3.3.4 ERP Memory Maintenance Results

The ERP elicited by the memory array can be seen in Figure 3.3. Mean amplitudes at PO7/8 (450-800ms) were submitted to a two-way repeated measures ANOVA, with factors for set size (2 or 4 items) and electrode side (ipsilateral or contralateral), which confirmed a greater negativity for contralateral, relative to ipsilateral, electrodes ($F(1,14) = 16.74$, $p=0.001$). Importantly, a significant set size by hemisphere interaction was observed ($F(1,14) = 11.52$, $p=0.004$), demonstrating a selective negativity increase for 4- relative to 2-items at contralateral ($p=0.05$), but not ipsilateral electrodes ($p=0.37$).

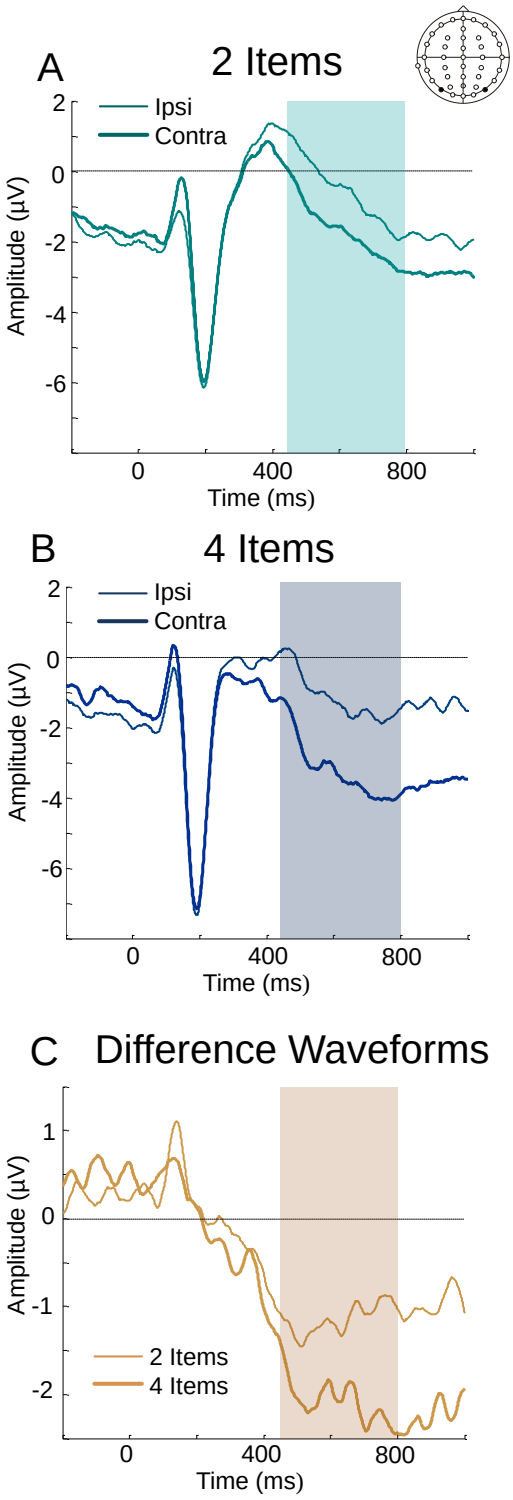


Figure 3.3: Grand-averaged ERPs time-locked to the memory array. Thick lines indicate activity from contralateral sites whereas thin lines indicate activity from ipsilateral sites. Shading highlights the time period of interest, during which

potentials differed significantly between ipsilateral and contralateral electrodes. [A] CDA – ipsilateral (thin line) and contralateral (thick line) activity from PO7/8 for 2 item trials from 450-800ms, [B] CDA – ipsilateral (thin line) and contralateral (thick line) activity from PO7/8 for 4 item trials from 450-800ms, [C] The difference waveform (contralateral minus ipsilateral activity) for the 2-item (thin line) and 4-item (thick line) trials from 450-800ms. Note that the ERPs and the subtraction waveforms do not begin at 0μV because a pre-cue baseline was used (see Section 3.2.6).

3.3.5 Electrophysiological Predictors of behaviour

Next, the relationship between the electrophysiological markers of preparatory attention reported above, and VSTM performance for each participant was explored. First, individual differences in ADAN magnitude predicted individual differences in d' cueing effect (difference in d' for cued and neutral trials; $r(13)=-0.50$, $p=0.03$). A similar trend was found for EDAN ($p=0.09$), but not for LDAP ($p=0.37$). Splitting the participants into those who showed a large or small advantage in d' for cued as opposed to neutral trials revealed a significant difference in EDAN magnitude ($t(13)=-3.49$, $p=0.002$) and a trend for ADAN ($t(13)=-1.68$, $p=0.059$).

Complementary effects were found while comparing the difference between neutral and valid asymptote estimates and the magnitude of the preparatory attention cueing effects. The difference in asymptote estimates between cued and neutral trials at the smallest set size was predicted by EDAN ($r(13)=-0.55$, $p=0.016$,

see Figure 3.4, top row), and ADAN (r(13)=-0.44, p=0.049, see Figure 3.4, bottom row). Independent samples t-tests performed on EDAN and ADAN magnitudes confirmed this result. EDAN (t(13)=-2.19, p=0.024, see Figure 3.4, top row) and ADAN (t(13)=-1.68, p=0.029, Figure 3.4, bottom row) magnitudes were greater (in a negative direction) for those who showed a large compared to a small cueing difference in asymptote. Once again, LDAP was not predictive of this behavioural cueing effect (correlation; p=0.12; split-half; p=0.947).

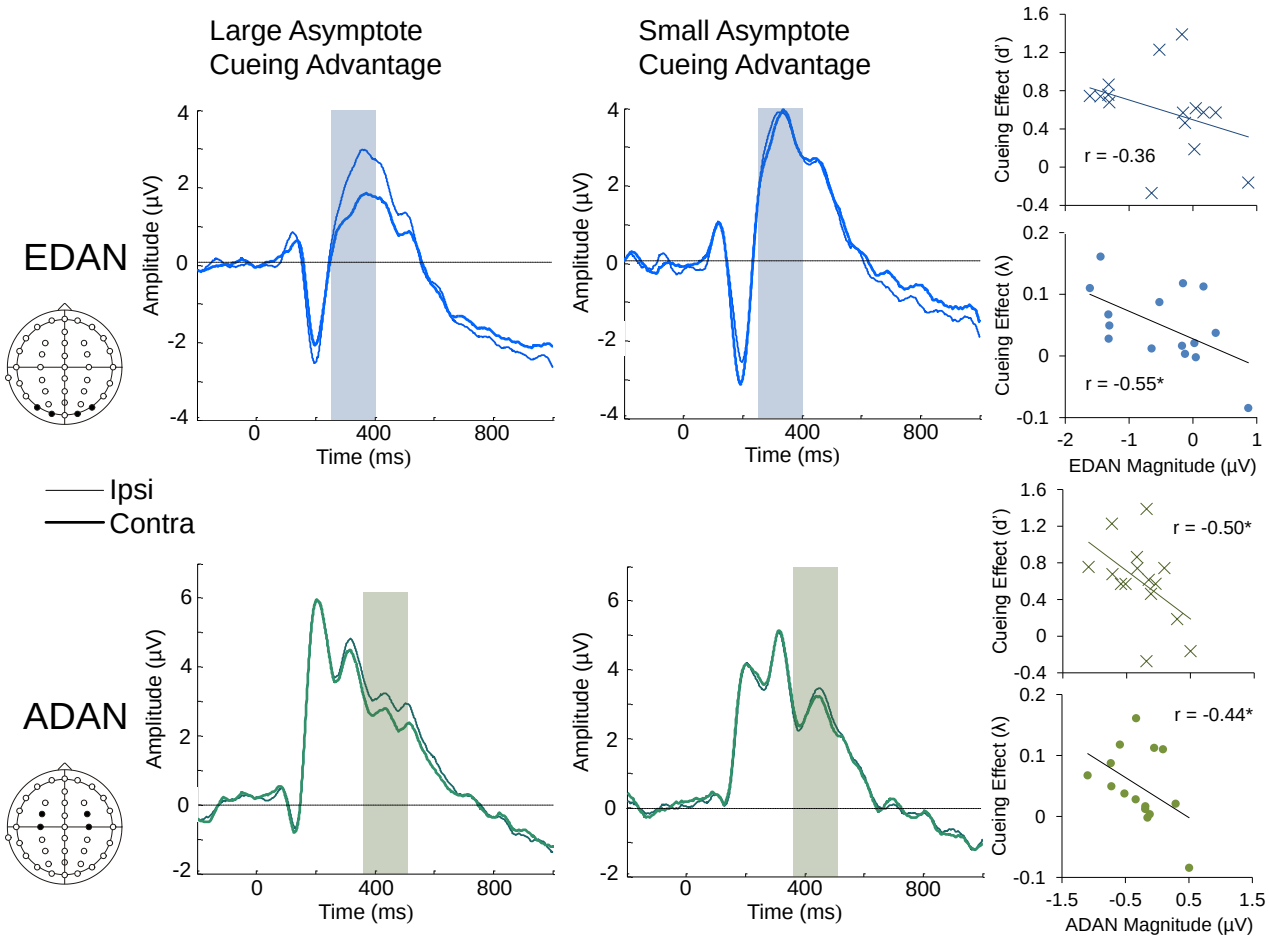


Figure 3.4: Neural predictions of the advantage in asymptote. The magnitude of the EDAN (top row) and ADAN (bottom row) effect split according to participants with

relatively large (left panels) or small (middle plots) difference in asymptote (neutral-cued). Shading indicates the time period of interest: 250-400ms for EDAN and 350-500ms for ADAN. During these time periods, there was a significant difference between participants who show a large compared to a small cueing advantage in asymptote. The right-hand panels show the correlations between cueing advantage for d' (cued-neutral) and for asymptote and EDAN magnitude (top two panels respectively) and ADAN magnitude (bottom two panels respectively). *Indicates a significant correlation ($p<0.05$).

In contrast to the brain-behaviour relationships that were observed for the cue-related behavioural advantage measured in d' and the asymptote of the psychometric function, there were not any similar relationships for the slope estimates. The difference in slope-parameter estimates between neutral and valid trials for the lowest set size was not predicted by EDAN (p=0.18), ADAN (p=0.09), or LDAP (p=0.90).

Finally, I also explored whether maintenance-related delay activity correlated with measures of performance in the task. Similar to the effects with EDAN and ADAN, CDA magnitude also tended to be related to an increase in the cueing advantage in asymptote. At the smallest set size, there was a trend suggesting that the differences in asymptote estimates between neutral and cued trials were related to differences in CDA (trend: $r(13)=-0.41$, p=0.067, see Figure 3.5, right panel; for all other behavioural cueing measures, $ps>0.1$). However, an independent samples t-test performed on the median split of CDA amplitude by cueing asymptote differences was not significant ($t(13)=-1.14$, p=0.14).

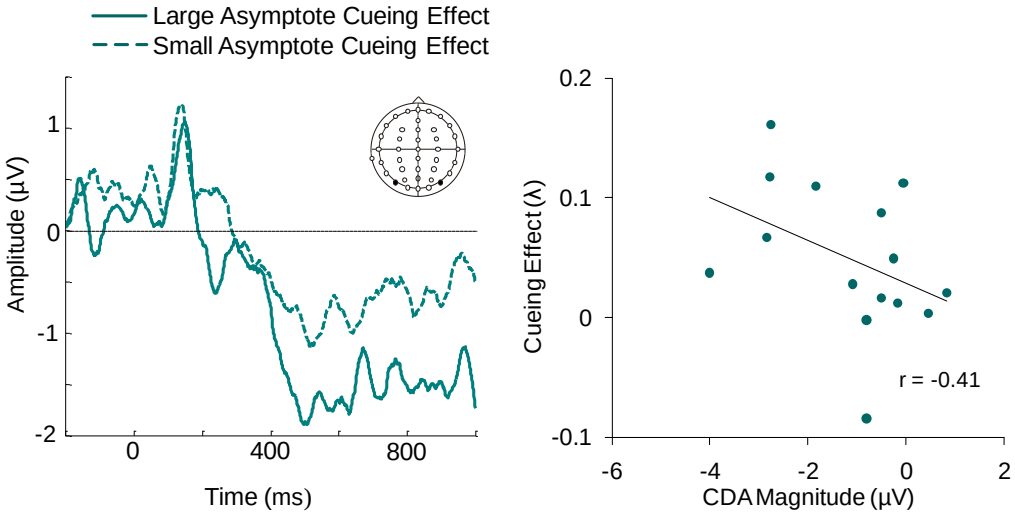


Figure 3.5: The relationship between CDA magnitude and the cueing advantage in asymptote. The left-hand panel shows the difference waveform between ipsilateral and contralateral sides of space for 2-item trials split according to whether the participants had a large (solid line) or small (dashed line) difference in asymptote for cued as opposed to neutral trials. The right-hand panel shows the relationship between maintenance activity and cueing advantage for asymptote estimates. Note these effects are not significant (during the CDA time period: 450-800ms) but are presented for completeness.

3.4 Discussion

EEG activity was recorded while participants performed a VSTM task that manipulated the spatial distribution of attention at encoding, the memory load, and the relative difficulty of the change discrimination at the memory probe. The parametric manipulation of change magnitude allowed us to model separately the

number of items held in VSTM (Zhang & Luck, 2008; Zhang & Luck, 2009), and the average precision of these memoranda (Bays & Husain, 2008). Selective encoding increased the number of task-relevant items that were available for recall. In contrast, there was only a trend for cue-related changes in precision. Importantly, the benefit in item-recall probability and d' for cued compared to neutral trials was predicted by preparatory measures of attention, including EDAN and ADAN. In contrast, there was no relationship between preparatory brain activity and effects of cueing on precision.

The implications of these results are important for a number of reasons. Firstly, at the behavioural level, the results demonstrate how preparatory orienting of spatial attention can influence the allocation of VSTM resources to favour task-relevant items. By modelling the slope and asymptote of behavioural psychometric functions for change discrimination between the memory array and test probe, the results suggest that attention primarily optimises the number of task-relevant items encoded into VSTM. There was only a trend for a cue-related increase in precision. Previously, Bays and Husain (2008) showed that increasing the number of items stored in VSTM reduces the precision with which each item is represented. Presumably, if participants are able to use the cue to encode selectively only the task-relevant subset of items in the memory array, then more resources can be allocated to each of these items, increasing the precision with which each item is represented. The observed trend for a cue-related increase in precision at the smallest set size is, therefore, consistent with a flexible resource model of VSTM capacity (Bays & Husain, 2008). However, the results are also compatible with less flexible models of VSTM capacity which allow for some flexibility for allocating

resources when the total number of items is below capacity limit (Zhang & Luck, 2008).

In this task, a sequence of neural markers for attentional orienting during the cue period was also observed. These potentials linked to preparatory attention have not typically been considered in selective VSTM tasks, but instead have been investigated in the context of tasks requiring perceptual judgements of incoming stimuli (e.g. Jongen et al., 2007; Nobre et al., 2000; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 2005). In these cases, ERP markers of preparatory attention have been associated with a modulation of the perceptual processing of cued stimuli (Hopf & Mangun, 2000; Jongen et al., 2007; Nobre et al., 2000; Talsma et al., 2005). The results extend these previous investigations by demonstrating that similar neural mechanisms of preparatory attentional selection can be engaged and are beneficial in preparing for selective VSTM encoding.

Critically, the results demonstrated a functional link between the neural mechanisms of selection signalled by EDAN and ADAN and subsequent VSTM performance, and were also able to shed further light on the functional mechanisms for these performance benefits. Participants who showed larger markers of preparatory attention (EDAN and ADAN) showed a greater cue-related advantage for recall probability (asymptote) and d'. This functional link suggests that the selection processes signalled by EDAN and ADAN increase the probability that only task-relevant items will be encoded. These findings are compatible with a related study that also suggests that ADAN is associated with filtering demands and the selection of task-relevant items (Seiss et al., 2009). In contrast, the preparatory mechanisms elicited by the pre-cue did not correlate with changes in precision,

suggesting that attention facilitates memory performance by biasing the quantity, rather than quality, of cued items that are encoded into VSTM.

As a corollary, the relationship between EDAN and cued behavioural advantages (for asymptote and d') also sheds light on the neural underpinnings of this potential. The functional significance of EDAN as a marker of spatial attention has been questioned (see Van Velzen & Eimer, 2003). Although explanations strictly based on the EDAN being linked to physical properties of cueing stimuli had been ruled out (Nobre et al., 2000), it remained possible that the EDAN reflected merely the 'spatial selection' of the aspects of the cue that were relevant to extracting its meaning. In this interpretation the EDAN is similar to the posterior lateralised N2PC potential elicited when a target is detected within a visual search array (e.g. Kuo et al., 2009). Explanations of this type do not readily apply to the current experiment, since identical cueing stimuli whose prominent side was factorially crossed with the cued side were used. More importantly, the functional relevance of this potential to spatial selection of items for subsequent encoding was clearly evident in the strong relationship between the magnitude of this potential and subsequent behavioural performance. In this respect, the results agree with Praamstra and Kourtis (2010) who suggest that the EDAN is the posterior precedent to the ADAN. More generally, the results demonstrate the functional significance of early markers of attentional orienting.

Interestingly, the results did not show any link between the later marker of preparatory changes in visual excitability (LDAP) and subsequent VSTM performance. The stimuli in the memory array were supra-threshold and easy to see, therefore, the main limits of performance were related to the number of items

available for encoding and the precision with which they had to be remembered. Consequently, heightened visual excitability may not have been advantageous for accurate performance in the current task. Rather, spatial selection of the relevant items to encode, reflected in the EDAN and ADAN, was presumably more important for performance than enhancing the initial visibility of items in the memory array (see Seiss et al., 2009).

In addition to the ERP signatures of preparatory attention, a load-dependant CDA was identified. Typically thought to index the number of items being maintained in VSTM (Jolicœur et al., 2008; Vogel & Machizawa, 2004; Vogel et al., 2005), CDA has also been linked to individual capacity limits (Vogel & Machizawa, 2004) and selectivity efficiency (Vogel et al., 2005). These results are consistent with load-dependent delay activity observed in this task. The observed trend relating CDA magnitude and the cueing difference in recall probability is also consistent with previous evidence linking maintenance activity with the ability to select task relevant items (Vogel et al., 2005).

The results of the current experiment provide important new insights into the neural mechanisms that mediate attentional selection for VSTM encoding. The study provides both behavioural and neural evidence that attention affects the probability that an item enters VSTM, and is successfully maintained. The results suggest that these mechanisms of attention critically shape the contents of VSTM to represent only the most behaviourally relevant visual information. Recent studies are beginning to show that VSTM performance can also be enhanced by cues presented after encoding, during the VSTM maintenance period (Griffin & Nobre, 2003; Landman et al., 2003). In future studies, it will be interesting to investigate

whether, at this later stage, attention can continue to influence the selection of items predicted to be relevant for behaviour or whether alternative mechanisms are employed, such as the improvement of precision with which the encoded items are represented.

CHAPTER 4

The Effect of Retrospective Orienting of Attention on the Capacity and Precision of VSTM

In chapter 4 the results show that selective attention can restore forgotten information to VSTM. In this VSTM task, all stimuli are equally task-relevant during encoding. During the retention interval, however, a cue predicts which of the memory items will be probed at the end of the delay. This dynamic shift in task-relevance improves memory recall for the cued item. Importantly, the results also demonstrate that attention can even improve recall probability for items that would have otherwise been irretrievable, providing critical evidence that attention can restore forgotten information to VSTM. In addition, psychophysical modelling of memory performance confirms that restoration of information in VSTM increases the overall probability that the cued item is available for recall, rather than changing the representational quality of memoranda.

4.1 Introduction

VSTM frees our behaviour from direct stimulus-dependency. By constructing a stable internal representation of the world, we can act on visual information that is no longer present in the environment. Although critical for flexible goal-directed behaviour, VSTM can only represent a very small proportion of the total sensory input (Phillips, 1974). We need, therefore, to be selective about how we focus our attention to ensure that only the most relevant information is encoded, and maintained, within this limited cognitive space.

Extensive research demonstrates that selective attention gates initial access to VSTM (Chapter 3; Bundesen, Pedersen, & Larsen, 1984; Gazzaley, 2011; McNab & Klingberg, 2008; Rutman et al., 2010). However, in everyday life, the importance of certain events may only become apparent after they have passed. In an ever-changing environment, it is important for VSTM to remain flexible and

under the influence of top-down control even after initial encoding (Stokes & Nobre, 2012). Recently, studies have shown that flexible control over VSTM does not end at encoding, but continues to shape memory representations during VSTM maintenance (Griffin & Nobre, 2003; Landman et al., 2003; Lepsien & Nobre, 2006; Makovski & Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007). In these experiments all stimuli are equally task-relevant at initial encoding, but attention cues presented during maintenance *retro*actively predict which item will be probed at the end of the trial. Retro-cues during maintenance significantly improve memory performance. Importantly, the effects of retro-cueing are not dependent on iconic memory (Astle et al., 2011; Sligte et al., 2008); rather, attention seems to modulate VSTM throughout the retention interval (Kuo et al., 2012).

Retro-cueing could engage mechanisms of attention to protect information in VSTM from forgetting (e.g. Gazzaley & Nobre, in press; Matsukura et al., 2007). By cueing an item during retention, memory load is effectively reduced thereby reducing the mnemonic demands of further maintenance (Kuo et al., 2012). Recent evidence suggests that the process of forgetting is discrete. For example, Zhang and Luck (2009) found that increasing the duration of retention increases the likelihood that a particular item will be forgotten. Rather than decaying gradually, they conclude that forgetting in VSTM involves a catastrophic “sudden death” (Zhang & Luck, 2009). If attentional orienting during maintenance reduces the likelihood that cued items suffer sudden death, one would expect retro-cues to increase the probability that a cued item will be recalled, but not necessarily influence the representational precision.

Attention could also, however, be important for transforming task-relevant information to a retrievable format. If, for example, information has already been forgotten, or is otherwise unavailable to retrieval mechanisms (e.g. Sligte et al., 2008), selective attention could trigger a state transition from a non-VSTM format to a representation that is directly accessible for recall. In this case, attention should be able to access information is otherwise unavailable to a memory probe.

To determine how attention dynamically optimises VSTM maintenance to accommodate shifting task-relevance, a novel paradigm was developed to manipulate the allocation of attention during the maintenance interval of a precision VSTM task (see Figure 4.1). Importantly, a number of control conditions are included to measure the quality and quantity of memory items at the end of an equivalent delay period (*neutral retro-cue* and *long no-cue* condition), or at the equivalent time of the retro-cue (*short no-cue* condition). The results show that retrospective attention improves recall for cued items, even if they were otherwise lost to VSTM (i.e., compared to the *short no-cue* condition). Moreover, psychophysical modelling confirms that attention during maintenance increases the probability that task-relevant items are available for report, consistent with a discrete transition between VSTM and non-retrievable formats.

4.2 Experiment 1: Spatial Retro-cueing

4.2.1 Method

4.2.1.1 Participants

Twenty volunteers aged between 20 and 32 (*M*=23.30, *SD*=2.31, 11 female) took part in Experiment 1. All had normal or corrected-to-normal vision, and all but two were right handed as assessed by a handedness inventory (Oldfield, 1971). Participants gave informed written consent and were remunerated £8 for their time. All experiments were approved by the Oxford Central University Research Ethics Committee (CUREC).

4.2.1.2 Task

The task is illustrated in Figure 4.1. It incorporates the retro-cuing paradigm developed by Griffin and Nobre (2003; Landman et al., 2003) with a VSTM precision task used in Chapter 3, based on Bays and Husain (2008). On each trial, participants encoded an initial memory array of randomly oriented coloured arrows (4, or 8, equally distributed on both sides of the visual field; 200ms duration). Memory for one item was tested at the end of the trial. The memory probe was always one of the arrows from the memory array, but rotated 20° or 45° about its central axis. Participants judged whether the probe had rotated clockwise or anti-clockwise relative to the original memory item. On half the trials, a black rectangular cue was presented either in the location of the probe arrow (spatially informative *valid retro-cue* condition: 25% of trials) or around the fixation cross (uninformative *neutral retro-cue* condition: 25% of trials). Valid and neutral retro-cues were

presented for 200ms, following a 800ms delay from the offset of the memory array. Cues were followed by another 800ms delay before the presentation of the probe (200ms duration). On the remaining 50% of trials, there was no cue stimulus; rather the probe was presented either after 800ms or 1800ms (25% of trials each), thus equating the probe appearance in no-cue trials to the appearance of the cue (*short no-cue* condition) or the probe in the cued trials (*long no-cue*; see Figure 4.1B for schematic). These conditions allow us to probe the quantity, and quality, of visual memories at the time that the cue is presented on retro-cue trials, and after the full delay period. Importantly, this allows us to test directly the extent to which retro-cueing improves performance by reducing inter-item competition during the second delay period (Edin et al., 2009; Makovski et al., 2008). Once the probe was presented and response made, feedback was presented for 300ms. All trial types were randomised across the experiment.

The resulting design manipulated three within-participant factors of Cue-Type (*valid retro-cue*, *neutral retro-cue*, *short no-cue*, *long no-cue*), Set Size (4, 8), and Angle of Rotation (20°, 45°). Data for clockwise and anti-clockwise rotations were collapsed. Manipulating the change magnitude provides important insight into the precision of VSTM: to detect a small angular change requires a more precise representation than to detect a larger change (see modelling details in Experiment 2).

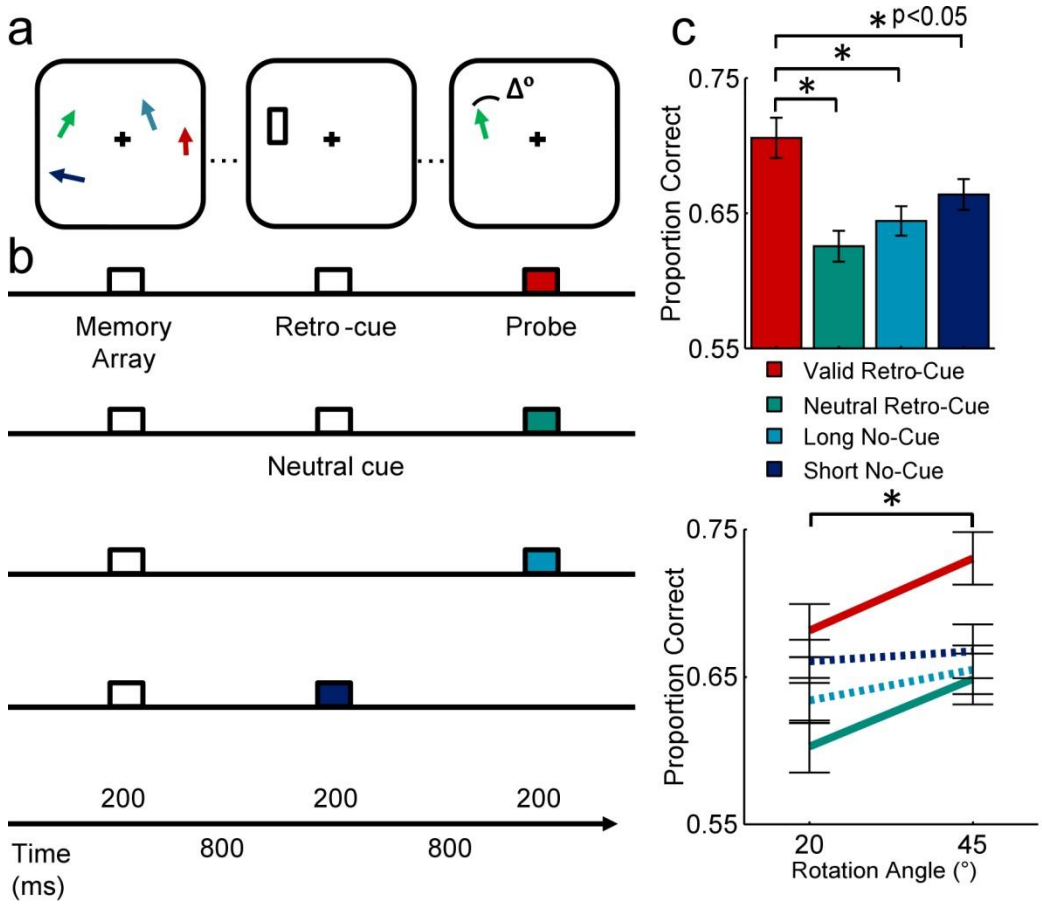


Figure 4.1: Paradigm and main results for Experiment 1. [a] Schematic of task format: Participants were instructed to encode an array of items and, after a delay, a single probe stimulus was re-presented except rotated (20° or 45°) clockwise or anti-clockwise. [b] Schematic of the timing of the four conditions for the four Cue Types: *valid retro-cue, neutral retro-cue, long no-cue*, *short no-cue*. Stimulus and delay durations are shown at the bottom of the panel. [c] The proportion of correct responses is shown as a function of cue condition, and [d] as a function of Angle of Rotation (20° and 45°; collapsed across set-size, clockwise and anti-clockwise rotations). Error bars represent ±1 s.e.m. *Indicates a significant comparison.

4.2.1.3 Stimuli

The task was programmed and presented using Presentation software (Neurobehavioral Systems v.13.0, 2009). All stimuli were presented against a light grey background. A black central fixation cross (0.86° by 0.86°) was presented throughout each trial, offsetting only when feedback was given. Arrow stimuli in the memory array were constructed within the task programme on a trial-by-trial basis. Their colours were chosen at random (without replacement) from a selection of highly discriminable colours (Red, Blue, Green, Cyan, Yellow, Magenta, Orange or White). Each arrow subtended approximately 1.43° of visual angle from base to tip, and a minimum distance of 2.39° between each stimulus ensured that there was no overlap, and reduced crowding effects. The cue was an unfilled black square (2.15° x 2.15°; 0.15° line thickness) presented either around the location of the task-relevant memory-array item (*spatial retro-cue)* or around the fixation cross (*neutral retro-cue*). Responses were made by turning the lever of a custom-built response device according to the direction of orientation change. Feedback about response accuracy was provided by replacing the fixation cross with either an “O” (correct) or an “X” (incorrect).

4.2.1.4 Procedure

Participants performed the computerised task in a quiet, dimly lit room viewing a CRT monitor (refreshed at 60hz) at a distance of 100cm. Eye-movements were monitored to ensure participants maintained fixation. There was a 20-trial practice block to familiarise participants with the task. In total, there were 768 trials,

presented across 10 blocks. The final analysis was based on 48 trials for each sub-condition of interest.

4.2.2 Results

The effects of the experimental variables upon accuracy were analysed using a 4 (Cue Type) x 2 (Angle of Rotation) x 2 (Set Size) repeated-measures Analysis of Variance (ANOVA). The ANOVA revealed a main effect of Cue Type on accuracy (see Figure 4.1, $F(3,57) = 14.35$, $p<0.001$). As shown in Figure 4.1, accuracy was highest for the *valid retro-cue* condition compared to the other Cue Types. Planned pairwise comparisons confirmed that accuracy was significantly higher for the *valid retro-cue* compared to all other conditions: *short no-cue* ($p=0.007$), *long no-cue* ($p=0.001$) and *neutral retro-cue* ($p<0.001$). Accuracy was significantly higher for the *short no-cue* compared to the *neutral retro-cue* condition ($p<0.001$, there were no other significant comparisons, ps>0.10). There was also a main effect of Set Size [accuracy for 4 items ($M=0.72$, $SE=0.12$) > 8 items ($M=0.60$, $SE=0.07$; $F(1,19) = 201.35$, $p<0.001$)], and Angle of Rotation (45>20: $F(1,19) = 15.55$, $p=0.001$).

Overall, the results suggest that directing attention to items in VSTM enhances the mnemonic representation, thereby improving recall performance. Cueing benefits were observed relative to all other conditions, including the short no-cue condition. Importantly, this condition provides an index of the contents in VSTM at the time of the retro-cue, and therefore demonstrates that the retro-cueing benefit cannot be explained by a simple reduction in effective duration of the

retention interval (e.g. Makovski et al., 2008). Rather, the results suggest that selection during VSTM maintenance can transform a relatively weak, or unstable, form of memory to a more robust representation to enable comparison to the probe (Makovski et al., 2008; Sligte et al., 2008). In this respect, attention can be used to access, and enhance, information that would otherwise have been lost and forgotten.

Interestingly, there was also a marginal interaction between Cue Type and Angle of Rotation ($F(3,57) = 2.42$, $p=0.076$; all other terms $p>0.09$). This trend could be attributed to greater cueing effects in the 45° relative to the 20° angular change trials. Correct small rotation change discrimination demands comparatively higher precision of the memory representation than large changes. Large changes, on the other hand, provide a closer estimate of the upper bound (or capacity) of VSTM performance (Bays & Husain, 2008; Zhang & Luck, 2008). If retro-cueing is most effective when the judgement task is relatively easy, this suggests that attention improves the likelihood of recall of the cued item, rather than the precision of the representation. This intriguing possibility motivated the design of the next, follow-up experiment.

4.3 Experiment 2: Individual Parameter Modelling

The purpose of Experiment 2 was to determine whether the cueing advantage observed in Experiment 1 was attributable to a change in the precision (or quality) of the VSTM representation, or the probability of memory recall. A finer-grained parametric modulation of change type was included to allow for formal modelling of

parameters for precision and upper-bound recall probability in each participant (Bays & Husain, 2008; Zhang & Luck, 2008).

4.3.1 Method

4.3.1.1 Participants

Participants (*N*=20, 11 female) were aged between 23 and 35 (*M*= 27.5, *SD*=3.59). All participants had normal or corrected-to-normal vision and were right handed as assessed by a handed inventory (Oldfield, 1971). Participants gave informed written consent and were remunerated £8 for their time.

4.3.1.2 Task

The task was almost identical to the one used in Experiment 1, except to estimate the shape of the psychometric function relating performance to change magnitude, a larger range of angular changes was tested: 5°, 15°, 30° or 45°. The same retro-cue manipulation was used as per Experiment 1, but to reduce trial numbers only 4 item trials were presented.

In total, there were 768 trials, presented across 10 blocks. The design included three factors: Cue Type (4 levels), Angle of Rotation (4 levels), and direction of angular rotation (2 levels). Direction of rotation was collapsed in ANOVAs testing for effects on performance accuracy, but was preserved for modelling. To compare models on an individual participant level, four participants completed 3 or 4 extra testing sessions.

4.3.1.3 Modelling and Analysis

Firstly, as with Experiment 1, a repeated-measures ANOVA was performed on the accuracy data at the group level (*N*=20). In a second step, the observed distributions of responses "Clockwise" were fitted to a cumulative Gaussian curve for each participant and condition (Figure 4.2). Responses were modelled as binary outcomes following:

$$y = \lambda + \frac{(1 - 2\lambda)}{2} \cdot erfc\left(\frac{-\beta}{\sqrt{2}}(x)\right)$$

Where erfc is the complementary Gaussian error function, β is the slope of the curve, and λ is its asymptote. Four asymptotes (λ), and four slopes (β) were estimated for each of the four Cue Types. The psychophysical model that was tested included separate parameter estimates for the precision (slope, β) and the probability (asymptote, λ) of items in memory (Bays & Husain, 2008; Zhang & Luck, 2008) for each participant. The upper and lower bound recall performance reflects the maximum number of items in VSTM, assuming the comparison judgment is infinitely easy (cf. Bays & Husain, 2008). An estimate of the asymptote, therefore, provides an estimate of the maximum number of items available in VSTM at the time of the test probe. In contrast, the estimate of the slope provides an index of the precision of available memory representations.

Parameter estimates were then assessed at the group level by using a repeated-measures ANOVA. In the analysis, both the slope and asymptote are estimated to index both the precision and probability of recall. Importantly, a failure to allow asymptotes to vary necessarily assumes that the upper bound of recall probability remains constant and therefore, forcibly attributes any change in

performance to a difference in slope (Cowan & Rouder, 2009; Wichmann & Hill, 2001a; Zhang & Luck, 2009).

In a third step, likelihood-ratio tests were performed for the four participants who completed multiple sessions of the same task, to identify the most parsimonious model to explain the data. If there were no significant differences in the goodness of fit between models with different asymptotes or slopes for each cue condition, then the optimal model has the lesser number of parameters (e.g. one asymptote and one slope for the four Cue Types).

4.3.2 Results

The group-level results are illustrated in Figure 4.2. Orienting attention during VSTM maintenance increased the probability of recall but had little, if any, influence on the precision of representations. Performance for all cue conditions increased as the Angle of Rotation increased until the curve reached a plateau at around ±20º to ±45º. The ANOVA revealed main effects of Cue Type ($F(3,57) = 19.74$, $p<0.001$) and Angle of Rotation ($F(3,57) = 78.34$, $p<0.001$) on accuracy. Pairwise comparisons confirmed higher accuracy for the *valid retro-cue* compared to the *short no-cue* ($p=0.003$), *long no-cue* ($p<0.001$) and *neutral retro-cue* conditions ($p<0.001$). Accuracy was also higher for the *short no-cue* compared to the *neutral retro-cue* condition ($p=0.001$). All other comparisons were non-significant ($ps>0.052$). The interaction between Cue Type and Angle of Rotation was not significant ($F(9,171) = 1.56$, $p=0.13$).

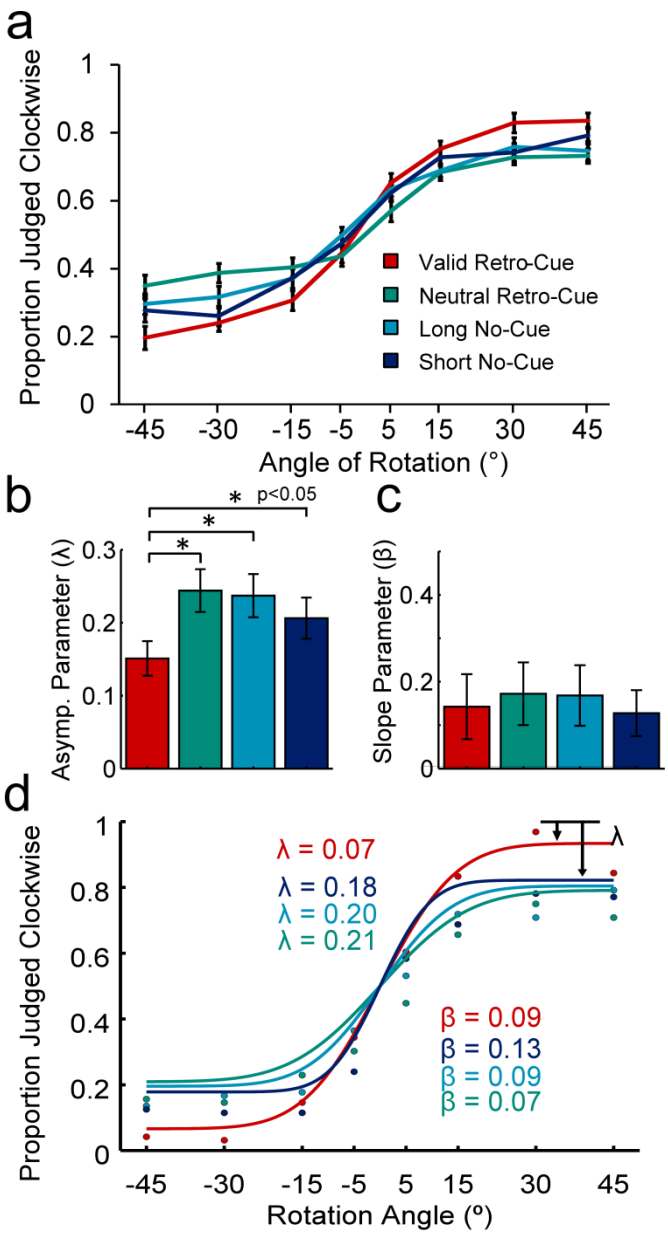


Figure 4.2: Behavioural results and parameter estimates for Experiment 2. [a] Proportion judged clockwise for the four cue conditions (*valid retro-cue*, *short no-cue*, *long no-cue*, and the *neutral retro-cue* condition) according to the Angle of Rotation change (5°, 15°, 30° and 45°, clockwise and anti-clockwise). [b] Average estimates of the probability of recall (λ) for the four cue conditions. For this measure a lower number indicates a smaller distance from maximal performance or higher probability of recall. [c] The β (slope) estimates for the four cue conditions. For this

measure, a larger number indicates higher precision. [d] The results of a representative participant who completed a total of four sessions of the task (96 trials per data point). Data points represent the proportion judged clockwise at each Angle of Rotation for the four cue conditions (*valid retro-cue*, *short no-cue*, *long no-cue*, and the *neutral retro-cue* condition). Slope (β) and estimates of asymptotes (λ) are given for each condition. The lines represent the fitted cumulative Gaussian functions with the estimates of the slope and asymptotes. Error bars represent ±1 Std. Error. *Indicates a significant comparison.

The estimated values for slope and asymptote were submitted to a repeated-measures ANOVA with Cue Type as a factor. For estimates of asymptote, there was a significant main effect ($F(3,57) = 3.56$, $p=0.02$, see Figure 4.2, Panel b). Post-hoc comparisons confirmed smaller asymptotes (λ) for *valid retro-cue* compared to the *short no-cue* ($p=0.037$), *long no-cue* ($p=0.006$) and *neutral retro-cue* conditions ($p=0.003$). As in Experiment 1, the comparison of the *valid retro-cue* and the *short no-cue* suggests that the cueing benefit cannot be accounted for by a simple reduction of the delay period. The cueing advantage relative to the early probe trials indicates that attention can directly increase the absolute number of items that can be retrieved at a given time point. In contrast, there was no evidence to suggest that attention could influence the precision (β) of representations: there was no main effect of Cue Type ($F<1$).

By collecting a larger number of trials in a subset of participants it was also possible to conduct a formal test to determine whether cue-related changes in

memory performance were best explained by models with separate parameter for asymptote and/or slope across the different cue conditions (see Table 4.1). Two participants performed a total of 4 sessions of the task (96 trials per condition) whereas another two performed 3 sessions of the task (72 trials per condition). Cumulative-likelihood tests (based on the cumulative data for all four participants, see Claessens & Wagemans, 2008) showed that a model with 1 slope (β) and 4 asymptotes (λ) best explained the data (N=4, all $\chi^2(12)>49.44$, $p<0.0001$, for individual data see Table 4.1). Individually, this effect held true for four out of four participants. These results replicate and extend the group results, showing that performance differences between Cue Type conditions are due to changes in asymptote, or the probability that an item remains in memory, rather than a change in the precision of the representation (slope).

Table 4.1 The group level and individual estimates for the full model and two comparisons: valid retro cue vs. short no-cue and short no-cue vs. long no-cue.

Type of Model	Model Parameters	Participant/Group Number	Log Likelihood	Akaike's Information Criterion
Full (All Data)	1T, 4S, 4A	Participant 1	-1909.96	3837.91
	1T, 4S, 1A		-1917.51	3847.02
	1T, 1S, 4A		-1911.49	3834.97*
	1T, 1S, 1S		-1926.88	3859.76
	1T, 4S, 4A	Participant 2	-1239.90	2497.8
	1T, 4S, 1A		-1246.75	2505.50
	1T, 1S, 4A		-1240.49	2492.98*
	1T, 1S, 1S		-1268.85	2545.69
	1T, 4S, 4A	Participant 3	-1118.60	2255.20
	1T, 4S, 1A		-1122.42	2256.85
	1T, 1S, 4A		-1121.45	2254.90*
	1T, 1S, 1S		-1128.66	2263.32
	1T, 4S, 4A	Participant 4	-1570.99	3159.98
	1T, 4S, 1A		-1612.73	3237.47
	1T, 1S, 4A		-1572.41	3156.81*
	1T, 1S, 1S		-1598.75	3203.50
Valid Retro-Cue vs. *Short No-cue* only	1T, 1S, 2A	Participant 1	-907.32	1822.63*
	1T, 1S, 1A		-910.60	1827.21
	1T, 1S, 2A	Participant 2	-547.32	1102.64*
	1T, 1S, 1A		-552.18	1110.37
	1T, 1S, 2A	Participant 3	-511.26	1030.51
	1T, 1S, 1A		-511.28	1028.57*
	1T, 1S, 2A	Participant 4	-701.42	1410.85*
	1T, 1S, 1A		-711.99	1429.99
Short No-cue vs. *Long No-cue* only	1T, 1S, 2A	Participant 1	-975.04	1958.09*
	1T, 1S, 1A		-977.12	1960.24
	1T, 1S, 2A	Participant 2	-629.19	1266.38*
	1T, 1S, 1A		-630.72	1267.43
	1T, 1S, 2A	Participant 3	-561.61	1131.22*
	1T, 1S, 1A		-565.40	1136.80

1T, 1S, 2A	Participant 4	-824.68	1657.36
1T, 1S, 1A		-825.65	1657.30*

Note. Full models are inclusive of all 4 cue-type conditions. The two other models only compare the data of interest: the *Valid Retro-Cue* compared to the *Short No-cue* condition and the *Long* and *Short no-cue* conditions. T = Threshold, S = Slope, A = Asymptote. *Indicates the optimal model.

As a strong test of the effects of retro-cues on the probability of item retrieval, the fitted models were directly compared across *valid retro-cue* and the most stringent control condition: *short no-cue.* The optimal model had 1 slope and 2 asymptote parameters (N=4, $\chi^2(4)=37.50$, $p<0.0001$). In addition to the cumulative effect, having two asymptote parameters was optimal for 3 out of 4 participants. As an aside, models for only the *short* and *long no-cue* conditions were compared. This also revealed that the model with 1 slope and 2 asymptotes gave the best fit (N=4, $\chi^2(4)=16.73$, p=0.002). This result held true for three out of four participants, supporting the idea of a 'catastrophic' loss of representations over time (Zhang & Luck, 2009).

4.4 General Discussion

The results show that VSTM can be dynamically modulated to accommodate changing behavioural contexts. These results demonstrate that attention, when directed to items already encoded and maintained in memory, improves the probability of recall. Moreover, attention also rescues information that would otherwise be lost or unavailable to retrieval processes, as indexed by the cueing benefit relative to the short no-cue condition. Finally, these benefits were not due to

an improvement in the recall precision of individual items (cf. Griffin & Nobre, 2003), but rather to an increase in the upper-bound probability of recall.

These results are at least partly consistent with the hypothesis that orienting attention during VSTM maintenance protects behaviourally relevant information from inter-item competition during the maintenance interval. According to this hypothesis, similar competitive dynamics that underlie perceptual processing also continue to influence mnemonic delay activity in the visual system (Edin et al., 2009; Stokes & Nobre, 2012). These winner(s)-take-all network dynamics could help organise VSTM to represent coherent task-relevant objects (e.g. Duncan, 1984) such that information about weaker, and/or less relevant competitors is lost. On-going inter-item competition could also contribute to forgetting in VSTM (Edin et al., 2009). Memory items that lose competitive advantage would be unable to be probed by conventional methods leaving little or no trace of the forgotten information at least in the robust form of VSTM. This information, however, may still be available to be cued and restored to a probable format. Consistent with this competitive account, Zhang and Luck (2009) show that increasing the memory retention interval reduces the overall probability of recall, rather than precision. Thus compared to gradual decay, this reduction in recall probability is likened to "sudden death" (Zhang & Luck, 2009), as if the doomed item has been suddenly forgotten to VSTM. The current results are also consistent with this account. By modelling behaviour of individual participants, it is clear that the *short* and *long no-cue* conditions were best explained by two asymptotes and one slope. This indicates that, on average, there were fewer items in VSTM at the end of the longer retention interval, with no corresponding reduction in precision. It may be the case,

however, that if the delay between the presentation of the memory array and the cue was shortened then the retro-cueing benefits may be able to prevent the loss of precision information due to inter-item competition or otherwise. This intriguing possibility should be directly addressed in future research.

Although retro-cues are too late to modulate initial sensory processing, top-down attention mechanisms may still be able to bias competition in visual "delay activity" to favour the retention of cued items (e.g. Kuo et al., 2012; Makovski et al., 2008). In particular, the comparison of memory performance in the *valid retro-cue* condition to performance in the two control conditions with the same retention interval (*long no-cue*, and *neutral retro-cue*) could be explained by biasing representations in VSTM. Within this framework, retro-cueing could bias inter-item competition in delay activity to favour the cued item, thereby increasing the likelihood that the most task-relevant information will survive the hazards of forgetting (schematised in Figure 4.3, left panels). Once an item is forgotten to VSTM it is no longer in a robust and probable form.

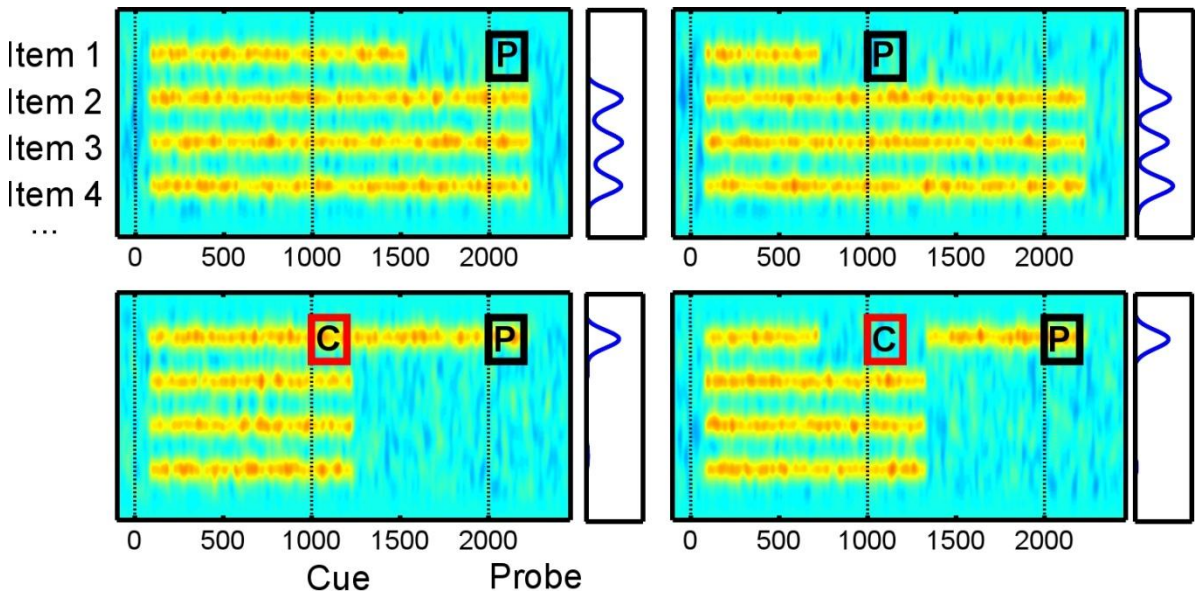


Figure 4.3: Schematic of persistent activation of neural populations coding for 4 memory items over time (see also Edin et al., 2009). The top panels represent a trial in which Item 1 is not able to be probed late (left), or early (right), during the maintenance interval of a respective long or short, no-cue trial. The memory probe is denoted by a black rectangle containing "P". If Item 1 is cued (red rectangle containing "C") before it is no longer in a robust, "probable" format (lower left), then the delay activity persists until the probe, perhaps also allowing other task-irrelevant items to be lost to VSTM, and thereby reducing inter-item competition (Matsukura et al., 2007). However, even if Item 1 is already unable to be retrieved normally at the time of the cue, the current results suggest that the representation in VSTM can be restored prior to the presentation of the memory probe (lower right panel).

However, evidence that retro-cueing improves recall probability relative to the *short no-cue* condition demonstrates that the effects of attention extend beyond biasing task-relevant information that is already in VSTM. Critically, the short no-cue condition provides an index of the contents in VSTM at the time of the retro-cue; thus, the retro-cue advantage in the probability of recall, relative to the short no-cue condition, demonstrates that attention can access information that would otherwise be unavailable to retrieval mechanisms (schematised in Figure 4.3, right panels, see also Makovski et al., 2008). Also, this suggests that there is more information retained in the visual system than is normally accessible (Astle, Nobre, & Scerif, 2010a; Sligte et al., 2008). Consider the tri-partite model of visual memory which dissociates robust, "probable" information in VSTM from both the iconic trace and a high capacity, fragile store (see Section 1.1, page 5 and Section 1.5.3, page

37). The retro-cue, in the case of the current experiment, may enable the consolidation of fragile item information into an accessible VSTM format before the probe is presented. In this way, the retro-cue can protect mnemonic representations from being overwritten by the probe (see also Makovski et al., 2008).

The psychophysical modelling results confirm that the apparent "resurrection" of lost items to accessible VSTM operates discretely: there was no evidence that retro-cueing improves the representational *quality* of the cued item. In this respect, restoration to VSTM can be thought of in complement to "sudden death" (Zhang & Luck, 2009). Both reflect a discrete transformation between items that are available, and those items which remain unavailable to retrieval mechanisms.

The study presented in Chapter 3 shows that directing spatial attention to items before they are encoded also influences recall probability, rather than memory precision. Combined, these results suggest that attention does not affect the quality of representations in VSTM, only the probability that task-relevant items will be encoded and maintained. These interactions between attention and VSTM contrast with evidence that attention modulates the *quality* of perceptual processing (e.g. Reynolds & Chelazzi, 2004). This difference could belie a fundamental distinction between attention for perception versus for VSTM. For perceptual tasks, in which responses are made directly according to perceptual judgements for low contrast or degraded stimuli, attention can facilitate processing to enhance perceptual analysis, and ultimately, to enhance the quality of the information that is available to post-perceptual processes, including VSTM. In VSTM tasks, however, the processing limit is not usually perceptual (e.g., stimuli are typically high-contrast

and not masked), but rather the behavioural challenge is to maintain over time as much task-relevant perceptual information as possible. Under these circumstances, mechanisms of attention do not influence the perceptual quality of the representations, but rather the likelihood that the results of perception are successfully maintained.

In sum, these data show that attentional control during VSTM maintenance influences the probability that a cued item will be recalled. Some of these results can be explained by biasing task-relevant information already encoded in VSTM, which could reduce inter-item competition, and therefore forgetting. The results, however, also show that attention improves performance for items that were otherwise irretrievable, demonstrating that the visual system retains more information than is normally accessible (Astle et al., 2010a; Sligte et al., 2008). By orienting attention to these otherwise inaccessible representations, it is possible to restore the lost information to VSTM.

CHAPTER 5

Fixed Trade-off between the Number and Precision of Items in VSTM

It is well established that increasing the number of items in VSTM decreases the precision with which each item is remembered, at least within capacity limits. This trade-off is relevant to a current debate between how VSTM resources are allocated between items. What has received little investigation, however, is the extent to which the trade-off between the number and precision of resources is under top-down control. Across four experiments, I manipulated the optimal setting of the trade-off required for task performance by changing expectations about the number of to-be-remembered items (Experiments 1-2), the precision required for the judgement (Experiment 3), or a combination of the two (Experiment 4). None of the experiments provided any evidence that the balance between the number and precision of items in VSTM is under top-down control. These null effects cannot be explained by a difficulty in changing the task expectations too rapidly or undermining the utility of the trade-off by biasing the number and precision settings independently (Experiment 4). Possible explanations for these resounding null effects are considered, such as the suppression of contextual information in favour of allocating resources based on the stimuli present at the time of encoding.

5.1 Introduction

Capacity limits in VSTM can be characterised by two features: the number of items and the quality with which they are remembered. Recent evidence suggests that the trade-off between these two features is a hallmark of VSTM. Increasing the number of items represented reduces the precision of each representation (Barton et al., 2009; Bays & Husain, 2008; Palmer, 1990; Zhang & Luck, 2008). This phenomenon has sparked an on-going debate in the literature regarding the flexibility over the allocation of VSTM resources according to the required number versus precision of representations (see Fukuda et al., 2010a).

On one hand, fixed-resolution accounts suggest that VSTM resources are discretely allocated to fixed item “slots” with high precision. Beyond this, no

information about the additional items is maintained, and there is little or no flexibility in the trade-off between quantity and quality of representations (Barton et al., 2009; Rouder et al., 2008; Zhang & Luck, 2008; Zhang & Luck, 2009). To account for the idea that items from smaller arrays are represented with higher precision, an amendment to the strict "fixed slot" account was proposed (see Zhang & Luck, 2008). Here, smaller numbers of items can be represented by multiple slots to improve the resolution of their representation. Alternatively, flexible resource models (e.g. Wilken & Ma, 2004) do not impose an upper item limit, and suggest that VSTM resources can be allocated fully flexibly, according to task demands (Bays et al., 2009; Bays & Husain, 2008).

Neither side of the debate, however, has directly addressed how the quantity-vs.-quality trade-off is resolved and whether it can be adjusted strategically. The flexible models do not describe how the allocation of resources to a certain number of items is decided and the fixed slot accounts do not describe when and how multiple "slots" are devoted to items. More importantly, it remains unknown whether the setting of the trade-off is under flexible control according to current task goals and expectations about the nature of memory representations required for performance.

A large literature shows that prior knowledge of a task goal or context can be used to optimise processing and adjust behaviour accordingly (Miller & Cohen, 2001). Top-down signals originating in prefrontal cortex (PFC) and other control regions can bias which information enters and is retained in the visual system and help determine the "winners" of the perceptual inter-item competition. For example, preparatory attention directed to spatial locations or attributes can facilitate task-

relevant sensory processing by modulating stimulus specific cortex (Hopfinger et al., 2000; Luck et al., 1997; Nobre et al., 2000; Stokes, Thompson, Nobre, & Duncan, 2009).

Similarly, in the VSTM literature, behavioural and neuroimaging experiments have revealed the beneficial effects of attentional orienting in preparing the brain to select or preferentially encode task-relevant information (Rutman et al., 2010; Zanto et al., 2011). The specific mechanisms of how pre-cues facilitate VSTM performance are still under investigation. The results of Chapter 3 provided evidence that orienting anticipatory attention to a sub-set of items could influence the probability of their recall. In this task, however, the task demands were constant and there was no anticipatory information regarding the kind of array that the participant would encounter. There was no systematic manipulation of the expectations of what would form the optimum trade-off between the number and precision of representations.

In order to determine whether the quantity-versus-quality trade-off in VSTM can be set voluntarily, in a series of four experiments, contextual information will be provided to participants regarding either the likely number of items in an upcoming array (Experiments 1 and 2), the precision with which they needed to be recalled (Experiment 3), or a combination of the two (Experiment 4). The contextual cues will indicate the likely demands in a change-detection task in which different degrees of orientation change of a single probe presented after the memory array varied (see Chapters 3-4; Bays & Husain, 2008). Here, the discrimination of small changes require high precision (or high-quality) memory representations, whereas discrimination of large changes could be performed with coarser representations.

This study asks whether it is possible to deliberately represent fewer items in order to have each representation be a higher resolution or choose to represent more items by sacrificing the quality of each representation. Across the four experiments, however, there was a resounding lack of evidence to suggest that the deployment of VSTM resources was under flexible control. Together, the results suggest that the allocation of VSTM resources is either automatically driven by the current stimulus parameters on any particular trial and/or not under contextual top-down control.

5.2 Experiment 1: Trial-by-trial Top down Control over capacity limits in VSTM

The first experiment was designed to examine whether the trade-off between the quality and quantity of items in VSTM can be adjusted flexibly according to the task demands. Prior to the presentation of the memory array in each trial, participants were informed that the number of to-be-remembered items would be comparatively low (2 or 4) or high (4 or 6). If VSTM resource allocation is under flexible control (e.g. Bays & Husain, 2008), participants should be able to optimise the trade-off between quality and quantity to favour more precise representations when set size is expected to be small. For large set sizes, however, the optimal strategy would be to encode more items by trading-off quality for quantity. Accordingly, performance on trials with the common Set Size (4 items) should be more precise when participants anticipate a small set-size compared to a large set-size.

5.2.1 Method

5.2.1.1 Participants

Thirteen participants took part in Experiment 1 (3 female). One was excluded due to low average behavioural performance (less than 55% accuracy). The 12 remaining participants were right handed as assessed by a handedness inventory (Oldfield, 1971), and had normal or corrected-to-normal vision. All participants were members of the University of Oxford, aged between 19 and 32 (*M*=22.3 years, *SD*=1.8). Participants were reimbursed £7 for participation in the experiment. All studies were approved by the Oxford Central University Research Ethics Committee (CUREC).

5.2.1.2 Task

The experiment consisted of a variant of a VSTM precision task used in Chapters 3-4, and based on the task designed by Bays and Husain (2008). The task schematic is presented in Figure 5.1 Panel a. On each trial, participants were presented with a set-size cue for 1000-1200ms, followed by a briefly presented array (200ms) of randomly oriented coloured lines to encode. After a variable delay of 1000-1200ms, memory for a single item was tested at the end of the trial. The memory probe was one of the lines from the memory array, but had rotated about its central axis (Angle of Rotation: ±5°, ±20° or ±45°). Participants judged whether the probe had rotated clockwise or anti-clockwise relative to the original memory item. Feedback was presented for 500ms after response.

There were four trial types, defined by the range of set sizes predicted by the Cue (*low* vs. *high*) and the number of items in the array. On *low set-size* trials, the memory arrays contained either 2 (25% of trials) or 4 items (25% of trials). On *high set-size* trials, arrays contained either 4 (25% of trials) or 6 items (25% of trials). All items within the memory arrays were equally distributed on both sides of the visual field. All trial types were randomised throughout the experiment. This design enabled the comparison of performance on a common condition (4 items) to determine whether the anticipation of the upcoming set size modulated the strategic allocation of VSTM resources.

5.2.1.3 Stimuli

The task was programmed and presented using Presentation software (Neurobehavioral Systems v.13.0, 2009). All stimuli were presented against a black background. Before each trial, the cue was a “2” for *low set-size* trials or “6” for *high set-size* trials (each approximately 0.83° by 0.83°) in grey (RGB: 100, 100, 100), Arial 28pt font. The cue was present throughout the trial, until the offset of the probe. A grey fixation cross (0.32° by 0.32°) was presented in the centre of the screen between each trial. Line stimuli in the memory array were constructed within the task programme on a trial-by-trial basis. Colours were chosen at random (without replacement) from a selection of highly discriminable colours (Red, Blue, Green, Cyan, Magenta, Yellow, Orange or White). Each line subtended approximately 1.43° of visual angle from base to tip, and a minimum distance of 2.49° between each stimulus ensured that there was no overlap, and reduced crowding effects. Participants pressed the right ctrl key for “clockwise” responses

with their right hand and the left ctrl key with their left hand for “anti-clockwise” responses on a standard keyboard. Feedback for response accuracy was provided by replacing the fixation cross with either an “$$” (correct) or an “X” (incorrect) in white, 28pt font (approximately 0.64° by 0.64°).

5.2.1.4 Procedure

Participants performed the computerised task in a quiet, dimly lit room viewing a CRT monitor (60hz refresh rate) at a distance of 90cm. A 16-trial practice block familiarised participants with the task. In total, there were 384 trials presented across four blocks. Participants were encouraged to use the cue to anticipate the likely number of items in the upcoming array. Rest periods were available between blocks.

5.2.1.5 Analysis

The direction of line rotation was not of interest, and data were collapsed across clockwise and anti-clockwise rotations, leaving 32 trials per condition. The resulting design manipulated three within-participant factors: Cue Type (*low set size* vs. *high set size*), Set Size (2 vs. 4, or 4 vs. 6 depending on the Cue Type condition), and Rotation Angle (5°, 20°, 45°). The most relevant analysis compared accuracy performance on the common set size (4 items) according to Cue Type and Rotation Angle using a repeated-measures ANOVA. For completeness, two additional 2x3 repeated-measures ANOVA also assessed performance for each Set Size and Angle of Rotation in the *low* and *high set-size* trials separately. Greenhouse-Geisser corrected p-values were reported when sphericity could not

be assumed (as assessed by Mauchly's test). Post-hoc pairwise comparisons of means were used to interpret results of interactions when necessary, and were Bonferroni corrected for multiple comparisons.

5.2.2 Results and Discussion

As expected, performance was better in trials with *low* compared to *high set sizes.* However, there was no difference in performance in the common four item condition between the two Cue Type conditions. Full details of descriptive statistics for all experiments are given in Appendix B.

The comparison of the performance on the common, 4-item condition, showed no significant main effect of Cue Type [$F(1,11) = 0.004$, $p=0.95$; Figure 5.1 Panel b] and no interaction between Cue Type and Angle of Rotation ($p=0.14$). As expected, there was a significant main effect of Angle of Rotation [$F(1,11) = 30.20$, $p<0.001$], owing to lower performance for 5° compared to 20° ($p<0.001$) and 45° angles of rotation ($p<0.001$). Performance for 20° and 45° rotations was equivalent ($p=0.32$).

Within each Cue Type, analyses revealed the expected decrements of performance as set size increased and as the judgement required greater precision. Main effects of Set Size occurred in both cases [*low set size*: $F(1,11) = 100.37$, $p<0.001$; *high* set size: $F(1,11) = 5.25$, $p=0.043$]. Main effects of Angle Rotation were also significant [*low* set size: [$F(2,22) = 68.10$, $p<0.001$; *high set size*: $F(2,22) = 21.80$, $p<0.001$]. Performance was significantly lower for 5° compared to 20° ($ps \leq 0.001$), and 45° angles of rotation ($ps \leq 0.001$), but was similar for 20° and 45°

rotations (*ps*≥0.29). Set size and Angle of Rotation did not interact for either Cue Type (*ps*≥0.20).

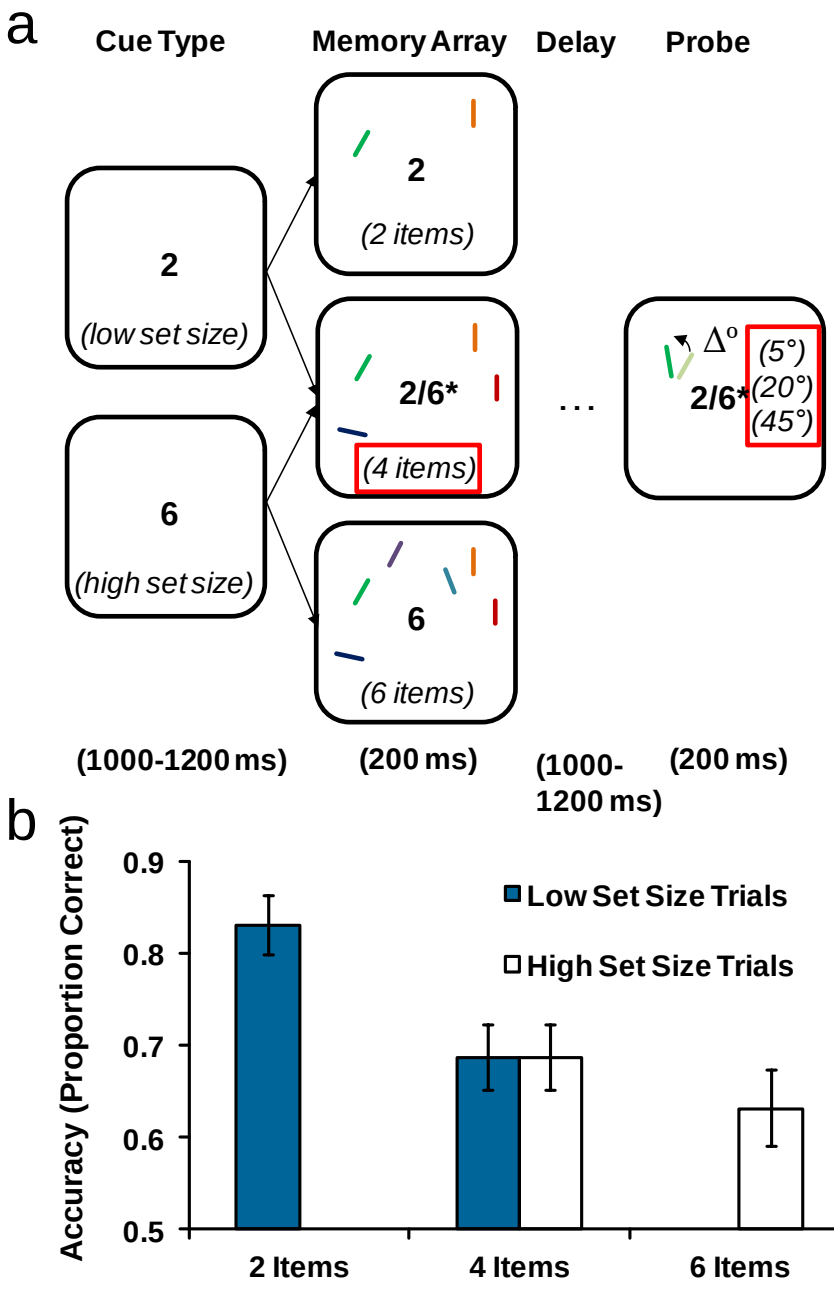


Figure 5.1: Task schematic and main results for Experiment 1. [a] A cue of either "6" or "2" was presented for 1000-1200ms to indicate the likely set size of the upcoming array. The memory array (presented for 200ms) consisted of either 2 or 4 oriented lines in the *low set-size* condition, or 4 or 6 lines in the *high set-size*

condition. After a variable delay (1000-1200ms), a single item was re-presented for 200ms, but rotated either 5°, 20° or 45° in a clockwise or anti-clockwise direction. Participants judged the direction of orientation change. Feedback was then presented for 500ms. Red boxes indicate common comparison conditions between the Cue Types: Angles of rotation (5°, 20° and 45°) and a Set Size of 4 items. *For this common condition the number at fixation corresponded to the Cue Type trial. [b] The proportion of correct orientation change discriminations is shown as a function of the Cue Type condition and Set Size. Error bars represent ±1 *SEM*.

If participants were able to use the cue information to optimise VSTM resource allocation, the precision of VSTM should vary as a function of the number of memory items that are likely to be presented. The critical comparison between common 4-item trials, however, showed no difference between the two cued task contexts. From these results, it would appear that mechanisms for top-down control were unable to optimise the distribution of VSTM resources in anticipation of the array.

There are two possible reasons for this null effect. Firstly, although the cue was predictive of a high or low set size, 50% of the time, the cue was followed by the common condition (i.e., a set-size 4 trial). This could have reduced the efficacy of the cue and thus reduced the effects of contextual cueing. The second reason may be because the control settings are not flexible enough to accommodate the trial-by-trial changes in set-size probability. Despite the strength of the cues, trial-by-trial fluctuations may be too rapid to allow a volitional change in VSTM resource allocation. These results, however, do not mean that top-down factors may not

operate on setting the quantity-quality trade-off according to the ongoing task context.

To rule out these two potential explanations, Experiment 2 tested whether participants could optimise performance when quantity probability is blocked, rather than manipulated trial-by-trial. In addition, the proportion of common set size was reduced to increase the validity of the cued task expectations.

5.3 Experiment 2: Allocation of Resources Blocked by Set Size

Experiment 2 was designed to explore whether the lack of effect in Experiment 1 was due to an inability to update the required allocation of resources on a trial-by-trial basis. In this design, participants were informed to expect either *low* or *high set size* trials at the beginning of each block. In addition, the proportional weighting of the 2- and 6-item trials in the *low* and *high set-size* blocks respectively was changed from 50% to 66.7%. Finally, increasing the trial numbers also enabled psychometric modelling of the precision and probability of recall of representations across the two Cue Types.

5.3.1 Method

5.3.1.1 Participants

Participants for Experiment 2 (*N*=20, 9 female) were aged between 20 and 34 (*M*=26.35, *SD*=4.17). Participants were remunerated £10 for their participation.

5.3.1.2 Task

The conditions of the task are illustrated in Figure 5.2. The design, task, procedure and analysis were very similar to those in Experiment 1. There were two important differences. Set-size probability was cued at the beginning of each block rather than on each trial. To increase the difference between blocks, the relative proportions of the items also changed from Experiment 1. In the *low set-size* blocks (cued as “Easy Block”), the memory arrays contained either 2 (66.67% of trials) or 4 items (33.33% of trials). The *high set-size* blocks (cued as “Difficult Block”) contained either 4 (33.33% of trials) or 6 items (66.67% of trials) in the memory array. All items within the memory arrays were equally distributed on both sides of the visual field and presented for 200ms. As in Experiment 1, this design enabled the comparison of performance on a common condition (4 items) to determine whether the contextual effects of having relatively small or large numbers of items to encode modulated the strategic allocation of VSTM resources.

5.3.1.3 Stimuli

Memory arrays consisted of oriented coloured arrows rather than lines. Stimuli were presented against a light grey background (RGB: 192, 192, 192). Before each block, the text “Easy Block” (5.09° by 0.83°) or “Difficult Block” (6.37° by 0.83°) was presented in black, Arial 34pt font as a contextual cue about the likely number of items in each trial in the upcoming block. A black fixation cross (0.32° by 0.32°) was presented throughout each trial, offsetting only when feedback was given. The colours of arrows were chosen at random (without replacement) from a selection of highly discriminable colours (Red, Blue, Aqua, Magenta, Orange,

Purple, Black or White). The spacing and size of the stimuli were approximately the same as Experiment 1. Responses were made by turning the lever of a custom-built response device according to the direction of orientation change. Feedback for response accuracy was provided by replacing the fixation cross with either an “O” (correct) or an “X” (incorrect) (approximately 0.64° by 0.64°).

5.3.1.4 Procedure

In total, there were 1080 trials presented across 5 *low* and 5 *high set size* interleaved blocks, the order of which was counterbalanced across participants. Angles of Rotation and relevant Set Sizes were randomised within each block. Eye-movements were monitored to ensure participants maintained fixation. Participants were instructed that the cue information presented at the beginning of each block provided information about the number of items per trial in the upcoming block.

5.3.1.5 Analysis

As in Experiment 1, the direction of arrow rotation was not of interest so data were collapsed across clockwise and anti-clockwise rotations, leaving 90 trials per condition. The resulting design manipulated three within-participant factors of Cue Type (*low* vs. *high set size*), Set Size (2, 4 or 6 depending on the Cue Type), and Rotation Angle (5°, 20°, 45°). Of critical interest for this experiment was the comparison of accuracy on the common Set Size (4 items) according to Cue Type and Rotation Angle using a repeated-measures ANOVA.

For completeness, performance was compared for each Set Size and Angle of Rotation for each Cue Type separately using two 2x3 repeated measures

ANOVA. Also, the proportion of trials for the two Set Size conditions was not equivalent within each Cue Type condition. Data were, therefore, randomly sub-sampled to equate trial numbers in the *low* condition and the 6 item trials in the *high* condition with the respective 4 item conditions.

The increase in trial numbers compared to Experiment 1, also enabled a more sophisticated modelling of the behavioural data to estimate two psychometric parameters: the slope and asymptote of the psychometric function. Specifically, I wanted to compare estimates of the probability of recall (using estimates of asymptote) and the precision of representations (using estimates of slope) for the common 4-item trials in the two Cue Type conditions. Data were modelled using a cumulative normal distribution by a Matlab toolbox Palamedes (Prins & Kingdom, 2009) for each participant. For modelling procedures and further details see Section 2.3. Differences in slope and asymptote estimates were compared between the *low* and *high set-size* conditions using paired sample t-tests.

5.3.2 Results and Discussion

Analysis of performance on the common, 4-item condition revealed no significant main effect of Cue Type [$F(1,19) = 0.49$, $p=0.50$] and no significant interaction between Cue Type and Angle of Rotation [$F(2,38) = 1.61$, $p=0.21$]. As expected, there was a significant main effect of Angle of Rotation [$F(1,19) = 51.82$, $p<0.001$] and follow-up analysis revealed that, for every comparison, accuracy was higher for larger angles of rotation ($ps<0.009$).

Comparisons of the estimates of the modelling parameters also failed to reveal an effect of Cue Type on performance at set-size 4. There was no significant difference between slope-parameter estimates [*low set size*: M_{slope}=0.13, SE_{slope}=0.07; *high set size*: M_{slope}=0.24, SE_{slope}=0.10; $t(19)=1.46$, $p=0.16$, 2 tailed] for the Cue Type conditions. Similarly, there was no significant difference in estimated asymptotes between the *low* ($M_{asymptote}$=0.20, $SE_{asymptote}$=0.03) and *high set size* ($M_{asymptote}$=0.22, $SE_{asymptote}$=0.03) conditions [$t(19)=0.51$, $p=0.61$, 2 tailed].

As expected, within each Cue Type, analyses revealed lower performance for higher Set Sizes and smaller Angles of Rotation. Main effects of Set Size occurred in both cases [*low set size:* $F(1,19) = 301.95$, $p<0.001$; *high set size:* $F(1,19) = 51.73$, $p<0.001$]. Main effects of Angle of Rotation were also significant [*low set size:* $F(2,38) = 146.69$, $p<0.001$; *high set size:* $F(2,38) = 24.70$, $p<0.001$]. Performance was consistently significantly higher for larger angles of rotation (ps<0.049). In each Cue Type, the interaction between Set Size and Angle of Rotation was also significant [*low set size:* $F(2,38) = 4.65$, $p=0.016$; $F(2,38) = 3.51$, $p=0.04$]. For *low set size* blocks, accuracy was significantly higher for 2 compared to 4 item trials for each Angle of Rotation (ps<0.001). For *high set size* blocks, the differences in performance between the two Set Sizes were significant at both 45° ($p<0.001$) and 20° ($p=0.006$) but not at 5° ($p=0.36$).

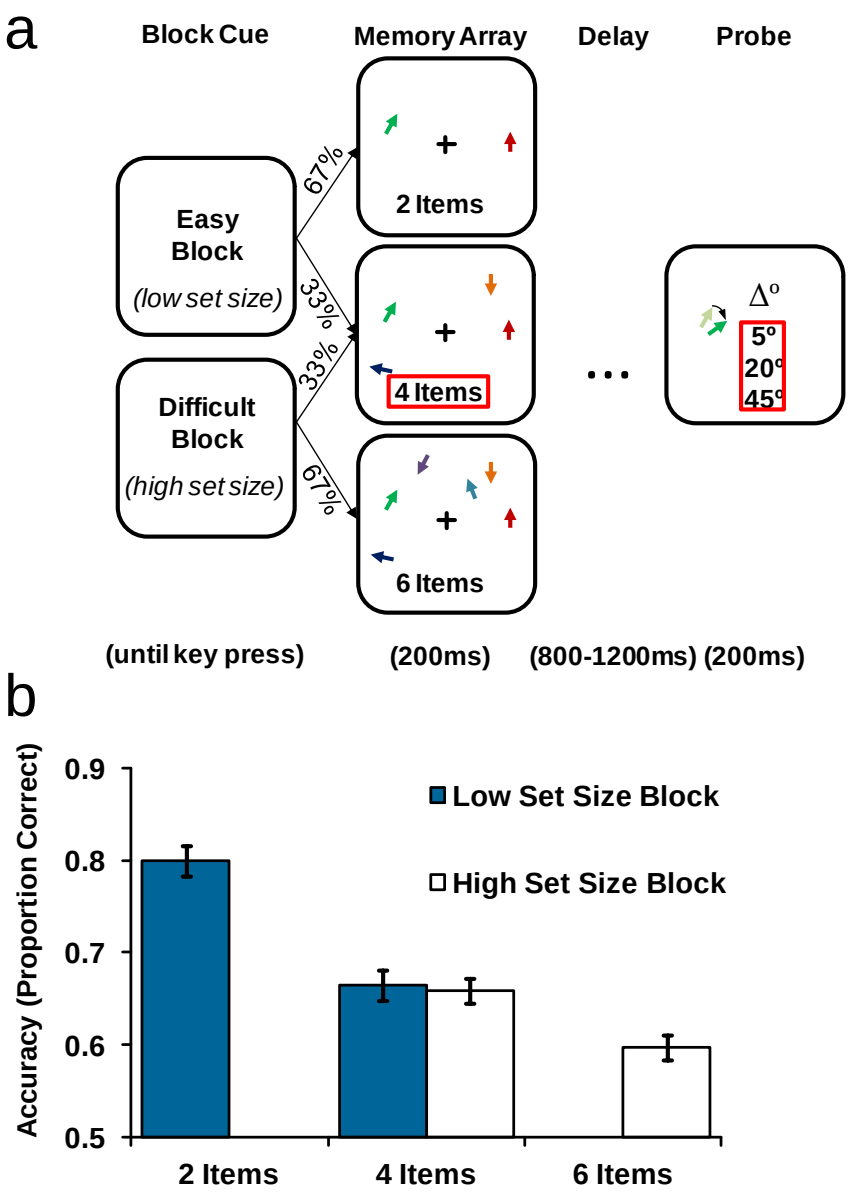


Figure 5.2: Task schematic and main results for Experiment 2. [a] In *low set-size* blocks participants attempted to encode 2 or 4 items (top) or 4 or 6 items in the *high set size* blocks (bottom). Red boxes indicate common comparison conditions between the Cue Type conditions: Angles of rotation (5°, 20° and 45°) and a Set Size of 4 items. [b] The proportion of correct orientation-change discriminations is shown as a function of the Cue Type condition and Set Size. Data shown are the average across all trials. Error bars represent ±1 s.e.m.

Across two experiments, there was a distinct lack of evidence that foreknowledge of the likely number of memory items can be used to optimise the allocation of memory resources. This was the case when the context was set by trial-by-trial cueing, or was blocked. The decrease in the proportion of common trials across the two cue conditions to emphasise the differences between them, furthermore, did not appear to facilitate the use of the contextual information. In Experiment 2 I was able to estimate the psychometric parameters thought to reflect the precision and probability of recall. Again, there was no evidence to suggest that expectation of the upcoming size of the array could affect the allocation of resources.

An alternative explanation may be that the trade-off could be established at encoding, upon presentation of the memory array. This is possible because the cue type is based on a property (set size) which is intrinsic to the memory array, meaning that participants can wait until the array is presented to allocate resources. This may be especially true since an albeit small, but sizeable proportion of the time, the cue is followed by the common condition which undermines its utility. In this case, therefore, it may be advantageous to simply wait until the presentation of the memory array to allocate resources. As such, the physical number stimuli present in the memory array may override the contextual information given by the cue.

To eliminate this potential explanation, the expectation of the necessary precision of representations required to complete the task was manipulated in Experiment 3. By basing the contextual information on the required precision, rather

than the set size, there is no intrinsic perceptual aspect of the memory array that can automatically shape the trade-off and override the block context. In Experiments 1 and 2, the set size was immediately apparent when the memory array was presented, so participants could allocate resources to encode items according to the number of stimuli present. By cueing the required precision, however, one should expect a greater reliance on the cued task context because the task demands would not become apparent until the presentation of the probe. Participants should then use the cued context rather than the stimuli present to allocate resources and optimise encoding.

5.4 Experiment 3: Allocation of Resources Blocked by Precision

Experiment 3 followed the same structure as Experiment 2. However, instead of manipulating set-size probability, the likely precision required to discriminate between the rotational change: *low precision* (45° or 20°) or *high precision* (20° or 5°) was manipulated. The question is whether expectations of different levels of precision required to perform the task are able to bias the balance between the number and precision of items in VSTM in the absence of any possible perceptual effects. This design could be more effective in motivating optimal trade-off during encoding because, unlike Set Size, the required precision will only be known upon presentation of the probe. In Experiments 1 and 2, the information about set size was no longer useful once the memory array had been presented. Even if there was an anticipation, this could be reset by the presentations of the array and participants could use the physical stimuli present to determine the trade-off

between the number and precision of representations. Here, however, cued context regarding the precision required will be useful throughout the entire duration of the trial. If participants can optimise resource allocation, it is expected that performance in the common condition (20°) will be more accurate in the *high precision* blocks relative to *low precision* blocks, owing to the higher overall demand for precise representations in those blocks.

5.4.1 Method

5.4.1.1 Participants

Twenty three volunteers with normal or corrected-to-normal vision were recruited for the study. Three participants were excluded due to poor behavioural performance (overall average accuracy less than 55%). The remaining 20 participants, aged between 19 and 34 (*M*=25.85, *SD*=4.74, 11 female) were included in the analysis. All participants except one were right handed as assessed by a handedness inventory (Oldfield, 1971).

5.4.1.2 Task and Stimuli

The Cue Type conditions are illustrated in Figure 5.3, panel a. The task design and stimuli parameters were the same as Experiment 2, with the exception that here the expected magnitude of rotation change is manipulated, rather than the number of to-be-remembered items. In the *low precision* blocks, the probe was rotated by 45° (66.67% of trials) or 20° (33.33% of trials). In the *high precision* blocks, the probe rotated 20° (33.33% of trials) or 5° (66.67% of trials). This design

enabled us to compare performance on a common condition (20° Angle of Rotation) to determine whether the prior knowledge of the likely precision required for the probe modulates the strategic allocation of VSTM resources. After collapsing over clockwise and anti-clockwise rotations, the resulting design manipulated three within-participant factors of block Precision (*low* vs. *high*), Rotation Angle (5° vs 20°, or 20° vs 45° depending on the block) and Set Size (2, 4 or 6 items).

5.4.1.3 Procedure and Analysis

Procedures and analyses were the same as Experiment 2, except participants were instructed that the cue information presented at the beginning of each block predicts the likely degree of angular change of the probe stimulus. The critical comparison was based on performance on the common 20° condition. Psychometric modelling was not possible for this experiment, because such modelling requires a range of angular changes (rather than a range of set sizes) within the common condition.

5.4.2 Results and Discussion

In a similar way to the previous experiments, performance on the common 20° change condition, did not differ as a function of Precision block [$F(1,19) = 0.14$, $p=0.72$] and the interaction between Precision block and Set Size was not significant [$F(2,38) = 0.52$, $p=0.60$]. As expected, the main effect of Set Size [$F(2,38) = 231.05$, $p<0.001$] was significant. Accuracy was significantly higher for lower Set Sizes at every comparison (ps<0.001).

Within each Precision Block condition, analyses revealed the expected lower accuracy for higher Set Sizes and smaller Angles of Rotation. Main effects of Angle of Rotation were significant in both cases [*low precision*: $F(1,19) = 5.01$, $p=0.037$; *high precision*: $F(1,19) = 120.43$, $p<0.001$]. Main effects of Set Size were also significant [*low precision:* $F(2,38) = 169.55$, $p<0.001$; *high precision*: $F(2,38) = 104.69$, $p<0.001$]. For both Precision types, at every comparison, lower set sizes were associated with higher performance ($ps \leq 0.001$). The interaction between Angle of Rotation and Set Size was also significant in both cases [*low precision:* $F(2,38) = 3.46$, $p=0.042$; *high precision*: $F(2,38) = 21.71$, $p<0.001$]. For the *low precision* blocks, the difference in accuracy between the two Angles of Rotation was only significant for the 2 item trials [$p<0.001$; other comparisons: $ps>0.17$]. In contrast, the differences in accuracy between the Angles of Rotation were significant for each Set Size ($ps<0.02$) for the *high precision* blocks.

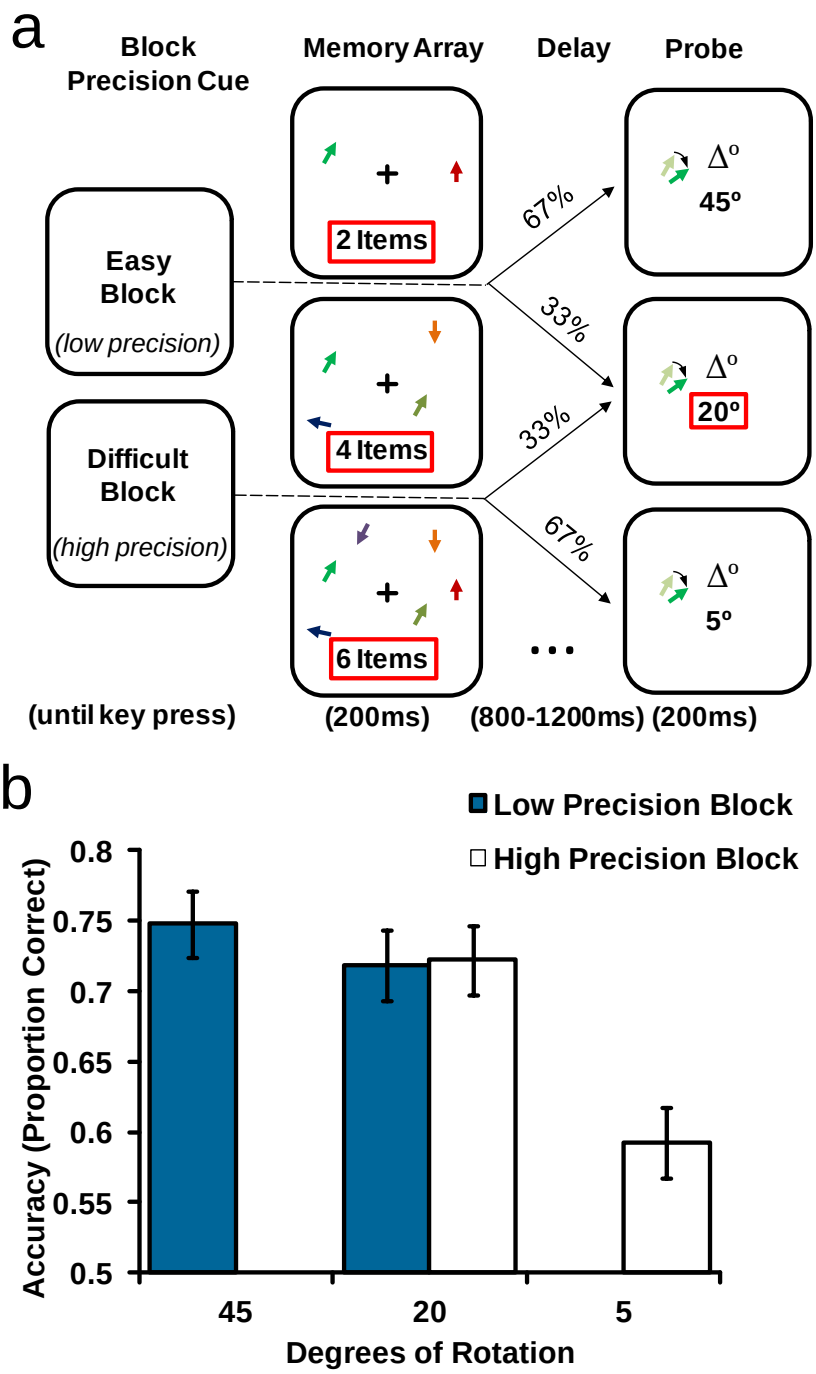


Figure 5.3: Task schematic and main results for Experiment 3. [a] Schematic of the Precision manipulation: In the *low precision* condition the Angle of Rotation of the probe was 20° or 45° (top). In the *high precision* condition, the Angle of Rotation of the probe was either 5° or 20° (bottom). Red boxes indicate common comparison

conditions between the Precision conditions: Set Size (2, 4 and 6 items) and 20° Angle of Rotation. [b] The proportion of correct orientation change discriminations is shown as a function of Precision and Angle of Rotation. Data shown are the average across all trials. Error bars represent ±1 *SEM*.

Once again, there was no evidence that participants could use prior knowledge to influence the balance between the quality relative to the quantity of information in VSTM. Specifically, comparing accuracy in the common 20° Angle of Rotation condition across the two types of Precision Blocks suggested that setting a context by the degree of precision required does not influence the way that resources are allocated. This was even the case when the expectations were manipulated on a stimulus dimension which could not be determined at encoding. Participants could not reset their expectations when the memory array was presented because the task expectations were regarding the precision, which would only be apparent upon presentation of the probe. Despite this, it appears the contextual information still did not influence performance.

A possible reason for the null effect across all three experiments thus far, may be because the expected quantity or quality of the upcoming trial/blocks was manipulated separately. Despite the cued context, participants always had to be prepared for trials requiring high load and difficult judgement requiring high precision which may have undermined the utility of the trade-off. In the next experiment, these characteristics will be combined to maximise the possibility that participants could optimise the trade-off. In Experiment 4, if a high precision judgement is required, then only small set sizes will be presented. Alternatively, if

large arrays are presented then only coarse discriminations will be required. This should encourage participants to represent small arrays with high precision and large arrays with low precision and should be the ultimate test of the flexibility of the trade-off between the precision and number of representations.

5.5 Experiment 4: Trade-off Between Precision and Capacity Demands

Experiment 4 was conducted to determine whether participants could optimally adjust their allocation of VSTM resources when the task context explicitly encourages a combined different trade-off between quality and quantity settings. Previously, the number and precision requirements were biased separately meaning that participants may have had to represent large arrays with high precision which undermined the utility of the trade-off. The combination of the two characteristics maximises the potential advantage of preparatory allocation of memory resources to quality or quantity.

To this end, one task context (*precision*) encouraged encoding and maintenance of a low number of items with high precision. Set sizes in the memory array were lower (1, 2 or 4 items) but the precision judgements were more difficult (Angles of Rotation: 5°, 15° or 25°). The other emphasised the number of representations (*load*) by presenting arrays with large set sizes but required comparatively more coarse representations. In the *load* blocks the Set Sizes were high (4, 8 or 12 items), but the precision judgements were easier (25°, 35° or 45°). In this experiment, the common condition was, therefore, a combination of a particular load (Set Size: 4 Items) and precision (Angle of Rotation: 25°). If

participants are able to flexibly set the trade-off, the balance between the precision and number of items, then there should be a difference in performance in this experiment. Specifically, it was expected that performance on the common condition would be better in the *precision* condition, if the context can be used to represent items with comparatively higher precision depending on expected set size.

5.5.1 Method

5.5.1.1 Participants

Participants for Experiment 4 (*N*=20, 14 female) were aged between 18 and 34 (*M*=23.20, *SD*=4.67). All participants had normal or corrected-to-normal vision and were right handed as assessed by a handedness inventory (Oldfield, 1971). All participants gave informed written consent and were remunerated £10 for their participation.

5.5.1.2 Task and Stimuli

The task design and stimuli parameters were similar to those in Experiments 2 and 3. The defining difference was that here both the expected magnitude of rotation change and the number of items in the array was manipulated (see Figure 5.4 panel a). Before each block, the text “Be Prepared for: Large Changes BUT Large Arrays” (Cue Type: *precision*) or “Be Prepared for: Small Arrays BUT Small Changes” (Cue Type: *load*) was presented in black, Arial 34pt font as a contextual cue about the likely precision and number of items in number of items in each trial

in the upcoming block. In the *precision* blocks, there were one, two or four items in the array, and participants were required to make angular change judgements when the probe had rotated by 5°, 15° or 25°. In contrast, in the *load* blocks, the arrays contained 4, 8 or 12 items, and the probe rotated by 25°, 35° or 45° compared to the corresponding item in the memory array. Three levels of each Angle of Rotation and Set Size were used to maximise the subjective differences between the conditions in an attempt to maximise the utility of the contextual information.

This design enabled the comparison of performance on a common condition with four items and a 25° Angle of Rotation to determine whether the prior knowledge of the combination of the number of items and the precision required could modulate the allocation of VSTM resources.

5.5.1.3 Procedure and Analysis

Participants were instructed that the cue information presented at the beginning of each block would predict the likely number of items in the array and the degree angular change of the probe stimulus. Similar to Experiment 3, accuracy was the only dependent variable of interest. The precision and probability of recall could not be modelled because the common condition only contained one Rotation Angle so performance over a range of precision conditions could not be compared. After collapsing over clockwise and anti-clockwise rotations, the resulting design manipulated three within-participant factors of Block Type (*precision* vs. *load*), Rotation Angle (5°, 15°, vs. 25°, or 25°, 35°, vs. 45° depending on the block) and Set Size (1, 2, vs. 4 or 4, 8, vs. 12 items depending on the block). The critical comparison was a paired samples t-test performed on performance for the common

4 item, 25° Angle of Rotation condition as a function of Block Type. For completeness, the effects of Rotation Angle and Set Size were analysed using a repeated measures *ANOVA* for the *precision* and *load* blocks separately.

5.5.2 Results and Discussion

Critically, the comparison for the 4 item, 25° Angle of Rotation condition (common across the two types of block), showed no significant effect of Block Type [$t(19) = 0.63$, $p=0.53$; see Figure 5.4 panel b].

Analysis of accuracy in both the Cue Type blocks revealed the expected decrease in performance for higher Set Sizes [*precision:* $F(2,38) = 112.27$, $p<0.001$; *load:* $F(2,38) = 69.06$, $p<0.001$] for each level of comparison ($ps \leq 0.001$). The Angle of Rotation was only significant for the *precision* block [*precision*: $F(2,38) = 125.63$, $p<0.001$; *load*: $F(2,38) = 1.54$, $p=0.23$] with significantly higher performance for larger angles at every comparison ($ps<0.03$). The interaction between Set Size and Angle of Rotation was also only significant for the *precision* block [*precision:* $F(4,76) = 3.93$, $p=0.006$; *load:* $F(4,76) = 0.20$, $p=0.94$]. In the *precision* block, the differences in accuracy between the Set Sizes were significant for each Angle of Rotation condition [low set size>high set size; all $ps<0.024$].

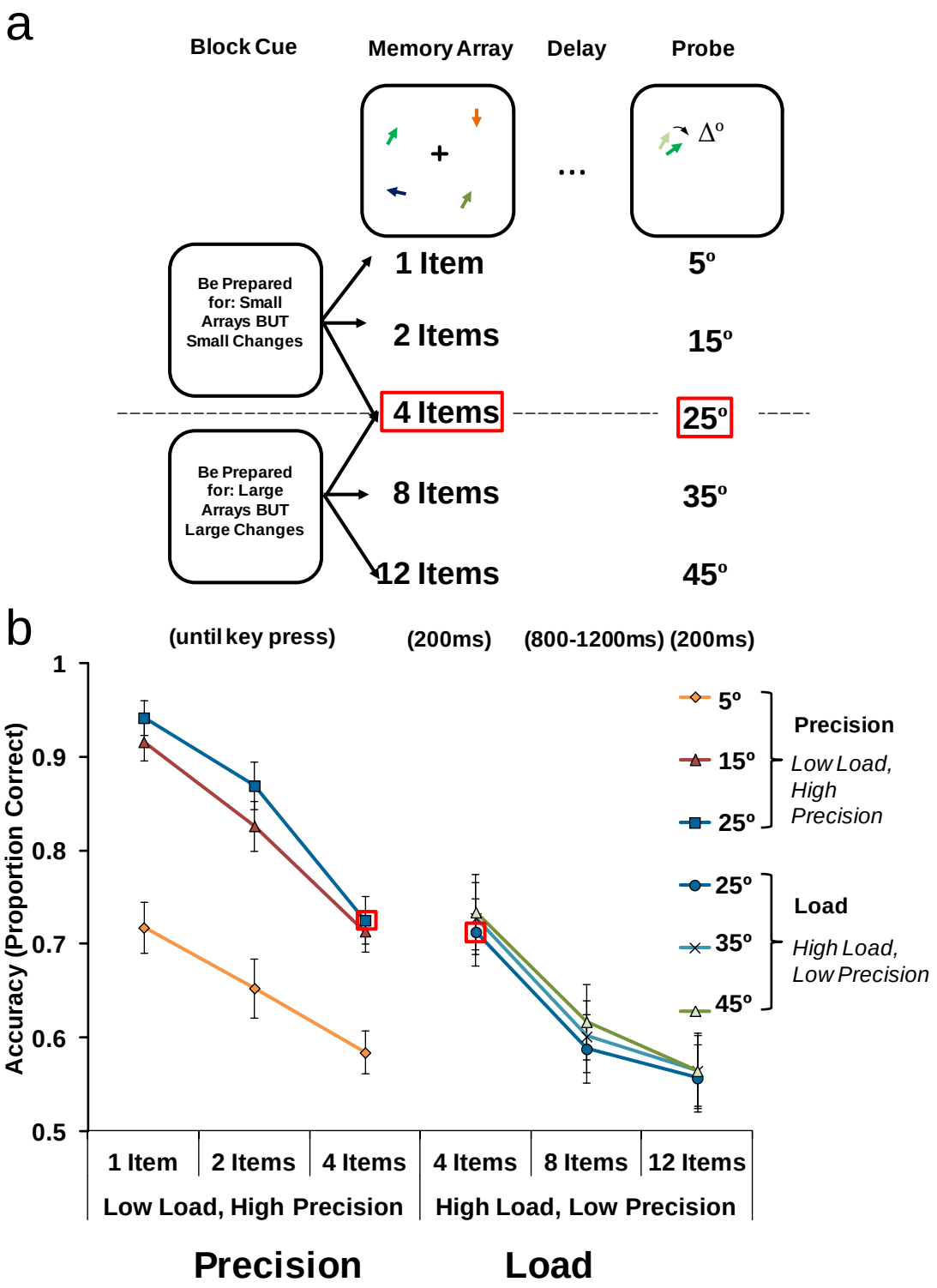


Figure 5.4: Task schematic and main results for Experiment 4. [a] Schematic of the task manipulation. In the low load, high precision condition (*precision*) condition (top row), participants could expect 1, 2 or 4 items, and a probe rotated by either 5°, 15°

or 25°. In the high load, low precision condition (*load*) condition, participants expected 4, 8 or 12 items, and a final probe rotated by either 25°, 35° or 45°. [b] The proportion of correct orientation change discriminations as a function of the Block Type *precision* is shown on the left, and *load* on the right. Data points represent accuracy as a function of Set Size (1, 2, vs. 4, or 4, 8 vs. 12 items) and the Angle of Rotation (5°, 15° vs 25°, or 25°, 35° vs 45°). Red boxes indicate common comparison conditions between the two conditions: 4 items and a 25° Angle of Rotation. Error bars represent ±1 s.e.m.

As in Experiments 1-3, there was no difference in VSTM performance between the two trade-off contexts. Specifically, there was no difference in performance between the critical common condition of 4 items and a 25° Angle of Rotation across the two block types. This null result, in combination with the results of Experiments 1-3, suggests that participants were unable to trade-off flexibly the quantity of items and the quality with which they are represented. This final experiment shows that even directly encouraging the trade-off by setting the task context to require small arrays to be represented with high precision or large arrays to be represented with low precision could not affect performance. This eliminates the possibility that the null results thus far were due the trade-off being undermined by encouraging one setting (e.g. high precision) without reducing the requirements to code the other (e.g. high set size). For example, in Experiments 1 and 2, it may not have been optimal to represent a large number of items with coarse precision because some trials still required fine discriminations. Likewise, in Experiment 3, some high precision trials still required participants to encode large numbers of

items. The utility of the trade-off was undermined in these cases. In this experiment, however, such situations did not arise; participants were required to either represent large arrays with low precision or small arrays with low precision; the trade-off was optimal in this experiment. It can be surmised, therefore, that the data repeatedly suggest that top-down mechanisms are not able to control the allocation of VSTM resources.

5.6 General Discussion

Across four experiments, there is no evidence that participants can control the trade-off between the precision and number of items in VSTM. The experimental context was manipulated according to the upcoming task requirements, defined by either the number of to-be-remembered items (Experiments 1 and 2), the precision required (Experiment 3), or a combination of the two (Experiment 4). There was a resounding lack of evidence that contextual information can affect the trade-off of VSTM resources. These consistent null effects provide convincing evidence that top-down control mechanisms cannot bias resource allocation for VSTM.

In addition to the lack of significant effect main effect of Cue-Type across Experiments 1-4, it is also important to consider the interaction terms. Specifically, it is worth considering how (if at all) the trade-off occurs between the different Angles of Rotation (Experiments 1 and 2) or different Set Sizes (Experiment 3) for the common conditions across the Cue Types. This is important to see whether differences in strategic allocation of resources favours precision or number of items changes in the different levels of condition which is common to the two Cue-Types.

For Experiments 1-3, this critical interaction term was not significant *(p*=0.14, *p*=0.21, *p*=0.60 respectively), which suggests that the patterns of resource allocation were similar across the different levels of angular change (Experiments 1 and 2) and Set Size (Experiment 3) for the common condition between the two cue-types. Furthermore, results from Experiments 1 and 2 suggest that, if anything, the pattern of behaviour is in the opposite direction to what would be predicted. Although one should be cautious about interpreting a non-significant interaction, performance was slightly higher on the common set size condition for small rotations (5°) for the high set size Cue Type condition compared to the equivalent low set size conditions. It may be the case that in the high set size Cue Type condition, participants are extra vigilant to prepare for the large upcoming array and, therefore, encode items more carefully (hence the higher performance for 5° rotations). This benefit is lost for large rotations, perhaps due to a violation of expectations if participants are deliberately coding precisely. In addition, the benefit for the high set size condition is lost for large set size trials, possibly because there are insufficient resources to deliberately encode items precisely. Nonetheless, the lack of interaction between Cue Type and Angle of Rotation (Experiments 1 and 2) and Set Size (Experiment 3) only strengthens the argument that participants did not use the contextual information to influence the trade-off between precision and number of representations.

One possible reason to account for the lack of differences in the common condition across easy and difficult trials in Experiment 1 was the inability to switch the strategic allocation of VSTM resources on a trial-by-trial basis. However, results from Experiments 2-4 suggest that any limitations in the ability to rapidly change set

size expectations trial-by-trial were not sufficient to explain the null results in Experiment 1.

Despite the similarity of the results and the task structure of Experiments 1-2, and 3, there is a fundamental asymmetry in the manipulation. When difficulty was defined by the set size, regardless of the block type the actual set size is immediately apparent at encoding and can reset any prior expectations. If there is no advantage in preparing the mnemonic mechanisms for the expected encoding demands, then resource allocation can simply wait until the memory array is presented. At this point, there is no difference between the contexts: VSTM resources can be deployed optimally for that trial. When the task expectations are defined by the required precision, however, an explanation is not so straightforward. On a trial-by-trial basis, the ultimate precision required for the task cannot be ascertained from the memory array and is only apparent upon presentation of the probe. One would expect a greater reliance on contextual effects to optimise VSTM resource allocation. Surprisingly, this was not the case.

Potentially, the results in Experiments 1-3 could be attributed to the task design undermining the utility of the trade-off by emphasising the importance of the number or resolution separately. In these experiments, the trade-off was encouraged in one setting (e.g. high precision) without reducing the requirements to code the other (e.g. a high set size). For example, despite prior knowledge of a high set size, in some circumstances, participants may have still been required to make fine discriminations. As such, it may not have been advantageous to rely on the cued context. From Experiment 4, however, it is clear that this is not the case because here the task only required situations in which the trade-off was optimal:

either high resolution for a small array of items, or low resolution representations of relatively large arrays were required. If the trade-off between capacity and resolution in VSTM was under top-down control, one should expect to see evidence of it in this experiment.

One potential drawback of the design of Experiment 4 is the inability to differentiate between two strategies participants may use to allocate resources. With the current design, performance on the common conditions would be the same if participants selected a certain proportion of items to represent with near perfect precision (for example, three out of four items) or coded all items with sufficient precision to make correct discriminations on 3 out of four trials[17]. Future experiments should address this particular issue by including at least two common conditions. For example, if a common set size is used between two Cue Type conditions over a range of angles of rotation, rather than just one, it may give greater insight into strategic differences in the trade-off between the number of items and the precision with which they are remembered (see Table 5.1). The proposed design includes five Angle of Rotation conditions and three Set Sizes, and every combination of each condition is included in both Cue Type conditions. The difference between Cue Types is the relative weighting of trial numbers so there is a greater proportion of low set size, small angle of rotation trials in “Favour Precision” trials compared to the relatively large proportion of large rotation angle, large set size trials in the “Favour Set Size” Cue Type condition.

[17] Thank you to my *viva vocce* examiner Dr. Nick Yeung for this point.

Table 5.1: Proposed proportion of trial numbers for future trade-off experiment. Shading indicates the common trials between the two Cue Type conditions (*favour precision* and *favour set size*).

	Set Size			
Cue Type Block	2 Items (Proportion of Trials %)	4 Items (Proportion of Trials %)	6 Items (Proportion of Trials %)	
Favour Precision				
5° Rotations	6	3	2	
15° Rotations	6	3	2	
25° Rotations	5	3	2	
35° Rotations	5	3	1	
45° Rotations	5	3	1	
			Total %	50
Favour Set Size				
5° Rotations	1	3	5	
15° Rotations	1	3	5	
25° Rotations	2	3	5	
35° Rotations	2	3	6	
45° Rotations	2	3	6	
			Total %	50

Another possibility to explain the inability to trade-off the quality and number of items is the notion that these two characteristics of VSTM are separate and do not share resources. There is both behavioural (Awh et al., 2007), and neural (Xu & Chun, 2006, 2009) evidence to suggest that the number and content (or quality) of representations are dissociable and operate independently. Research based on individual differences suggests that precision and number of representations are best explained by orthogonal factors (Fukuda et al., 2010b). The two are also affected differently by expertise in perceptual judgements (Scolari et al., 2008) and by psychiatric disorders (Gold et al., 2010). If, indeed, number and precision are separate and based on separate resource pools, then one would not expect any

evidence of a trade-off. Such a possibility, however, would need to be reconciled with the evidence to suggest that resolution decreases as the number of items increase (e.g. Barton et al., 2009; Bays & Husain, 2008). It might be the case that the limitation in performance is the ability to integrate the two characteristics into coherent objects, rather than in an intrinsic limitation in the quality or number of resolutions themselves. Future research could aim to dissociate these abilities using transcranial magnetic stimulation (TMS) to differentially affect the precision or the number of representations in VSTM.

In addition to questioning the flexibility of top-down control, the implications of the current results can also give some insight into the way VSTM resources are distributed. According to the flexible resource models, resources should be allocated flexibly according to task demands (Bays et al., 2009; Bays & Husain, 2008). Although there is clearly a trade-off between the number of to-be-remembered items and the relative precision with which they are recalled, the resources should be optimally divided between items currently available on that trial. In this way, the results of the current experiment are in keeping with this model. However, the fixed-resolution account would also predict that the precision should remain constant, at least within capacity (Barton et al., 2009; Rouder et al., 2008; Zhang & Luck, 2008; Zhang & Luck, 2009). In order to differentiate between the slots vs. resource debate, future experiments should explicitly examine the ability to trade-off the quantity and quality of representations above and below capacity limits.

In a recently published study, Zhang and Luck (2011) manipulated the degree of precision required to respond in a delayed colour discrimination task.

Participants either responded by clicking on a continuous colour wheel (requiring high precision, as per Zhang and Luck (2008)) or by selecting a homogeneous colour wedge (requiring comparatively lower precision). The tasks were analogous to Experiment 3 in the current study because participants had to rely on the context of the response condition to bias the allocation of resources at encoding. Like the current study, Zhang and Luck (2011) found that participants were unable to trade-off resolution and capacity in VSTM, even when given financial incentive to do so. In contrast, there was evidence of flexibility over the trade-off between quantity and quality of representations when memory was probed before the decay of the iconic trace. This suggests another functional dissociation between VSTM and the high capacity, iconic trace (e.g. Phillips, 1974). It may be the case that the flexibility in the control over the number and precision of VSTM is lost once representations are consolidated from a fragile state into the robust but limited-capacity VSTM form (Chapter 4; Sligte et al., 2008). The current study, therefore, also concurs with this idea, and shows that the biasing of VSTM resources in the trade-off between *quantity* and/or *quality* is not under flexible control.

It appears that the trade-off between the quality and number of representations is determined at encoding and this is not amenable to top-down control. It may be the case that the current participant samples were already optimally allocating resources and thus did not benefit from the use of contextual information. This argument concurs with the current literature which suggests encoding strategy (Linke et al., 2011) and efficiency (Vogel et al., 2005) is a major determinant of VSTM performance. Linke and colleagues (2011), for example, found that differences in encoding strategies between low and high capacity

participants accounted for differences in VSTM performance. In a sub-optimal fashion, low capacity participants were more likely to attempt to encode all memory array items even when the set size far exceeded capacity. Unlike high-capacity individuals who were already allocating resources efficiently, low-capacity participants benefited from strategic cues to encourage the encoding of a sub-set of items. Future studies should, therefore, specifically test groups who vary dramatically in capacity to investigate individual differences in the use of the strategic information like the current task.

If it was possible to find evidence of the ability to flexibly allocate VSTM resources to favour the number or quality of representations, it would have been interesting to extend the study to a neuroimaging setting. In complement to the findings of Edin and colleagues (2009), prefrontal areas may be engaged in anticipation of arrays with large arrays in order to pre-empt and supplement parietal VSTM capacity limitations. The effects would be especially interesting, however, when prior knowledge of the required precision was available. In such contexts, it may be the case that more stimulus-specific, early visual areas specialising in the coding of shape or orientation (like Harrison & Tong, 2009; Serences et al., 2009; Stokes et al., 2009) may be up-regulated in anticipation of difficult trials. Multivariate pattern analyses would, in this case, be useful to detect the subtle stimulus-specific patterns across neuronal ensembles.

In summary, the current study calls into question the volitional flexibility of top-down control to guide the allocation of resources to optimise the encoding and maintenance of behaviourally relevant information. Across four systematically conducted studies, there was a resounding lack of evidence to suggest that

participants were strategically allocating their VSTM resources according to contextual information. Surprisingly, it appears that resources were allocated once memoranda were physically present. It may be the case, however, that the precision and number of representations are separate characteristics, based on separate resources. Further research is needed to fully elucidate the extent to which the precision and number of representations are dissociated and whether resource allocation is in fact under flexible control.

CHAPTER 6

Do Competitive Inter-Item Interactions Extend into VSTM?

Recent evidence suggests that visual areas involved in perceptual coding also support the continued maintenance of items in memory. This raises the question of whether similar competitive processes that constrain perception also continue to influence VSTM maintenance. In a series of four experiments, the degree of inter-item competition was manipulated along task-irrelevant dimensions to determine whether competitive perceptual dynamics extend into VSTM maintenance or are resolved at encoding. Firstly, the spatial proximity of items was manipulated while testing colour for memory (Experiment 1). VSTM performance (accuracy, VSTM capacity (k) and sensitivity) was lower for items in close proximity. Two control experiments (1) showed equivalent performance for the two competition conditions in a perceptual search task and (2) showed that the stimulus presentation parameters did not constrain encoding for the high competition condition. The final experiment manipulated competition along a non-spatial stimulus feature (colour) and tested memory for orientation. Like the effects of spatial competition, performance was higher when items were all different colours (low competition) rather than the same. Across the four experiments, it is possible to conclude that the competitive dynamics between items during perception continue into VSTM maintenance.

6.1 Introduction

It is becoming increasingly clear that many of the same neuronal populations in visual areas engaged during perceptual processing also contribute to maintenance of representations in VSTM. This converging evidence is from both single unit (Woloszyn & Sheinberg, 2009) and advanced analyses of human imaging data (Harrison & Tong, 2009; Serences et al., 2009). For example, Harrison and Tong (2009) used multivariate pattern analyses of fMRI data to show that VSTM for orientation can be decoded in areas V1-V4 during maintenance, despite low levels of gross BOLD activity. VSTM maintenance is supported in these posterior, visual areas as well a network of multisensory parietal and frontal areas (e.g. Gazzaley et al., 2005a; Gazzaley et al., 2007). The arrangement appears analogous to the

network of areas involved in the selective processing of task-relevant items during perception, during which top-down signals in parietal and frontal cortex prioritise processing in visual areas. The analogy suggests that representations being maintained in VSTM may continue to be natural candidates for top-down modulation in a similar way to perceptual processing. The question then arises of whether some of the same mechanisms which constrain perception may also continue to influence VSTM performance.

Not all information in the visual scene can be perceived. Perceptual processing is inherently competitive. Competition is established when multiple attributes or objects occur simultaneously within the same Receptive Fields (RF) of neurons, and compete to drive neuronal activity (Desimone & Duncan, 1995; Kastner et al., 1998; Kastner & Ungerleider, 2000). The "winners" of the competition then remain active and are available for further processing. The organisation of RFs in the visual system is such that the size of the RF become increasingly larger as information is integrated through the visual hierarchy (e.g. Kastner et al., 2001).

The overlap of neuronal populations coding nearby items may explain why items presented in close proximity can reduce visual processing efficiency. For example, during perceptual search, the identification of a target became increasingly difficult as the distance between four potential target items decreased (Müller-Plath & Elsner, 2007)[18]. Analogous results have been shown in attentive tracking paradigms; performance for tracking multiple objects decreased as the target-target distance was reduced (Shim et al., 2008). The detrimental effect of spatial crowding may arise because the inter-item competition begins earlier along

[18] Note that the opposite effect occurs when close proximity can assist in perceptually grouping distracters (Müller-Plath & Elsner, 2007). See also Alexander and Zelinsky (2011).

the visual hierarchy, starting in visual areas with smaller RFs. The increase in spatial overlap in more visual areas in turn reduces the possibility of disambiguating items across RFs (Kastner et al., 2001).

Like perception, VSTM is also a limited capacity resource. Only a limited portion of the available information in the visual scene can be encoded and maintained (e.g. Phillips, 1974). In order to be adaptive, therefore, VSTM must also be extremely selective. Traditionally, it was thought that VSTM was simply the end product of selection during encoding. Recent evidence suggests, however, that like in perception, representations already in VSTM can be cued, biased and enhanced through top-down attentional processes (see Chapter 4; Griffin & Nobre, 2003; Stokes & Nobre, 2012). Furthermore, in addition to the overlap in activity in early visual areas between perception and VSTM, there is evidence that VSTM is arranged in a spatiotopic fashion; in an analogous way to perception (Dell'Acqua et al., 2010; Eimer & Kiss, 2010; Kuo et al., 2009). Taking all this evidence, the notion that emerges is that VSTM and perception are not anatomically, or functionally, decoupled; but VSTM is instead an extension of the perceptual process.

Though there are multiple points of correspondence between VSTM and perception, it remains unclear whether the competitive mechanisms present in perception also extend into VSTM maintenance. To my knowledge, very little formal investigation of competition occurring during VSTM maintenance has been conducted (for a discussion see Shapiro & Miller, 2011). One notable exception is a study conducted by Lin and Luck (2009), which tested the influence of item similarity on VSTM representations. They found that presenting an array of items with highly similar colours facilitated VSTM performance for colour compared to

when one or more dissimilar items were included. This effect suggests that colour similarity created a condition of co-operation rather than competition. One aspect of their design, however, makes it difficult to interpret the nature of their results. The feature dimension along which similarity was manipulated (colour) was the same dimension required to perform the colour task. This may have resulted in strategic differences during encoding of similar versus dissimilar hues which may have accounted for the result, such as participants paying more attention to individuate similar colours.

In order to provide a rigorous test for the presence of continued competitive interactions operating during VSTM maintenance, I investigated whether the spatial proximity among items encoded and maintained in VSTM affected judgements about a non-spatial feature of the items. Manipulating a *task-irrelevant* feature dimension can address whether competitive interactions interfere with VSTM performance, while minimising the influence of any changes in coding strategies (cf. Lin & Luck, 2009). For example, if participants were asked to report locations of items, they may spend more effort encoding locations with greater precision when spatial proximity increased.

One could envisage two possible types of inter-item dynamics to operate within VSTM. Firstly, as a consequence of selective encoding, the competition between the few items which come to occupy VSTM has already been resolved, so that stable and differentiated representations can be actively maintained without further competitive interactions. Alternatively, the competitive dynamics present at perceptual analysis could continue to operate during VSTM maintenance.

Experiment 1 used a variant of the change-detection task in which the spatial competition between items is manipulated and participants report memory for the colour of probed item. Items presented in close proximity should compete for representation earlier in the processing hierarchy. If competitive interactions persist during VSTM, proximity should have a negative effect on VSTM performance. Furthermore, this effect should outweigh the effects that would be expected to result from spatial competition during selective perception and encoding of the original stimuli. Experiments 2 and 3 were designed to assess the contribution of perceptual competition during encoding to decrements in VSTM performance. In Experiment 4, the investigation of competitive interactions during VSTM was extended by asking whether similarity along an irrelevant non-spatial feature dimension (colour) would similarly damage VSTM performance.

The results suggest that inter-item interactive mechanisms continue to shape representations during VSTM maintenance. The results showed that VSTM performance suffered from spatial competition among items, in a way which may have exceeded effects occurring only during perceptual encoding. In accordance with expectations, unique but task-irrelevant information benefitted performance. This suggests that spatial and non-spatial based competitive dynamics operate in similar ways.

6.2 Experiment 1: Effects of Spatial Competition on VSTM

To determine whether competitive inter-item dynamics continue to operate during VSTM maintenance, the spatial proximity between items in a memory array

was manipulated. The aim was to create two conditions of Competition: items were either separated by 132 pixels in the *low competition* condition or 44 pixels in the *high competition* condition (equivalent to 3° or 1° at fixation). Participants were required to judge whether a probe item changed colour compared to the previous presentation in memory array. This meant that the competition dimension was orthogonal to the task demands; spatial information was *not* required to complete the task. This was important in order to eliminate differential coding strategies from explaining any differences in performance between the competition conditions (see Lin & Luck, 2009). It was expected that the increased spatial proximity in the *high competition* condition would result in greater inter-item competition. This should lead to greater confusion between representations because items will not be able to be disambiguated across receptive fields at early stages of the visual processing hierarchy. In contrast, performance should be higher in the *low competition* condition because the greater spacing between items means that inter-item competition should occur only in fewer, higher-order visual areas with larger RFs. If competition occurs later in the processing stream, this should also reduce the confusability between items in VSTM maintenance.

6.2.1 Method

6.2.1.1 Participants

Nineteen volunteers with normal or corrected-to-normal vision were recruited for the study. Four participants were excluded due to poor behavioural performance (*d*' < 1.0 for one more condition). The remaining 15 participants, aged between 20

and 35 (*M*=25.94, *SD*=4.37, 5 female) were included in the analysis. All participants were right handed (self-report), gave informed written consent and were remunerated £7 for their time. All four experiments were approved by the Oxford Central University Research Ethics Committee (CUREC).

6.2.1.2 Task

A task schematic is presented in Figure 6.1, panel a. Participants performed a variant of a VSTM change-detection task (Luck & Vogel, 1997). They were required to detect changes in colour for the probe item compared to a previous presentation in the memory array. In each trial, participants attempted to encode an array of four differently coloured squares presented for 200ms in either the upper left or upper right visual quadrant. The squares were positioned in four of 16 regularly arranged invisible placeholders (see Figure 6.1, panel b). For all conditions, one of the four items was placed in the most extreme corners of the invisible matrix within each hemifield. To compare the effect of spatial competition among items on VSTM the distance among the items was manipulated. On half the trials, there was large spacing between the items (*low competition*), and on the other half they were placed in close proximity (*high competition*).

After a variable delay (between 1500 and 2000ms), memory of the colour of one item was probed. The probe (presented for 200ms) appeared in the same location as one of the squares but may have changed colour (50% *match*, 50% *no-match*). On *no-match* trials the colour of probe was different from all four colours presented in the memory array. This design eliminated the possibility of binding errors contributing to the results. Once the probe was presented and the response

was made, feedback was presented for 300ms. All trial types were randomised across the experiment.

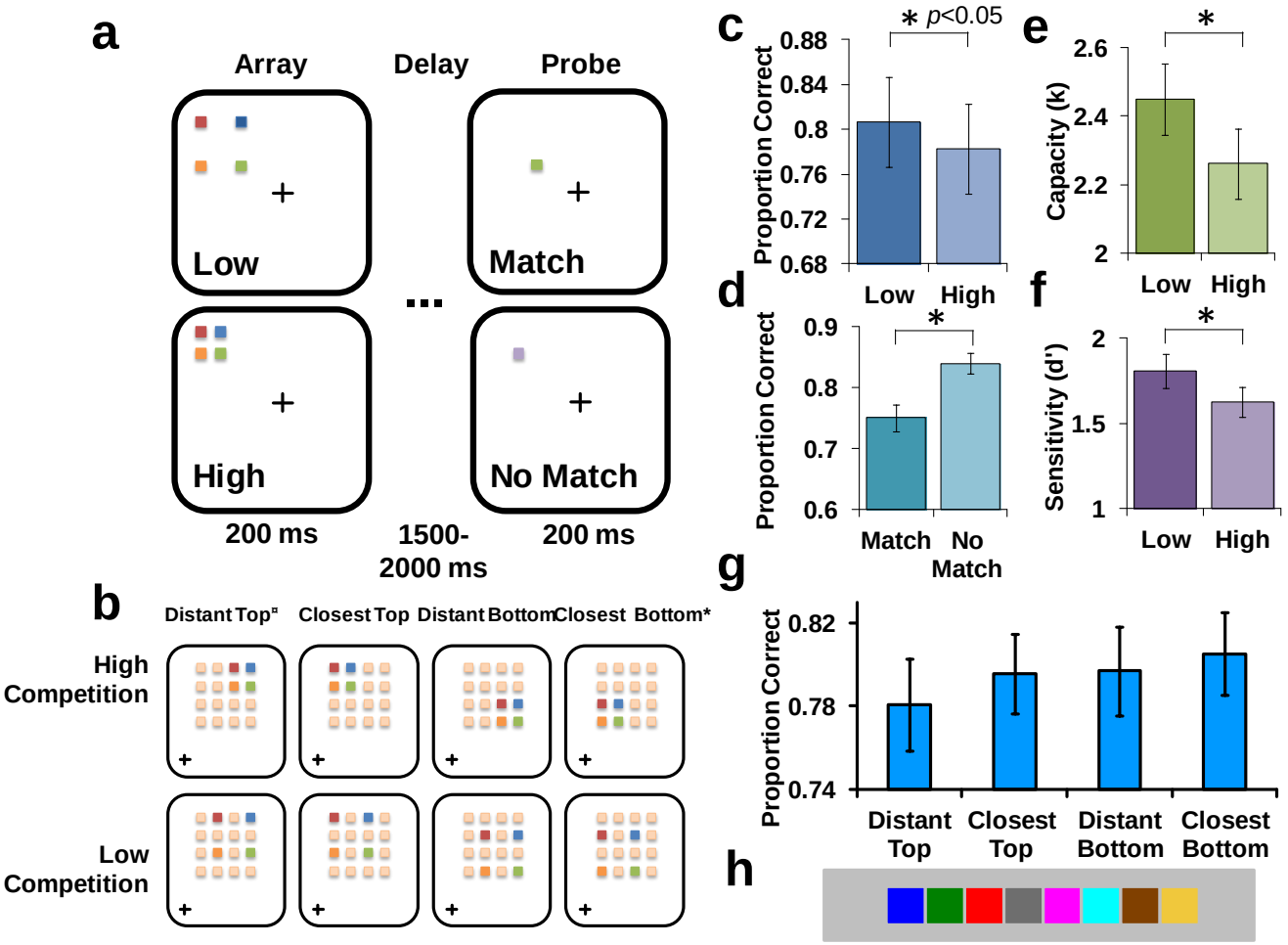


Figure 6.1: Experimental task and main results for Experiment 1. [a] Schematic of task format: Participants were instructed to encode an array of four squares (presented for 200ms) separated by either 3° (*low*) or 1° (*high competition*). After a variable delay (1500-2000ms), a single probe was presented (200ms), which either matched or did not match the colour of original stimulus at that location. [b] The four sets of potential item locations for the *high* (top) and *low competition* (bottom) condition: *distant top*, *closest top*, *distant bottom*, *closest bottom*. The brightly coloured squares represent item the positions against the invisible placeholders

(shown here in light beige; only right hemifield shown). [c] The proportion of correct colour-change discriminations is shown as a function of Competition condition (*low* vs. *high*) and [d] whether the colour of the probe matched the colour that was presented in the memory array (*match* vs. *no-match*). [e] The difference in the Capacity measure (k) and [f] sensitivity (d') between the *low* and *high competition* conditions. [g] Performance (proportion correct) for the four Corner positions averaged across both hemifields and Competition conditions. [h] The eight possible colours of items. ¤Indicates the positions furthest from fixation. *Indicates the positions closest to fixation. *Indicates a significant effect ($p < .05$). Error bars represent ±1 *SEM*.

6.2.1.3 Stimuli

The tasks were programmed and presented using Presentation software (Neurobehavioral Systems v.13.0, Albany: USA). All stimuli were presented against a light grey background [RGB: 192, 192, 192]. A black centrally presented fixation cross (0.72° by 0.72°) was presented throughout each trial, offsetting only when feedback was given. Stimuli in the memory array were constructed within the task programme on a trial-by-trial basis. Their colours were chosen at random (without replacement) from a selection of eight highly discriminable colours (Blue [RGB: 0, 0, 255], Green [RGB: 0, 128, 0], Red [RGB: 255, 0, 0], Dark Grey [RGB: 110, 110, 110], Magenta [RGB: 255, 0, 255], Cyan [RGB: 0, 255, 255], Brown [RGB: 128, 64, 0] and Gold [RGB: 240, 200, 60]). Each memory item was a square 44 x 44 pixels (equivalent to 1° x 1° of visual angle if presented at fixation), and during the presentation of the memory array, four squares were presented in a square

formation. Each item was separated by 44 pixels in the *high* and 132 pixels in the *low competition* conditions (equivalent to 1° and 3° respectively if presented at fixation). There were 16 possible arrangements of the arrays: in both upper quadrants (left and right), there were four “high” and four “low” competition conditions (see Figure 6.1, Panel b). Responses were made by a mouse button click (left: *match*, right: *no match*). Feedback about response accuracy was provided by replacing the fixation cross with either an “O” (correct) or an “X” (incorrect) after response for 300ms.

6.2.1.4 Procedure

Participants performed the computerised task in a quiet, dimly lit room viewing a CRT monitor (refreshed at 60Hz), with 1280 x 1024 pixel resolution, at a distance of 80cm. Eye movements were monitored to ensure participants maintained fixation. A 16-trial practice block familiarised participants with the task. In total, there were 576 trials, presented across 10 blocks. Participants were encouraged to respond as accurately as possible. For the final analysis across the eight possible locations (for both left and right) were collapsed so there were 144 trials per condition of interest

6.2.1.5 Analysis

The initial analysis used a repeated-measures ANOVA to test the effects of Competition (*high* vs. *low*), Change Type (*match* vs. *no match*), array Side (*left vs. right*), and spatial Position of the array (*distant top, closest top, distant bottom vs. closest bottom*). After showing no significant effects or interactions of array Side or

Position, all subsequent analyses collapsed over the eight (four left and four right) potential arrays. Accuracy, therefore, was analysed using a 2x2 repeated-measures ANOVA testing the factors of Competition (*high* vs. *low*) and Change Type (*match* vs. *no match*).

By combining the information from both *match* and *no-match* trials, the sensitivity (d') for change discrimination was calculated (Green & Swets, 1966; Macmillan & Creelman, 2005). The d' scores were calculated with respect to the standardised proportion of trials in which participants responded "match" on *match* (hits) versus *no-match* trials (false alarms):

$$d' = z(hits) - z(false\ alarms)$$

In a similar way, to compare the VSTM capacity between the two Competition conditions, k was calculated for each participant according to the following formula (Cowan, 2000; Pashler, 1988):

$$k = (H + CR - 1)N$$

where k is VSTM capacity, H is the hit rate (proportion of "match" responses on *match* trials), CR is the correct rejection rate (proportion of "no match" responses on *match* trials) and N is the number of items in the array (in this case N=4). Differences in performance between the *high* and *low* Competition conditions were assessed using paired samples t-tests.

6.2.2 Results and Discussion

The initial ANOVA testing, whether effects varied as a function of array side or position, showed no significant differences according to array Side [*F*(1,14)=1.85,

p=0.20] or array Position [*F*(1,14)=1.56, p=0.21; see Figure 6.1, panel g], and no significant interaction terms (*ps*>0.18). Only the main effect of Competition was significant, revealing significantly higher performance for the low compared to high competition condition [*F*(1,14)=6.94, *p*=0.02]. Analyses subsequently collapsed over array side and position.

Overall, performance was better in the *low* compared to the *high* Competition condition across all measures: accuracy, capacity and sensitivity. An *ANOVA* revealed a main effect of Competition: accuracy was significantly higher for the *low* compared to the *high competition* condition [see Figure 6.1: Panel b, *F*(1,14) = 6.94, *p*=0.02]. There was also a significant main effect for Change Type [*no match*>*match*, *F*(1,14) = 13.35, *p*=0.003; see Figure 6.1: Panel b]. The interaction was not significant [*F*(1,14) = 1.53, *p*=0.24].

A paired-samples t-test on the k measure for each Competition condition revealed that VSTM capacity was significantly greater for the *low* compared to the *high competition* condition (*t*(14) = 2.64, *p*=0.02; see Figure 6.1: Panel d, top). Similarly, the d' scores for the two Competition conditions revealed that sensitivity was significantly greater for the *low* compared to the *high competition* condition (*t*(14) = 2.85, *p*=0.013; see Figure 6.1: Panel d, bottom).

Overall, the results provide evidence that VSTM performance is affected by the spatial proximity of memoranda in a similar way to processes involved in perception. Under conditions of higher competition, it appears that memory capacity is reduced. This is possibly due to a greater overlap in neuronal populations which work to maintain items in memory. In this respect, the competitive mechanisms

underlying the perception of visual information may continue to influence representations throughout VSTM maintenance.

An alternative explanation may be that the detrimental effects of high versus low spatial proximity on VSTM performance do not occur from continued competitive processes during maintenance, but reflect different perceptual limits during the encoding process. The perceptual demands in the *high competition* condition could simply have unduly compromised encoding into VSTM. Given that the influence of competition on the perception of items is well established, it is important to ensure that participants are able to encode the items similarly in high and low spatial competition arrays, within the current set of stimulus parameters. Two control experiments followed, to show that the perceptual differences between the two Competition conditions did not constrain performance before the items were encoded into VSTM. Participants completed two tasks: (1) to show that performance on a perceptual search task was roughly equivalent between the two conditions when arrays were exposed for 200ms and (2) to show that increasing the possible time to encode the memory array did not change the pattern of results between the *high* and *low* Competition conditions.

6.3 Experiments 2 and 3: Controlling for Perceptual Differences

To ensure that the perceptual conditions known to create ‘competition’ did not unduly affect perception to the extent that information could not be encoded into VSTM, two control experiments were conducted. Experiment 2 was a perceptual search task: participants searched for a target in an array with the same spacing

parameters as Experiment 1, and judged whether the colour of the corresponding item had changed or not. In Experiment 3, I tested whether the reduced performance in the *high competition* condition was due to 200ms being insufficient time to encode the items into VSTM. This was achieved by varying the duration of the presentation of the memory array and testing the effect on VSTM performance for the two competition conditions.

6.3.1 Method of Experiment 2: Perceptual Search Control

6.3.1.1 Participants

The same sixteen participants (10 female) took part in Experiments 2 and 3. They were aged between 20 and 35 (*M*=24.31, *SD*=3.89), had normal or corrected-to-normal vision, and were right handed (by self report). All participants gave informed written consent and were remunerated £10 for their participation in both experiments. The order of Experiments 2 and 3 was counterbalanced across participants.

6.3.1.2 Task

The basic task structure is shown in Figure 6.2, panel a. Stimulus parameters and experimental procedures were the same as those in Experiment 1, except that the order of the single-item and multi-item arrays was reversed. Participants judged whether a single target changed colour when re-presented as part of an array. The target was presented for 200ms and, after a variable delay, an array of four squares was presented for 200ms. The proximity among the items was

manipulated using the same parameters as in the *high* and *low competition* trials in Experiment 1. Also following Experiment 1, the target changed colour in the subsequent array (*no match*) on half of the trials. Participants were encouraged to respond as quickly and accurately as possible. In total, there were 128 trials presented across 3 blocks.

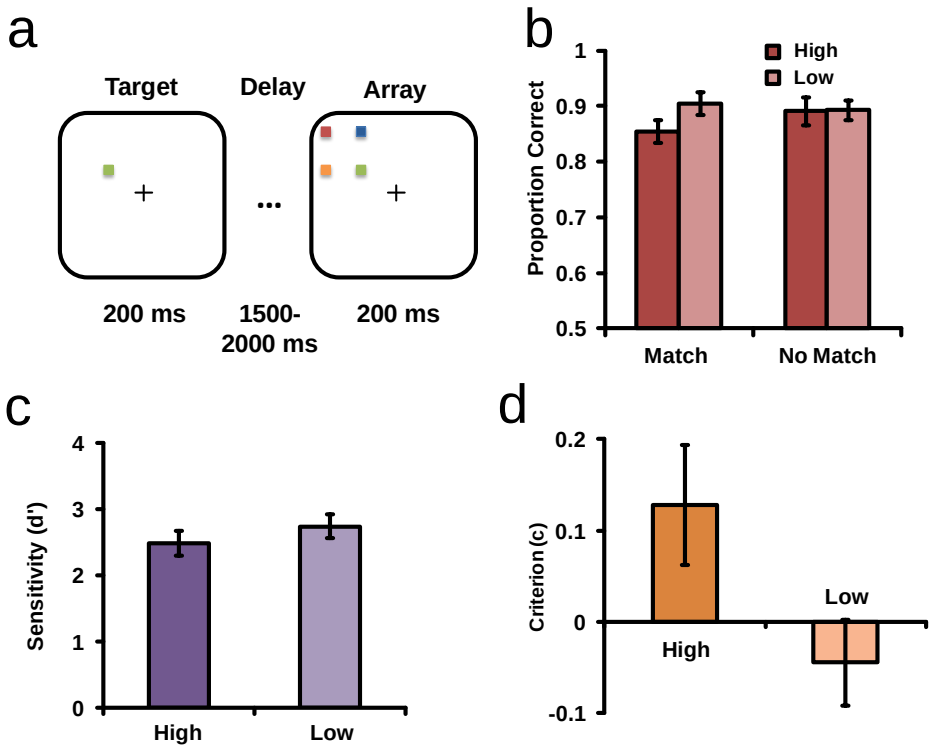


Figure 6.2: Paradigm and main results for Experiment 2. [a] Schematic of task format for Experiment 2: Participants were instructed to encode a target (presented for 200ms) and then, after a variable delay (1500-2000ms), to judge whether the corresponding item in the test array had changed colour or not. Items in the test array were separated by either 3° (*low*) or 1° (*high competition*) and were presented for 200ms. [b] The proportion of correct colour-change discriminations is shown as a function of Competition condition (*high* vs. *low*) and whether the colour of the probe matched the colour that was presented in the memory array (*match* vs. *no-*

match). [c] Sensitivity (d') is shown as a function of Competition (*high* vs. *low*). [d] Criterion (c) is shown as a function of Competition (*high* vs. *low*). Error bars represent ±1 *SEM*.

6.3.1.3 Analysis

The main factors of interest, manipulated in a factorial design, were Competition (*high* and *low*) and Change Type (*match* and *no match*). Performance data were collapsed over the eight potential array positions for the *high* and *low competition* trials. Of primary interest was correct performance on the perceptual search task which was assessed with an analysis of accuracy and sensitivity. Repeated-measures ANOVAs evaluated effects on accuracy and RT. RT was also analysed in this experiment to gain some insight into the difficulty of the perceptual search across the two Competition conditions. Analysis of sensitivity (d') combined *match* and *no match* trials; differences between the *high* and *low* Competition conditions were, therefore, assessed with a paired samples t-test.

In addition to the analyses described in Experiment 1, the criterion (c), which characterises the response propensity to respond *no-match* compared to *match* was also calculated (Green & Swets, 1966; Macmillan & Creelman, 2005). Often, this is used when hits and false alarms are valued differently, but can also be used to measure how different perceptual conditions influence the decision-making process, as in the current experiment. This can give further insight into what is underlying effects in accuracy and sensitivity. The *c* scores were calculated with respect to the standardised proportion of trials in which participants responded "match" on *match* (hits) versus *no-match* trials (false alarms):

$$c = -0.5 * (z(hits) + z(false\ alarms))$$

A higher criterion score represents a greater propensity to respond “no match”, which would result in and fewer false alarms but also possibly fewer hits. In turn, a negative criterion score represents a heightened propensity to respond “match”, which would result in more hits but also more false alarms. Like sensitivity, differences in criterion between the *high* and *low* competition conditions were assessed using a paired samples t-test.

6.3.2 Results and Discussion

The results for Experiment 2 are shown in Figure 6.2, panels b, c and d. Overall, performance (in terms of accuracy, and sensitivity) was approximately equal across the two competition conditions. Interestingly, however, there was a comparatively lower criterion score in the *low competition* condition.

Analysis of accuracy revealed no significant main effect of Competition [$F(1,15) = 3.01$, $p=0.10$; see Figure 6.2: panel b], Change Type [$F(1,15) = 1.42$, $p=0.25$], or interaction between the two factors [$F(1,15) = 2.48$, $p=0.14$]. RT data revealed similar results: no significant main effect of Competition [$F(1,15) = 2.40$, $p=0.14$] or Change Type [$F(1,15) = 0.57$, $p=0.46$]. The interaction between the two factors, however, was significant [$F(1,15) = 5.87$, $p=0.028$]. The difference in RT between the two Competition conditions was significant for *match* trials [M_{high}=519.74, SE_{high}=47.77; M_{low}=477.86, SE_{low}=46.03; $p=0.008$], whereas RT did

not differ between the two Competition conditions for *no match* trials [M_{high}=480.87, SE_{high}=32.13; M_{low}=489.93, SE_{low}=41.83; p=0.58][19].

Sensitivity did not differ significantly between the two Competition conditions, although there was a trend towards higher sensitivity in the *low* condition [t(15)=1.93, p=0.072; two-tailed, see Figure 6.2, panel c]. Similarly, a trend was also obtained on criterion scores, with higher scores for the *high* compared to the *low competition* condition [t(15)=1.95, p=0.07; two-tailed, see Figure 6.2, panel d].

Overall, the results of this control experiment are inconclusive. Although there was no main effect of Competition on VSTM performance, there was a trend towards higher sensitivity and lower criterion in the *low competition* condition. Such a pattern of results suggests that the spatial competition conditions may have compromised the initial perception and encoding of a multi-item array. In the search task here, there was no need to encode and maintain the multi-item array, and there were already trends toward performance (d') decrements. On the other hand, this task also places additional pressures of selecting an item from a perceptual array under time pressure, which is not the case in Experiment 1. This could have been the site at which spatial competition had its influence (although only a trend here). One way to enhance the relevance of this experiment would be to design a more typical visual search task with large arrays to compare the effect of competition on visual search times[20]. In this task, participants would respond weather a single target was present or absent in the test array. The test array would

[19] An analysis of inverse efficiency was conducted to combine the RT and accuracy data to ensure that there was no speed-accuracy trade-off. As predicted, there was better performance for the low competition condition (F(1,15) = 4.68, p=0.05). This, combined with the fact that analysis of both RT and accuracy show effects in the same direction, suggests there is no obvious speed-accuracy trade-off.

[20] Thank you to Professor Kimron Shapiro for this idea.

have similar spacing parameters as Experiment 1, however, many more items would be presented. This design would give more insight into the perceptual differences between the competition conditions of Experiment 1 affect basic perceptual processing. A direct test of whether spatial proximity compromised the perception and encoding of the multi-item sample array in Experiment 1 would be to manipulate the exposure duration of this array. This potential was addressed in another control task: Experiment 3.

6.3.3 Method of Experiment 3: Encoding Time Control

Experiment 3 used a similar design as Experiment 1, but manipulated the presentation time of the memory array. The aim was to test whether the 200ms display duration used in Experiment 1 was sufficient to ensure sufficient perception and encoding of the items in the array. If so, the effects of spatial competition observed in Experiment 1 should also be observed when display durations are longer and provide ample time for item perception and encoding (but see also Vogel et al., 2001). Shorter display durations were also tested in order to test for the possible effects of limitations in perception and encoding of the array.

6.3.3.1 Participants

See Figure 6.3, panel a, for a schematic of the structure of Experiment 3. Stimulus parameters and experimental procedures were the same as those in Experiment 1, except that the duration of the memory array was varied systematically. The presentation time of the memory array could take one of six

durations: 50, 100, 150, 200, 300 or 500ms. There were 576 trials presented across 10 blocks.

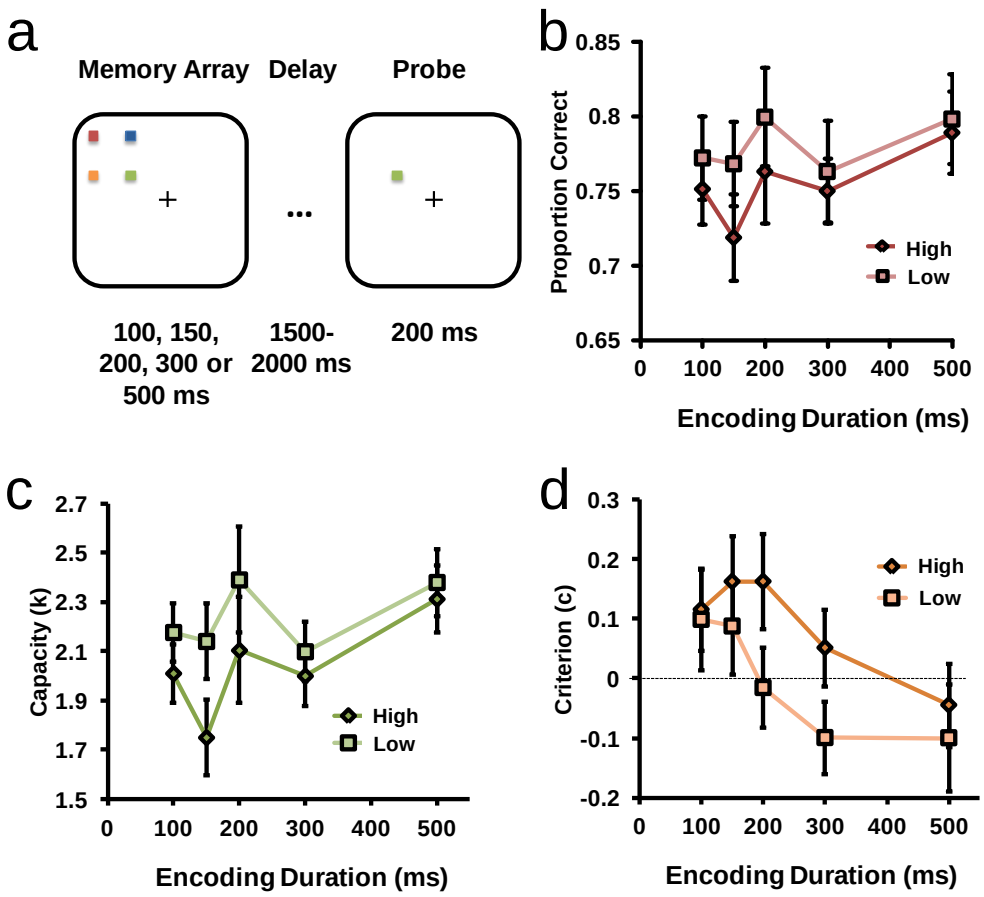


Figure 6.3: [a] Schematic of task format for Experiment 3. The task format was the same as Experiment 1 except the memory array was presented for either 50 (not shown), 100, 150, 200, 300 or 500ms. Performance is shown as a function of Encoding Time condition (100, 150, 200, 300 and 500ms) as a function of Competition (*high* vs. *low*) for [b] Proportion of correct colour judgments [c] Capacity (k) and [d] Criterion (c). Error bars represent ±1 *SEM*.

6.3.3.2 Analysis

There were three experimental factors of interest, manipulated in a factorial design: Competition (*high* vs. *low*), Change Type (*match* vs. *no match*), and Encoding Duration (50, 100, 150, 200, 300 or 500ms). Each resulting cell contained 24 trials. Only the last five durations were included in the analyses due to the presence of a brief after-image, which led to an inability to strictly control the presentation time in an unmasked array at the 50ms duration. Accuracy, therefore, was analysed using a 2x2x5 repeated-measures ANOVA. Analysis of capacity and criterion combined *match* and *no match* trials, and so effects were assessed using a 2x5 repeated-measures ANOVA. Accuracy, capacity and criterion were the primary variables of interest to assess correct VSTM performance. Capacity was chosen as a dependent variable for this experiment because of its similarity to sensitivity in calculation and predominance in the field when testing effects on VSTM maintenance. The speed of retrieval of representations was not important to the current study so RT was not calculated. To test for systematic variation across the Encoding Duration specifically, linear contrasts were conducted and, if appropriate, pairwise comparisons were tested between adjacent pairs. Greenhouse-Geisser corrected p-values were reported when sphericity of variance could not be assumed. When appropriate, post hoc analyses used the Bonferroni correction for multiple comparisons.

6.3.4 Results and Discussion

Overall, accuracy and capacity measures were higher, on average, for the *low* compared to the *high* c*ompetition* condition. Criterion scores were higher for *high* compared to *low competition* trials and remained consistently so for all but the first Encoding Duration.

The repeated-measures *ANOVA* conducted on accuracy revealed a significant main effect of Competition [*low >high; F*(1,15) = 7.69, *p*=0.014; see Figure 6.3: panel b]. The main effect of Change Type was not significant [*F*(1,15) = 0.79, *p*=0.39]. In contrast, the main effect Encoding Duration was significant [*F*(4,60) = 4.01, *p*=0.006]. This was explained by a significant linear contrast [*F*(1,15) = 5.58, *p*=0.032] which was followed-up by a comparison of adjacent encoding duration conditions. When corrected for multiple comparisons, only differences in performance between 150ms and 200ms (*p*=0.08) and 300ms and 500ms (*p*=0.06) tended towards significance (others *ps*>0.44).

Critically, the interaction between Competition and Encoding Duration was not significant [*F*(4,60) = 0.59, *p*=0.67] and there was no interaction between Competition and the linear contrast of Encoding Duration [*F*(1,15) = 1.44, *p*=0.25]. The interaction between Change Type and Encoding Duration was significant [*F*(4,60) = 5.08, *p*=0.001; see table 6.1 for descriptive statistics]. This was not explained by a significant linear interaction contrast [*F*(1,15) = 0.12, *p*=0.73]. Follow-up analyses suggested that there were no significant differences between adjacent Encoding Duration conditions except a trend between 100ms and 150ms

for *no match* trials (p=0.04). No other adjacent pairwise comparisons were significant ($ps \geq 0.16$).

Table 6.1 Accuracy means and standard errors of the mean for Experiment 3, according to each Encoding Duration and Change Type condition.

	Encoding Duration (ms)				
	100 (*SEM*)	150 (*SEM*)	200 (*SEM*)	300 (*SEM*)	500 (*SEM*)
Change Type					
Match	0.73 (0.03)	0.75 (0.03)	0.78 (0.03)	0.74 (0.03)	0.77 (0.03)
No-match	0.80 (0.02)	0.73 (0.02)	0.78 (0.02)	0.78 (0.02)	0.82 (0.02)

Similar effects were found for the analysis conducted on VSTM capacity estimates for the two Competition conditions. The repeated-measures ANOVA revealed significant main effects of Competition [*low* >*high*; $F(1,15) = 7.62$, p=0.015; see Figure 6.3: panel c] and Encoding Duration [$F(4,60) = 4.02$, p=0.006]. This was explained by a significant linear contrast [$F(1,15) = 5.49$, p=0.033]. Follow-up comparisons between adjacent Encoding Duration conditions revealed a trend towards a difference in capacity between 150ms and 200ms (p=0.072) and, 300ms and 500ms (p=0.064; others ps>0.44). Critically, the interaction between Competition and Encoding Duration was not significant [$F(4,60) = 0.59$, p=0.67] and there was no interaction between Competition and the linear contrast of Encoding Duration [$F(1,15) = 1.49$, p=0.24].

Analysis of the criterion scores revealed a trend for higher criterion scores for *high* compared to *low competition* trials [$F(1,15) = 3.49$, p=0.08; see Figure 6.3: panel d]. There was a significant main effect of Encoding Duration [$F(4,60) = 7.54$,

p=0.015]. This was explained by a significant linear contrast [*F*(1,15) = 16.14, *p*=0.001]. Follow-up comparisons between adjacent Encoding Duration conditions revealed a trend towards a difference in criterion scores between 200ms and 300ms (*p*=0.076; others *ps*>0.44). Importantly, the interaction between Competition and Encoding Duration was not significant [*F*(4,60) = 0.98, *p*=0.43] and nor was there an interaction between Competition and the linear contrast of Encoding Duration [*F*(1,15) = 0.26, *p*=0.62].

Overall, the results of Experiment 3 suggest that performance remained higher for low compared to the high competition condition across all Encoding Durations. Importantly, none of the analyses showed an interaction between Encoding Duration and Competition condition. This suggests that the differences between the high and low competition conditions remained relatively unchanged as the encoding time differed.

Caution must be taken, however, in the interpretation. Despite the fact that the interaction between Competition and Encoding Duration is not significant, the difference between high and low Competition Conditions appears to be reduced at the longer Encoding Durations. This suggests that the perceptual inter-item competition may be resolved before the items enter maintenance. As such, it is not possible to categorically conclude that the results from Experiment 3 are exclusively due to competition during maintenance. It may be possible that perceptual competition contributed to this effect.

An alternative way to test the effects of inter-item competition during maintenance would be to present the items sequentially[21]. Previously sequential

[21] Once again, I thank Dr. Nick Yeung for this idea.

presentation of stimuli has been used as a baseline with which to compare the effects of perceptual competition (e.g. Kastner & Ungerleider, 2001). If indeed inter-item competition extends into VSTM then it would still be evident even if items are not presented simultaneously. Care would be needed, however, to disentangle sequential from competitive effects. Future research should validate the results of Experiment 1 using such a sequential presentation method.

Despite the possible limitations, the current results do give further weight to the effects found in Experiment 1, and suggest that the effects of competition can continue to affect VSTM throughout maintenance. The results of Experiment 2, however, were not so straightforward. From the trend towards higher performance for the low competition condition in Experiment 2, it may appear that the perceptual differences between the competition conditions elicit different processing demands for the items from the high and low competition conditions. Considering the different task demands of Experiments 1 and 2, however, I suggest that the results of Experiment 3 are more pertinent in determining the perceptual constraints placed on the two competition conditions. For both accuracy and capacity in Experiment 3, the critical interaction between competition and Encoding Duration (and the corresponding linear contrast) suggest that the effect of competition was not simply due to 200ms stimulus presentation duration placing unnecessary encoding demands on the high competition condition. This suggests that the perceptual stimulus parameters presented in this series of experiments, therefore, are insufficient to account for all the differences in VSTM performance. From these results, at least that some of the inter-item dynamics which are well established in perceptual processing (e.g. Desimone & Duncan, 1995) may also extend into

VSTM maintenance. Future research should be conducted, however, with the aim to prevent perceptual contributions from potentially confounding results.

In order to extend this effect into other stimulus dimensions, I investigated whether colour variance could also create situations of competition akin to spatial proximity in Experiment 1. In a similar way to the previous experiments, this tested the effect of feature-based competition on an orthogonal stimulus dimensions: orientation change.

6.4 Experiment 4: Non-Spatial Feature-Based Competition in VSTM

Experiment 4 was conducted to determine whether non-spatial, feature-based competition among items can also influence VSTM performance. Perceptual competition is typically only considered in the spatial dimension, where the overlap of different items within receptive fields triggers competitive interactions. Competition can also be conceived, however, to occur along non-spatial feature dimensions. For example, if there are limited resources for coding colour in visual cortex, one might expect that multiple items with the same colour should compete for representation.

This experiment tested for possible effects of non-spatial competition in a VSTM precision task. The level of colour competition was manipulated by presenting all array items in the same colour (*high competition*) and in different colours (*low competition*). The participants' task was to discriminate the direction of a change in orientation between a single probe and the spatially corresponding item previously presented memory array. Colour was therefore an irrelevant stimulus

dimension and the item-colour manipulation was orthogonal to the task requirements.

In order to test how colour-based competition may influence VSTM performance, VSTM load was varied systematically; arrays contained 2, 4 or 6 items. If colour similarity triggers competitive interactions, the effects might increase as more items compete for resources. In addition, the angular rotation change between the memory array and probe was also varied systematically (±5°, ±20° or ±45°), like in Chapters 3-5. It is expected that the effects of Competition may become more apparent in trials requiring a greater precision of representation. In the Experiments in Chapters 3-5, different colours for each stimulus in the memory array were used, under the apprehension that additional colour information may help to individuate and separate items in memory.

6.4.1 Method

6.4.1.1 Participants

Twenty volunteers aged between 22 and 29 (*M*=25.74, *SD*=1.97, 11 female) were recruited for the study. All participants had normal or corrected-to-normal vision, and all except two were classed as right handed by self-report. Participants gave written informed consent and were remunerated £7 for their time.

6.4.1.2 Task

Figure 6.4, panel A, contains a schematic of the task. The design was based on the VSTM precision task used in Chapters 3, 4 and 5. On each trial, participants

encoded an initial memory array of randomly oriented coloured arrows. Arrays appeared for 200ms and contained 2, 4, or 6 arrows, equally distributed on both sides of the visual field. The arrows in the memory array were either the same colour (*high competition*, 50% of trials) or were all different, highly discriminable colours (*low competition,* 50% of trials). Memory for a single item was tested at the end of the trial, after a randomised interval between 800 and 1200ms. The memory probe was always one of the arrows from the memory array, but rotated 5°, 20° or 45° about its central axis (also presented for 200ms). The participant judged whether the probe had rotated clockwise or anti-clockwise relative to the original memory item. Parametric manipulation of the change magnitude enables us to estimate the precision of VSTM: to detect a small angular change requires a more precise representation than to detect a larger change. Feedback was presented after the response for 300ms. The intertrial interval varied randomly between 1500 and 2000ms. All trial types were randomised across the experiment.

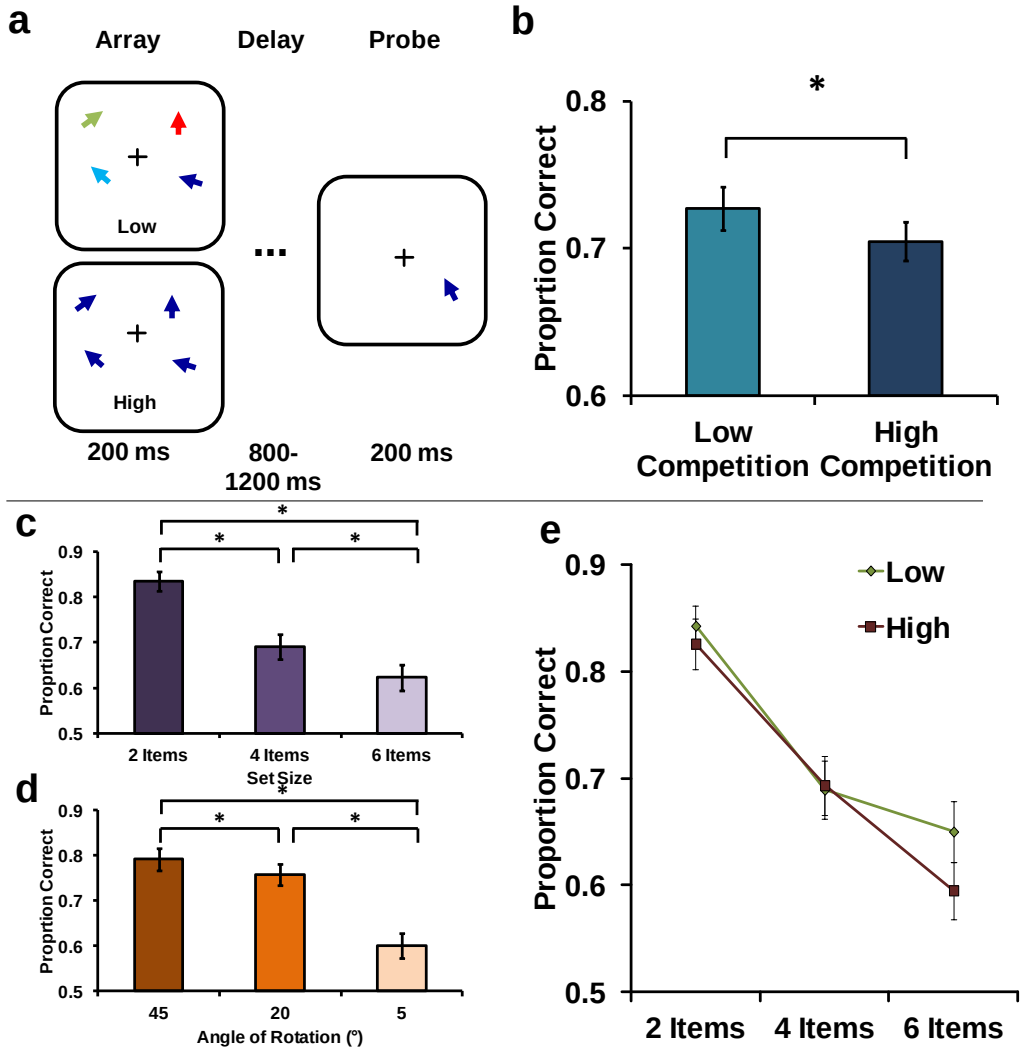


Figure 6.4: Experimental task and main result for Experiment 4. [a] Participants encoded an array of 2, 4 or 6 arrows (presented for 200ms), which were either all the same colour (*high competition*) or all different colours (*low competition*). After a variable delay (800-1200ms), a single probe was presented (200ms), rotated either clockwise or anti-clockwise to the original stimulus by 5°, 20° or 45°. [b] Proportion correct as a function of Competition (*low* vs. *high*). [c] Proportion correct according to each Set Size (2, 4 or 6 Items). [d] The proportion correct for the orientation change discrimination (5°, 20° or 45°) as a function of Competition condition: *high* (darker bars) vs. *low* (lighter bars) for 2-item trials, [e] The proportion correct for the

Set Size Conditions as a function of Competition condition: *low* (olive) vs. *high* (red). Note this interaction is not significant but shown for illustration purposes. Error bars represent ±1 *SEM*. *Indicates a significant comparison.

6.4.1.3 Stimuli

Arrow stimuli in the memory array were constructed within the task programme on a trial-by-trial basis. The possible colours of the arrows were chosen at random from a selection of highly discriminable colours (Blue [RGB: 0, 0, 255], Red [RGB: 255, 0, 0], Aqua [RGB: 0, 150, 150], Purple [RGB: 128, 0, 150], Olive [RGB: 128, 128, 0], Orange [RGB: 255, 128, 0], Black [RGB: 0, 0, 0] and White [RGB: 255, 255, 255]). On multi-colour trials, colours were drawn randomly and without replacement. Each arrow subtended approximately 1.43° of visual angle from base to tip. A minimum distance of 2.39° between the centres of each stimulus ensured that there was no overlap and reduced crowding effects. Responses were made by turning the lever of a custom-built response device according to the direction of orientation change. Feedback about response accuracy was provided by replacing the fixation cross with either a black “O” (correct) or “X” (incorrect), approximately 0.64° by 0.64°. All other aspects of the stimuli and procedure were the same as in Experiment 1.

6.4.1.4 Procedure

Participants performed the computerised task in a quiet, dimly lit room. They viewed a CRT monitor (refreshed at 60hz) at a distance of 90cm. A 16-trial practice

block familiarised participants with the task. In total, there were 360 trials presented across nine blocks.

6.4.1.5 Analysis

There were three experimental factors of interest manipulated in a factorial design: Competition (*high* vs. *low*), Set Size (2, 4 or 6 items) and Angle of Rotation (5°, 20°, 45°). Direction of rotation was not of primary interest, and data were collapsed over clockwise and anti-clockwise accordingly. Data were also collapsed across individual stimulus colours. Each experimental cell contained 20 trials. The main dependent variables of interest were accuracy and sensitivity to assess the effects of the competition, stimulus variables on presence and precision of representations. Sensitivity analysis was calculated by combining information from the proportion of correct of clockwise trials (hits) and the proportion of clockwise judgments for anti-clockwise trials (false alarms). Because any difference in the propensity to respond clockwise or anticlockwise was not of interest in this study, criterion was not analysed. In addition, the differences in the presence and precision of representations were of central interest rather than the speed of retrieval so RT was not analysed. To maintain consistency with previous experiments using this task in this thesis, sensitivity was chosen rather than capacity. Linear contrasts were used to test between the three Angles of Rotation and Set Sizes and, if appropriate, pairwise comparisons were tested between adjacent pairs. The relatively small number of trials per condition precluded modelling of the probability of recall and precision of representations.

A separate subsidiary analysis was carried out to test whether any effects of colour competition were carried by only a subset of colours. To explore this possibility, I tested whether performance differed as a function of Competition condition for each target colour. This was investigated using a 2 (Competition) x 8 (Target Colour) repeated-measures *ANOVA.* Greenhouse-Geisser corrected p-values were reported when sphericity of variance could not be assumed. When appropriate, post hoc analyses used the Bonferroni correction for multiple comparisons.

6.4.2 Results and Discussion

Results for the accuracy ANOVA revealed main effects of all three experimental factors. As predicted, accuracy was higher in *low* colour competition trials compared to *high competition* trials [$F(1,19) = 5.01$, $p=0.04$; see Figure 6.4: Panel b]. There was a significant main effect of Set Size [$F(2,38) = 179.45$, $p<0.001$; see Figure 6.4: Panel c], which was explained by a significant linear contrast [$F(1,19) = 512.03$, $p<0.001$]. Adjacent pairwise comparisons revealed that accuracy was significantly higher for lower compared to higher set sizes (*ps*<0.002). The main effect of Angle of Rotation was also significant [$F(2,38) = 116.04$, $p<0.001$; see Figure 6.4: Panel d]. This relationship was also explained by a significant linear contrast [$F(1,19) = 186.03$, $p<0.001$], and adjacent pairwise comparisons revealed that accuracy was significantly higher for larger compared to smaller Angles of Rotation (*ps*<0.024). In contrast to expectations, Competition did not interact with Set Size [$F(2,38) = 1.97$, $p=0.15$; see Figure 6.4: Panel e]. There

was, however, a significant interaction between Set Size and Angle of Rotation [$F(4,76) = 7.64$, $p<0.001$; see Table 6.2] and this interaction was explained by a linear relationship [$F(1,19) = 23.73$, $p<0.001$]. Follow-up pairwise comparisons show that accuracy was significantly higher for 2 compared to both 4 and 6 ($ps \leq 0.006$) item trials at each Angle of Rotation. Accuracy only differed between 4 and 6 items for 45° and 20° rotations ($ps<0.02$) but did not for 5° rotations ($p>0.1$). There were no other significant interaction terms ($ps>0.51$).

The results of the analysis of sensitivity also revealed main effects of all three experimental factors (see Table 6.3). Sensitivity was significantly higher in *low* compared to *high competition* trials [$F(1,19) = 5.36$, $p=0.03$]. There was a significant main effect for Set Size [$F(2,38) = 166.02$, $p<0.001$] which was explained by a significant linear contrast [$F(1,19) = 399.81$, $p<0.001$]. Follow-up adjacent pairwise comparisons revealed that sensitivity was significantly higher for lower Set Sizes for both comparisons ($ps<0.002$). The main effect of the Angle of Rotation was also significant [$F(2,38) = 126.06$, $p<0.001$] and was explained by a significant linear contrast [$F(1,19) = 183.30$, $p<0.001$]. Adjacent pairwise comparisons revealed that sensitivity was significantly higher for larger compared to smaller Angles of Rotation ($ps<0.02$). Level of Competition did not interact with Set Size [$F(2,38) = 2.34$, $p=0.11$].

The interaction between Set Size and Angle of Rotation was significant [$F(4,76) = 11.44$, $p<0.001$], and this interaction was explained by a linear relationship [$F(1,19) = 37.23$, $p<0.001$]. Follow-up pairwise comparisons show that sensitivity was significantly higher for 2 compared to both 4 and 6 ($ps \leq 0.01$) item trials at each Angle of Rotation. Sensitivity only differed between 4 and 6 items for

45° and 20° rotations (*ps*<0.02) but did not for 5° rotations (*p*>0.1). There were no other significant interaction terms (*ps*>0.51).

Table 6.2: Accuracy results for Experiment 4. Proportion correct and standard error of the mean (SE) for each Competition, Set Size and Angle of Rotation condition.

	2 Items			4 Items			6 Items		
Angle of Rotation (°)	45 (*SE*)	20 (SE)	5 (SE)	45 (*SE*)	20 (SE)	5 (SE)	45 (*SE*)	20 (SE)	5 (SE)
Competition									
Low Competition	0.94 (0.01)	0.91 (0.01)	0.68 (0.03)	0.75 (0.03)	0.73 (0.03)	0.59 (0.03)	0.68 (0.03)	0.69 (0.03)	0.58 (0.03)
High Competition	0.94 (0.02)	0.89 (0.02)	0.63 (0.03)	0.78 (0.03)	0.71 (0.02)	0.59 (0.03)	0.65 (0.03)	0.61 (0.02)	0.52 (0.03)

Table 6.3: Sensitivity results for Experiment 4. Sensitivity (d') and standard error of the mean (SE) for each Competition, Set Size and Angle of Rotation condition.

	2 Items			4 Items			6 Items		
Angle of Rotation (°)	45 (*SE*)	20 (SE)	5 (SE)	45 (*SE*)	20 (SE)	5 (SE)	45 (*SE*)	20 (SE)	5 (SE)
Competition									
Low Competition	2.86 (0.11)	2.56 (0.1)	1.05 (0.19)	1.50 (0.19)	1.35 (0.17)	0.51 (0.15)	1.07 (0.18)	1.14 (0.18)	0.43 (0.15)
High Competition	2.79 (0.14)	2.47 (0.17)	0.86 (0.16)	1.69 (0.18)	1.26 (0.15)	0.51 (0.19)	0.88 (0.19)	0.63 (0.13)	0.07 (0.15)

The salience of particular target colours (for example high contrast stimuli presented in black or white) may have resulted in comparatively higher performance when all the colours in the array were different because the target contrast may have drawn resources from less salient items (for more information see Itti & Koch, 2001). The results of the follow-up colour based analysis can be seen in Figure 6.5. The *ANOVA* revealed no main effect of Competition [*low>high*; $F(1,19) = 2.80$, $p=0.11$][22]. There was no Target Colour main effect [$F(7,133) = 1.36$, $p=0.23$] and, critically, there was no interaction with competition [$F(7,133) = 0.88$, $p=0.53$].

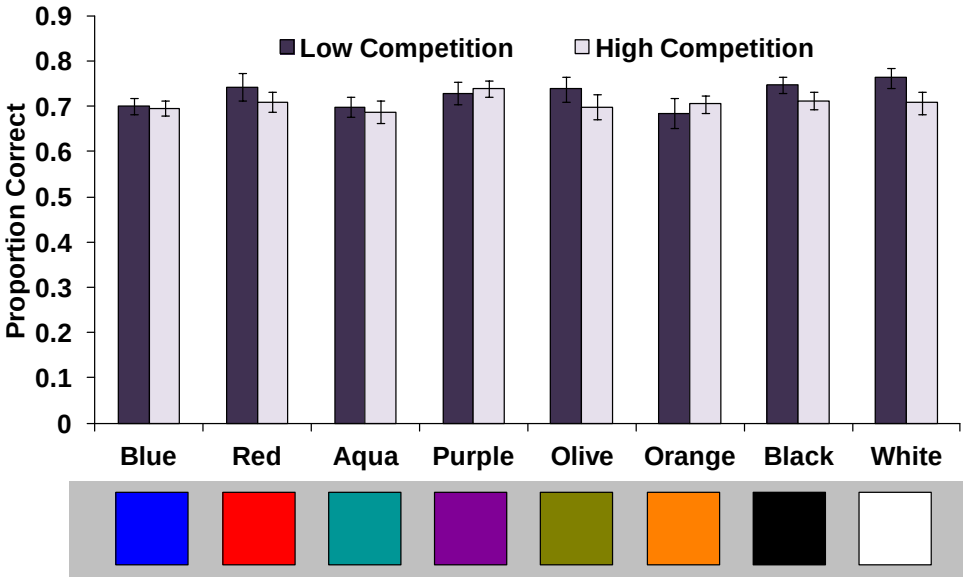


Figure 6.5: Results for the follow up colour analysis. Proportion correct for each of the eight colours used in the experiment as a function of whether the arrows were all the same colour (*high competition)* or all different colours (*low competition*). A

[22] Note: The discrepancy with the previous analysis is due to differences in trial numbers for the eight target colours within each competition condition. This led to subtle differences in the weighting of each condition for each participant. For an infinite number of trials and an infinite number of participants, this comparison would yield exactly the same results as the previous ANOVA.

representation of each colour is shown below the *x*-axis against the background colour used in the experiment.

Overall, the results suggest that colour can induce inter-item competition in a similar way to spatial-based competitive dynamics. Similarity in colour triggers competitive interactions that are ultimately detrimental to VSTM performance. It appears that the additional colour information can aid recall despite the additional computations needed to code this information. Similarly, previous research has found no additional cost of storing additional object features and this process is automatic (e.g. Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). This experiment, however, suggests that this additional information can actually facilitate performance. This result, furthermore, could not be explained by differences in low-level colour or contrast salience between stimuli in the *low competition* condition.

These results extend the findings of a recent study conducted by Lin and Luck (2009) who manipulated the similarity in colour between to-be-remembered in a memory array and tested memory for colour using a change detection task. For both simultaneous and sequential displays of the memory array, VSTM performance was higher when items were all similar colours compared if one or more dissimilar colour(s) were included. They concluded that feature-based similarity can facilitate performance perhaps by local inhibitory mechanisms sharpening similar representations of colour. They speculated that additional attention may have been required to encode the arrays with similar colours and as such, their results may have been explained by differences in encoding strategy between the colour conditions. The findings of the current experiment, however,

suggest that similarity in colour elicited competitive rather than co-operative dynamics among items. This may be due to an important design element in the current study which eliminates encoding strategy as a possible explanation. Because the difficulty of discrimination was varied orthogonally to the manipulation competition, competition was task irrelevant thus, attentional and strategic effects should not explain the results. It shows that unique but task-irrelevant information can facilitate VSTM performance, possibly by individuating items in memory.

6.5 General Discussion

In this series of four experiments there is evidence that inter-item interactions can extend into VSTM maintenance. Furthermore, the differences in performance cannot be accounted for by the perceptual differences between the two conditions. Interestingly, the effects of competition were consistent across spatial and feature-based (colour) manipulations. Higher spatial inter-item competition led to a reduction in VSTM performance, presumably due to an inability to disambiguate items across overlapping receptive fields. Similarly, memory arrays of the same colour (high competition) were detrimental to performance. The consistency with this competitive effect of closely spaced and monochromatic arrays suggest that space and other stimulus features, at least in the tasks presented here, are affected by similar dynamics and constraints in the visual system.

Interestingly, the results of Experiment 1 were in accordance with expectations but were in contrast to the results of previous research (e.g. Lin & Luck, 2009; Shapiro & Miller, 2011). Importantly in the current design, the stimulus

dimension along which inter-item competition was created was not needed to perform the task. Because colour was task-relevant in the design used by Lin and Luck (2009), differences in strategies for the similar colour condition may have led to the subtle differences between items being coded, which consequently led to improved performance and a co-operative benefit for similar (high competition) items. Here this confound was eliminated by showing that task-irrelevant features were still able to affect VSTM performance. The exact mechanisms of stimulus relevance, however, should be investigated in future studies and extended to other feature-based dimensions.

Given that the design of the current experiment was based on a manipulation known to influence perception (e.g. Müller-Plath & Elsner, 2007; Shim et al., 2008), it was difficult to ensure that the differences in VSTM performance were not due to effects at perception and encoding. Although there was a trend towards a difference in perceptual search performance between the two conditions in Experiment 2, this may be due to the increased selection pressures in the search task. As such, one can argue that the design of Experiment 3 may have been more suitable to assess the constraints on encoding in Experiment 1. Critically, differing the potential encoding time from 200ms did not differentially change the pattern of differences between the two competition conditions. This suggests that encoding time did not differentially affect performance in the *high* and *low competition* conditions and thus the parameters enabled the testing of effects on VSTM, not perception in Experiment 1.

If we can conclude that the competitive effects are due to maintenance, not encoding, then the question remains, where do competitive interactions emerge?

The retinotopic organisation of visual cortex and increasing RF size as more information is integrated up the processing hierarchy means that it may be possible to track the evolution of spatially based competition. The results may suggest that the increased spatial proximity between items created a situation of inter-item competition earlier (should be approximately V1 for the high spatial competition condition or V2+ for the low spatial competition condition; Kastner et al., 2001) in the visual processing hierarchy which ultimately reduced VSTM performance. Competition in early visual areas is important for two reasons. Firstly, some of the early visual areas which are involved in perceptual processing are also directly involved in maintenance (e.g. Harrison & Tong, 2009). Secondly, the earlier in the system items compete, the more time items can interact and these competitive dynamics can ultimately affect performance. The recurrent feedback loops between visual and associative areas during maintenance also suggests that greater competition in early areas can still potentially affect performance (see Raffone & Wolters, 2001).

The explanation is not so intuitive when it comes to the competitive feature-based effect of Experiment 4. It was expected that if there are limited resources to represent each colour, then multiple items of the same colour would need to compete for representation. Although these results are in accordance with expectations, they do contrast with those found by Beck and Kastner (2007). In their fMRI task, BOLD suppression in visual areas was used as an index of inter-item competition. Participants were presented with homogeneous and heterogeneous displays in an unattended, peripheral location. BOLD suppression was lower for homogeneous compared to heterogeneous stimuli suggesting that

heterogeneous arrays elicit greater inter-item competition. In the current task, however, the stimuli were all task relevant and any item could have potentially been a target. High competition (similar arrays) may have facilitated some sort of grouping mechanism that could assist in the processing of the items as a single unit rather than as individual items. Such principles are based on perceptual groups which are fundamental efficient visual search performance (Alexander & Zelinsky, 2011; Duncan & Humphreys, 1989). Despite item similarity assisting visual search performance, it did not assist performance in this task, especially since a single probe was presented to encourage the coding of individual items to reduce reliance on configural or perceptual groups. Ultimately, however, in the *low competition* condition, there was more information to encode overall. The results are especially interesting, therefore, because colour information was task-irrelevant but it still managed to facilitate performance.

An alternative interpretation of the competition model, however, may have predicted opposite results to those found in Experiment 4. Instead of considering resources being limited to each colour (e.g. each item competes for limited "red" resources on *high competition* trials), there may be a limited generic "colour" resource pool, so when multiple colours are presented, each colour category must compete for representation (see also Scalf & Beck, 2010; Shapiro & Miller, 2011). When there is only one colour (like *high competition* condition in Experiment 4), there is no "inter-category" competition, so only one colour needs to be coded. This explanation concurs with the literature which suggests that changing the number of perceptual groups (e.g. colours) has a fundamental effect on the organisation of perceptual analysis for visual search (Bundesen & Petersen, 1983) and implies that

suppressive influences act between rather than within perceptual categories (see also Beck & Kastner, 2007). The results of Experiment 4, however, suggest that task-irrelevant but unique information can assist recall possibly by forming multiple perceptual groups to individuate items. Future research should directly compare performance for memory and visual search efficiency for this type of task.

Lin and Luck (2009) proposed a number of reasons to account for their increase in VSTM performance for items from similarly coloured arrays. They suggest that local inhibitory mechanisms may sharpen similar representations and stabilise them during maintenance over time. For successful performance in this task, it is important to have sharp, precise representations to make correct colour judgements. In the current experiment, colour was not task-relevant and so was not coded and maintained in the same way. Rather than identically coloured, future research should include a condition with similarly coloured items to see whether the subtle differences between items can sharpen the representation, even when task irrelevant.

It is important to note, that the equivalent perceptual controls for Experiment 4 were not run like the ones for Experiment 1[23]. Ideally one should test that 200ms is sufficient time to encode the multi-coloured arrays by differing the encoding duration (like Experiment 3 presented here). The effect of inter-item competition can also be investigated via the effect of orienting attention to the target item during maintenance (see Chapter 4). Here, the perceptual demands are equal at encoding because the target item is still unknown. If there is indeed inter-item competition during maintenance, then one would expect to see greater cueing benefits for

[23] An analogous task to Experiment 3, however, was conducted to ensure 200ms was sufficient to encode arrays of the same colour (equivalent to the *low competition* condition in Experiment 4; see Appendix C).

higher set sizes because the resolution of competition would occur during maintenance rather than at the presentation of the probe. Specifically, as set size increases, the greater the relief when the inter-item competition is resolved as early as possible. If inter-item competition is resolved at encoding, however, then the cueing benefit should be equivalent across set sizes because the limited number of VSTM representations has already been determined and the “winning” items no longer interact.

Future research should also extend the findings of the current study by testing competition in other feature-based, non-spatial dimensions (e.g. line orientation). Orientation is unique in the way comparatively large arrays of items of similar orientations can create illusory contour effects (see Greenwood, Bex, & Dakin, 2010) which may facilitate memory performance for an orthogonal stimulus dimension. Orientation similarity would be particularly interesting due to the regular organisation of orientation columns in early visual areas (e.g. Hubel & Wiesel, 1968). Like spatial competition, the regularity in columnar organisation means it should be easy to track inter-item competition in neural ensembles using multivariate decoding approaches of neuroimaging data (e.g. fMRI or MEG; see Haynes & Rees, 2005).

The results of the current experiment not only provide an interesting insight into the dynamics of inter-item competition in VSTM but raise a range of possibilities for future research. This suggests that inter-item competition does affect VSTM performance, even on an orthogonal dimension to what is task relevant. It is this specific manipulation which is the ultimate test of competition because differences in strategy cannot account for differences in performance (cf.

Lin & Luck, 2009; Shapiro & Miller, 2011). Critically, the results provide evidence that competition does affect VSTM, even when accounting for the differential perceptual constraints of the two competition conditions. Future research, however, needs to concentrate on examining the effects of competition throughout the VSTM maintenance period. Additionally, the results suggest a greater correspondence between neuronal populations underlying VSTM and perception (e.g. Harrison & Tong, 2009; Serences et al., 2009; Stokes & Nobre, 2012; Woloszyn & Sheinberg, 2009). The results of the current experiments can, therefore, provide a unique insight into the mechanisms underlying VSTM and suggests that VSTM is not a static storage unit but a dynamic representation that may, like perception, continue to be shaped by inter-item interactions.

CHAPTER 7

General Discussion

The General Discussion is divided according to the main themes explored in the thesis by drawing upon the results presented in the experimental Chapters. Invariably, in science, experiments ultimately result in more questions than were considered in the initial aims. These resulting questions are often more important than the “answers” themselves. As such, after the discussion of each theme, if applicable, I shall outline some of the unanswered questions brought about by the work of the thesis and discuss how future research could extend the current results. This chapter will then close with a brief summary and conclusions to the ideas discussed.

7.1 Themes Explored in the Thesis

The series of experiments presented in the previous four experimental chapters manipulated both attentional and perceptual mechanisms to investigate the characteristics of capacity limits of VSTM. Novel paradigms were applied to age-old debates regarding how processing in our visual system is organised and modulated in order to optimise VSTM performance according to task goals. This section of the discussion will draw upon results presented in this thesis to give new insight into the limitations which define VSTM. Six main themes will be discussed.

7.1.1 The Number and Precision of Items in VSTM – Slots versus Infinite Flexibility

This thesis differs from most previous research addressing the debate about the flexibility of allocating VSTM resources by investigating the effects of selective attention upon the number versus precision of items in VSTM. Building upon the previous knowledge of anticipatory and retrospective attention outlined in Section 1.5.2, the experiments presented in Chapters 3 and 4 demonstrate how attention can modulate the precision and probability of recall of VSTM representations.

Overall, the effects of orienting attention were detected on the probability of recall, rather than on the precision of representations. As such, attention appears to operate by selecting (Chapter 3) or transforming (Chapter 4) whole-item representations into a robust form of VSTM. From the lack of evidence showing that precision is modulated by top-down signals, it appears that attention acts on items, represented perceptually (Chapter 3) or mnemonically (Chapter 4) rather than by enhancing the quality of the representation at the cued spatial location. The discrete nature of the current attentional results also concurs with previous work which suggests that the limitations in our visual attention are defined by the number of integrated objects presented simultaneously (e.g. Duncan, 1984; Scholl, 2001). The observed effects of selective attention on enhancing the probability of recall rather than precision of VSTM items add credence to the notion of discrete “slots” for representing items with high precision, regardless of task demands (Anderson et al., 2011; Awh et al., 2007; Buschman et al., 2011; Luck & Vogel, 1997; Zhang & Luck, 2008).

The inability to trade the number of representations for increases in representational precision is further evidence that the flexibility over the allocation of VSTM resources is highly limited (Chapter 5). The results suggest that resources are primarily allocated based on stimulus driven factors. Resources appear to be divided according to the number of items presented rather than by prior knowledge of the likely task demands. Importantly, this does not suggest that VSTM is static or inflexible, only that the particular ability to trade the number for an increase in the quality of representations is not under top-down control.

Although this thesis does lend some support to the slot-based models of VSTM resource allocation, it is not possible to conclude categorically that there is no effect of attention on the precision of items in VSTM. The experiments from this thesis did not systematically measure the effects of attention in situations above and below conventional item capacity limits. As such, the results did not show any evidence of the hallmark drop in precision once capacity was exceeded. Nonetheless, the evidence presented shows that both prospective and retrospective attention can enhance the probability that task-relevant representations are maintained without sharpening their representational precision.

Because the effects of anticipatory (Chapter 3) and retrospective attention (Chapter 4) were investigated in separate, non-comparable experiments, another study should be run to compare directly these effects on the precision and probability of recall of representations (akin to Griffin & Nobre, 2003). This would also be interesting for determining which type of attention has a greater effect on the probability of recall and for investigating any interactive effects between the two types of attention, especially at high loads.

One possible reason for the observed attentional affects on the probability of recall rather than the precision of representations was the use of suprathreshold stimuli. The interactions between attention and VSTM found in Chapters 3 and 4 contrast with evidence that attention modulates the *quality* of perceptual processing (e.g. Reynolds & Chelazzi, 2004). This difference could provide evidence for a fundamental distinction between 'attention for perception' versus 'attention for VSTM'. For perceptual tasks discrimination judgements are usually made about low-contrast or degraded stimuli. In these cases, attention can facilitate processing to enhance perceptual analysis, and ultimately, to enhance the quality of the information that is available to post-perceptual processes, including VSTM.

In all of the experimental chapters of the current thesis, the stimuli were high contrast and easily perceptible against the background colour. This is important, as it means that the processing limit in the experiments presented here is not perceptual, but rather the challenge is to maintain as much task-relevant information as possible. Interestingly, the results of Chapter 6 suggest that the use of multi-coloured arrays further facilitated performance and created highly discriminable, individuated items in memory. The limiting factor, therefore, is selection: either from the perceptual trace (as in Chapter 3) or from a fragile internal representation (as in Chapter 4). Under these circumstances, the results suggest that the mechanisms of attention do not influence the perceptual quality of the representations, but rather the likelihood that the results of perception are successfully maintained.

Presumably, there would have been a different pattern of results, however, if tilted Gabor patches had been used with individually calibrated near-threshold

contrasts. In this case, pre- and retro-cueing may have benefited performance by decreasing the contrast threshold for items to be perceived and subsequently maintained in VSTM. With this design, it is more likely that the ERP signatures reflecting enhanced cortical excitation in anticipation of perceptually difficult stimuli may be closely linked with performance e.g. LDAP (see Hopf & Mangun, 2000). Future research could explore these notions and determine whether there is direct evidence of a dissociation between attention for perception versus attention for VSTM. More likely, there are different consequences of attention when the limiting factor is perceptual discrimination versus selection of stimuli in either perceptual or VSTM tasks. Alternatively, the number and precision of representations in VSTM may be regulated by common mechanisms but it may simply be more difficult to influence precision. Another possible factor which may have contributed to the results of the current thesis is the use of a discrete, binary forced choice experimental design. The use of a continuous response “wheel” (see Zhang & Luck, 2008) may have yielded different results. Future research should determine whether this is the case.

Finally, the relative improvement of the reliability of source localisation of MEG, in comparison to EEG, would make this a useful technique to dissociate CDA sources from inferior and superior IPS (Anderson et al., 2011). Currently, there is no convenient online measure of the quality of item information in VSTM (Fukuda et al., 2010a). This may mean that the results of the current thesis may have been biased to interpret results (trends) in individual cueing benefits as only affecting the number of items being maintained as indexed by CDA amplitude.

It would also be interesting to examine the oscillatory[24] correlates of the encoding and maintaining precise (compared to coarse) representations. Precise representations may be associated with greater phase synchronisation, enabling greater communication between networks (see Fell & Axmacher, 2011). Greater phase coherence between the areas may facilitate integration and individuation of items in VSTM. In an analogous way to the experiment conducted in Chapter 3, it may be possible to observe a correspondence between the oscillatory reflection of anticipatory attention and VSTM performance. A greater contralateral alpha desynchronisation to the pre-cue may reflect a more attentive state which may result in more efficient selection of items or more precise encoding of relevant items which should ultimately impact upon VSTM importance.

7.1.2 The Number and Precision of Items in VSTM – Separate Mechanisms?

In parallel to the slots vs. resource debate regarding the nature of VSTM resource allocation, there has been a suggestion that the number and quality of representations are functionally distinct memory attributes (Chun, 2011). Current behavioural (Awh et al., 2007), individual differences (Fukuda et al., 2010b; Gold et al., 2010; Scolari et al., 2008) and neuroimaging (e.g. Xu & Chun, 2006, 2009) research supports this dissociation. The implications of two key results of the current thesis are relevant to this line of argument and may be consistent with this notion. The first is regarding the divergent effects of attention on the number and

[24] For more details of brain oscillatory brain activity, see Section 2.5.3.

precision of representations in VSTM (Chapters 3 and 4). The second is the inability to trade between number and quality of representations as shown in Chapter 5.

Firstly, the experiment in Chapter 3 provides evidence that preparatory spatial attention can dissociate the quality and probability of recall. Preparatory attention affected the probability that items were successfully recalled rather than the precision with which they were recalled. Furthermore, the magnitude of the electrophysiological signatures of anticipatory attention (EDAN and ADAN) also predicted the behavioural benefit gained from the cue, in terms of both sensitivity (d') and probability of recall (asymptote parameter λ). Similarly, retrospective attention only affected the probability of recall, rather than the precision of representations (Chapter 4). In both prospective and retrospective cases, therefore, attentional orienting only affected the number of items in memory rather than the quality of memories. This dissociation between the effects of attention on the precision of representations and the probability that they are successfully maintained is consistent with the argument that these abilities are distinct characteristics of VSTM.

In addition to the divergent effects of attention on the precision and probability of recall, the lack of evidence to show the ability to trade flexibly between the number and precision of representations is at least consistent with the idea that these attributes are separate. If indeed the number and precision of representations are determined by fundamentally different mechanisms, and supported by different neuronal populations (for analogous discussion see Xu, 2007; Xu & Chun, 2006, 2009), then it would not be possible to share resources flexibly between them, even if beneficial for task performance. Across four experiments, the results presented in

Chapter 5 showed a resounding inability to flexibly control the trade-off between the number and precision of representations. This was even the case when the task context strongly encouraged encoding and maintaining a low number of items with high precision, as in the final experiment (Section 5.5). Participants were simply unable to use the task context to optimise their performance. Such a result provides evidence that the flexibility in setting the balance between the number and quality of representations by contextual or voluntary factors is minimal or non-existent.

The notion that the number and precision of items are separate mechanisms is becoming increasingly popular in the literature (see also Chun, 2011). Although the following studies presented by Chun's group were not designed to test directly the number and precision of items in VSTM, the implications are very relevant for the current thesis. In their neural object-file theory of visual perception, Xu and Chun (2009) suggest that the first step of object identification involves the creation of a number of coarsely coded "object files" which correspond to the number of to-be-represented items (approximately four). Activity from the inferior IPS has been associated with this process by reflecting only the number of items in the display (see also Todd & Marois, 2004; Xu, 2007; Xu, 2009; Xu & Chun, 2006, 2009). The second stage then incorporates feature bindings and complex visual information by updating these object files, and identification can result. The limit of this higher order visual information is defined by the informational content regardless of the number of items, and is reflected by activity in the superior IPS and LOC (Xu, 2007; Xu, 2009; Xu & Chun, 2006). With the correspondence between VSTM and perception (see Chapter 6), this theory maps nicely onto the potential dissociation between the number and precision of items in VSTM.

If quality and number of representations are fundamentally distinct and based on separate resources, then one needs to reconcile this with the previous research suggesting that resolution decreases as the number of items increases (e.g. Barton et al., 2009; Bays & Husain, 2008). One possibility is that the limitation in performance comes from the ability to *integrate* the two characteristics into coherent representations, rather than from an intrinsic limitation in the quality or number of resolutions themselves. Accessing information about many objects simultaneously may result in an apparent loss of quality in each item, not because there are insufficient 'precision' resources but because there is a limitation in the ability to integrate representations into a coherent form. Estimates of the number of items which can be represented in VSTM and the number of items that can be attended, give support to the notion that attention is involved in this integration process (for a greater discussion on this see Section 7.1.3). Presumably, as the results of Chapter 5 suggest, there is little flexible control over whether information about number and identity of items or precision information is prioritised during access and transformation of items into VSTM.

Future experimentation should explore whether the number and precision of items in VSTM are indeed determined by separate mechanisms. Transcranial Magnetic Stimulation (TMS) is a natural candidate for testing whether separate neural structures are causally involved. It would be interesting to use TMS to test the proposed dissociation between the roles of inferior and superior IPS in determining the number and feature information in the perceptual analysis of the visual scene (Xu & Chun, 2009), and to test whether these areas play an analogous role in determining the number and precision of representations in VSTM. If this is

true, then applying TMS to the inferior or superior IPS during encoding or maintenance should influence the number or precision of representations selectively. This would provide causal evidence for the separability of VSTM number and precision both functionally and anatomically.

The results of Chapter 5 provide a resounding lack of evidence to suggest that the trade-off between the number and quality of representations is under top-down control. In a study recently accepted for publication, Zhang and Luck (2011) find a similar pattern of results, and also show no evidence that participants can trade-off the number of representations for an increase in precision, even if given financial incentive to do so. To test the generality of this notion, a future experiment should test whether feature-based reward manipulations can influence the trade-off between the probability of recall and the precision of representations. Rewarded features or items may “capture” VSTM resources and thus gain prioritised access into VSTM. If given such a direct entry into VSTM, these rewarded items may be represented with both a higher precision and probability of recall. If resources are unevenly distributed toward rewarded items, then it would be expected that the representations of non-rewarded stimuli would suffer accordingly. There may be mechanisms which boosts VSTM resources to represent rewarded items akin to PFC boosting posterior capacity limits (see Edin et al., 2009). It would be important to see how higher-order processes supplement or bias the allocation of VSTM resources to increase the precision or probability of recall of task-relevant information. It would be important, however, to separate the effects of attentional and reward-related orienting to items by fully crossing these factors and dissociating them by examining the separate and interactive effects (see

Rutherford, O'Brien, & Raymond, 2010). To do this, I would train participants to associate a stimulus feature (such as blue items) with a financial reward. It be may the case, however, that participants automatically attend to this feature. To dissociate attentional effects from reward associations, I would also pre-cue an orthogonal stimulus feature (e.g. vertical orientation) on some trials. As such, attention and reward association would be fully crossed: targets could be rewarded, attended, rewarded and attended or neither rewarded nor attended. Such a design would enable the examination of reward on the distribution of VSTM resources.

7.1.3 Is Attention the Limiting Factor for VSTM?

Attention has clearly been implicated in assisting the transfer of perceptual information into VSTM (Gazzaley, 2011; Schmidt et al., 2002). Also, consider the role of attentional orienting towards particular items to transfer relevant representations to a useful, probable format during maintenance (see Chapter 4, e.g. Griffin & Nobre, 2003; Sligte et al., 2008). The notion that attention is critical in the encoding of items (either during perception or during maintenance in the fragile visual store) into VSTM is becoming more established in the literature (Gazzaley & Nobre, in press; see also Lepsien & Nobre, 2006; Palmer, 1990). If the number and precision of representations are separate memory functions, attention may play an important role in selecting and integrating item representations into a coherent and retrievable format.

The number of items to which attention can be oriented in the perceptual domain coincides with the number of items that can typically be represented in VSTM (Bettencourt, Michalka, & Somers, 2011; Cavanagh & Alvarez, 2005; Culham, Cavanagh, & Kanwisher, 2001; Scholl, 2001). The similarity has even led people to suggest that spatial attention and VSTM are fundamentally based on the same mechanisms (for different accounts see Awh & Jonides, 2001; Cowan, 2001; Desimone, 1996; Kastner & Ungerleider, 2000). Both attention and VSTM can modulate processing in visual cortex in the absence of immediate sensory input, and there is a great deal of similarity between these signals, at least within these task designs (Chelazzi et al., 1993; Kastner & Ungerleider, 2000; Luck et al., 1997). Dovetailing these results, there is neuroimaging evidence that both attention and working memory are supported by highly overlapping networks involving prefrontal and parietal regions (for a review see Awh & Jonides, 2001; Desimone, 1998; Marois & Ivanoff, 2005).

As further evidence, results of previous experiments have shown the impairment of memory performance when a secondary, attentionally demanding task is performed during the delay period of a VSTM task (Fougnie & Marois, 2006; Makovski, Shim, & Jiang, 2006). Behavioural experiments have shown impaired spatial working memory when attention was directed away from the remembered location (Awh, Jonides, & Reuter-Lorenz, 1998). Interestingly, the results of a study conducted by Makovski and colleagues (2006) suggest that attending in either visual or auditory modality impairs visual change-detection performance, whereas passive viewing/listening has minimal impact. Structures in higher-order, associative areas, such as PFC are excellent candidates for the source of this

amodal mechanism which co-ordinates representations in earlier sensory areas (Curtis & D'Esposito, 2003; Postle, 2006). As previously discussed, PFC is functionally connected to visual areas and can modulate VSTM representations in light of new task-relevant information (e.g. Kuo et al., 2011; Lepsien & Nobre, 2006; Nobre et al., 2004). As further evidence, the changes in functional correlation between PFC and visual areas can predict the strength of top-down modulation and associated VSTM performance (Bollinger et al., 2010; Sergent et al., 2011). These effects are supported by a recent TMS study which provided direct evidence that perturbing PFC function diminishes the top-down attentional modulation of perceptual processing which ultimately undermined VSTM performance (Zanto et al., 2011).

The limit of attentional capacity reflects the number of items which can be attended simultaneously: about 4-5 items (Bettencourt et al., 2011; Cavanagh & Alvarez, 2005; Culham et al., 2001; Scholl, 2001). With this reasoning, it may be the case that VSTM capacity is also limited to this number because this is the maximal number of representations which attention can integrate successfully from object and feature information[25]. The results of the current thesis suggest that attention can prioritise the encoding and transformation of the task-relevant representations into robust VSTM. This was shown when anticipatory attention was directed to a visual hemifield (Chapter 3) and when attention was directed to a spatial location during a maintenance period (Chapter 4). These results are consistent with previous research which demonstrates the critical role that attentional efficiency and

[25] This is analogues to the model proposed by Wheeler and Treisman (2002) who emphasise the importance of attention in binding representations of disparate features into coherent objects.

strategy have in VSTM performance. For example, IIhssen and colleagues (2010) show increased capacity for arrays where items are sequenced or repeated over time. They suggest that these conditions can alleviate some of the problems of simultaneous presentation possibly because participants can pay attention to parts of the array at a time. The notion that emerges, therefore, is that attentional limitations are critical in determining VSTM performance, however, it is still controversial as to whether attention is the sole contributor to VSTM capacity limits.

To attempt to discern whether VSTM capacity is only limited by attention, Fougnie and Marois (2006) compared the dual-task costs of performing working memory tasks and visual attention multiple object tracking (MOT) task. For high loads, they found significant bi-directional dual-task costs when participants performed the (1) visual change-detection (CD) and MOT tasks, (2) the CD and verbal working memory task. The results suggest that attention is not the sole limiting factor, but limitations in attention clearly contribute to the limitations in VSTM.

Future research should explore directly whether the ability to orient attention to select and integrate relevant items during encoding and during maintenance correlates directly with VSTM performance. The experiments in Chapter 3 suggested a correlation between selective attention during encoding and subsequent VSTM performance by showing that individual differences in the electrophysiological signature of shifting anticipatory attention predicted the benefit gained from the cue. This approach could be adapted to explore whether attentional orienting during the maintenance period is involved in selecting items from a fragile store into a robust VSTM format. In a recent study conducted by Kuo and

colleagues (2012), the magnitude of the CDA dropped significantly after the presentation of a spatial retro-cue presented during the maintenance period. The effect was interpreted to reflect the reduction in VSTM load after selection of the relevant, cued item that needed to be maintained. The size of this drop in lateralised electrophysiological activity may be linked to the increase in the probability of recall gained from the retro-cue. Future research should extend the retro-cueing paradigm presented in Chapter 4 to determine the individual differences in the interaction between maintenance activity and the precision and probability of recall of representations.

Other lines of research based on individual differences could provide an important insight into the effects found in this thesis. In a recent study, for example, attention-related differences in item-selection strategy during encoding accounted for differences in VSTM performance between participants with high versus low VSTM capacity (Linke et al., 2011). Previous research, in addition, has suggested that intelligence is related to the number and not the precision of representations (Fukuda et al., 2010b). The number and precision of the representations of items in memory are, furthermore, differentially affected in those who suffer from psychiatric disorders (Gold et al., 2010).

The tasks used in the current thesis should be conducted, therefore, on a more diverse population of participants to determine how the attentional cueing benefits, ability to trade the number and quality of representations, and the effects of inter-item competition differ between individuals. This would give a complementary understanding of how attention and perception enhance or constrain VSTM performance. For example, it may have been the case that the

studied population did not benefit fully from the contextual trade-off information (Chapter 5) because they were already allocating resources optimally. This would suggest that the trade-off is under voluntary control at least under certain circumstances. If low-capacity participants did not benefit from the attentional cues presented (Chapter 3 and 4), it may give an insight into how attentional selection determines VSTM performance.

7.1.4 What does Attention Do?

The results of the current thesis suggest that attention only affects the probability that representations are successfully recalled rather than the precision with which they are recalled (cf. Bays et al., 2011)[26]. Despite the similarity in the results between prospective and retrospective orienting of attention on VSTM performance, however, I argue that the underlying processes for information entering VSTM from a perceptual compared to an internal representation are quite different.

In the case of orienting anticipatory attention (Chapter 3), the visual system can be prepared to select and encode only the task relevant items. This process was reflected by electrophysiological signatures of anticipatory attention (ADAN and EDAN). If the number of pre-cued items does not exceed capacity, like the case in the results presented in this thesis, then the selection process should transfer items directly from the perceptual representation to VSTM. There should be minimal or no

[26] This result, however, may be due to the use of two item arrays by Bays and colleagues as this is well below capacity limits. There may have been already sufficient resources to code and maintain both items so the benefits were observed in precision rather than the probability of recall.

inter-item competition because the issue of which information will be represented by the limited resources is resolved by the orienting of attention to a subset of items via the pre-cue. In this case, cues pre-select which integrated object representations are prioritised and maintained. The probability of recall should be increased (as was found), possibly due to the reduced inter-item competition.

In addition, the precision of pre-cued representations should be high because the selection mechanism should enable the integration and encoding of object features in VSTM. Because there was only a trend for an increase in precision for cued compared to neutral trials, the results of the current thesis only provide marginal support to the idea that pre-cueing should result in high precision of presentations. However, this may be attributed to the fact that it was only possible to model precision for the smallest set size, which is already well below capacity, even in the neutral condition. There may have already been sufficient resources to code all items in the neutral condition so the cueing benefits in precision may have been underestimated. Future research should concentrate on extending this type of paradigm to include larger set sizes.

In the case of retrospective orienting of attention, however, there is no indication from the beginning of the trial about which item(s) may be task relevant. The system should then code as much information as possible, which may result in lower representational quality per item. Attention may not, therefore, be able to restore the loss of “quality” of representations due to decay or inter-item competition before the cue onset (see also Palmer, 1990). In the volatile, pre-attentive state, item representations should compete for representation by robust VSTM. This competition is resolved, however, by orienting attention to one (Chapter 4) or more

items (Delvenne & Holt, in press; Lepsien et al., 2011b) during maintenance. Attention strengthens the representation and directs the allocation of resources to the item so it is more likely to "win" the inter-item competition and thus increase the probability that it is successfully recalled.

The orienting of retrospective attention to the cued item, however, does more than simply resolve the inter-item competition earlier during the delay period[27]. The results of Chapter 4 suggest that attention somehow transforms the representation into a format that is more robust than if memory was probed at that time during the delay (see also Makovski et al., 2008). The period of time between the presentation of the cue and the probe is crucial in consolidating the representation into VSTM (in Chapter 4 it was 800ms). If they reduced the delay period after the presentation of the cue, Sligte and colleagues (2008) found that the retro-cueing benefits were greatly diminished. Like the encoding from the perceptual representation to VSTM via a pre-cue, the orienting of attention during maintenance transfers the cued items from the high capacity visual store into VSTM. This suggests that there is more information present in the visual system than is readily accessible (see also Astle et al., 2010b).

In the absence of top-down signals (cf. Chapters 3 and 4) the items that will be available for further processing may be determined by a number of factors. Presumably, these successful items which enter VSTM are the "winners" of inter-item competition (see Chapter 6). Factors which affect this dynamic interplay may include the perceptual features of items such as visual salience or how unexpected

[27] Further evidence that attention is not only involved in reducing inter-item competition is the fact that the retro-cueing benefit does not increase as the set size is increased (Experiment 1 in Chapter 4; see also Makovski, Sussman and Jiang (2008)).

the stimulus is (Corbetta & Shulman, 2002; Itti & Koch, 2001). Competition is also likely to be biased toward information that is important for survival or relevant to current task goals. Information can still enter VSTM automatically, that is, without deliberate attempts to select items in particular.

Future research should be devoted to comparing the modulatory mechanisms triggered by orienting attention before encoding versus during the maintenance period. MEG[28] could provide novel insights into, for example, the source and evolution of the anticipatory signals in Chapter 3 and of the top-down signal elicited by the retro-cue in Chapter 4. However, unlike the well documented ERP signatures of attention and VSTM, the equivalent ERFs (Event Related Fields) are still under investigation (e.g. Robitaille et al., 2010). For the analyses conducted in Chapter 3 for example, it was important to have well defined signals to correlate with behaviour.

In the current thesis, only spatial attention was manipulated via either a hemifield pre-cue (Chapter 3) or a cue in the spatial location of the cued item (Chapter 4). It may not be the case, therefore, that these effects extend to cueing non-spatial features. One might expect that feature-based cueing may enhance the precision of representations as opposed to spatial cueing, which may facilitate the spatial indexing or individuating of items. Another key way to extend the work of the current thesis would be, therefore, to test the effects of feature-based attention in the precision and probability of recall of item representations. Further work could also asses the interaction between spatial and feature based attentional effects (see also Hillyard & Anllo-Vento, 1998).

[28] For more details on MEG see Section 2.5.1.

Recent evidence suggests that some of the effects of attention on VSTM performance can be attributed to the suppression of distracting information (e.g. Zanto & Gazzaley, 2009). In the current thesis, there were no known distracters present in the cued hemifield. That is, all cued items could potentially have been the target. It may be important to determine the effects of attention when items need to be selected from a cued location in combination with suppressing distracters along an orthogonal dimension (e.g. colour).

Another notion which is not explored in this thesis is the idea that, once in VSTM, these robust representations are simply the reflection of attention in anticipation of the probe (Lepsien, Thornton, & Nobre, 2011a). The similarity of the structure of typical tasks involving anticipatory attention and VSTM also concurs with this notion (Stokes, 2011). The period of anticipation after the presentation of the cue is analogous to the delay period of a VSTM task because the visual system is maintaining the identity and meaning of the cue. The intrinsic link between VSTM maintenance and perceptual anticipation makes good ecological sense, since VSTM is for guiding future behaviour. Accordingly, areas such as PFC, which are clearly involved in VSTM maintenance, are also critical in co-ordinating the prospective use of information (Sakai & Passingham, 2003). Both retrospective and prospective functions are essential in VSTM tasks, which involve comparing an internal mnemonic representation to the anticipated perceptual representations of the probe. In recent studies, there is evidence to suggest that at least some of the VSTM delay activity reflects the contents of attention, and not just memory (Lepsien et al., 2011b; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2012; but cf. Kuo et. al (2012)). VSTM delay activity, like the CDA in the current thesis, therefore, may not

simply reflect items being passively maintained but may also be shaped in accordance with expectations of the probe. Future research should be directed to untangle these conflated concepts, and task designs should separately manipulate demands related to item maintenance versus expectation.

7.1.5 The Correspondence Between VSTM and Perception

Although intuitively there is a distinction between VSTM and perception, the results of the current thesis provide support for the notion that there is a high correspondence between them. The results of Chapter 6 suggest that the competition conditions that were based on manipulations known to affect perception (e.g. Müller-Plath & Elsner, 2007; Shim et al., 2008) also affected VSTM performance. Despite being task irrelevant, the proximity between items (Experiment 1) and colour information (Experiment 4) was coded and affected performance. This may be because these perceptually distinct object features were bound into coherent representations in VSTM (Luck & Vogel, 1997; Vogel et al., 2001). Together, these results are in accordance with recent literature showing the ability to decode stimulus-specific maintenance activity in neuronal ensembles associated with perception and encoding during VSTM maintenance (Harrison & Tong, 2009; Serences et al., 2009; Stokes & Nobre, 2012; Woloszyn & Sheinberg, 2009). The results of this thesis are consistent with the notion that there is a great degree of overlap in the neuronal populations which underlie perceptual and mnemonic representations of items.

Future experiments should continue to explore the contribution that perceptual attributes and neural codes make to VSTM representations. For example, experiments could examine the effects of perceptual grouping on subsequent VSTM performance. Care was taken to ensure that inter-item spacing was sufficient to reduce crowding effects. Previous research suggests that consistent spatial regularity affects the relational coding between items but does not appear to affect VSTM capacity (Alvarez & Oliva, 2007). Future research could test whether these spacing parameters affect the precision and probability of recall of representations in the same way.

The results of Chapter 6 suggest that item similarity, which may aid in the formation of perceptual groups, can affect VSTM performance. In the current thesis, however, the orientation of arrow stimuli was fully randomised to reduce any illusory contour effects interacting with the manipulations of interest. Systematic manipulation of perceptual grouping should give a greater insight into how the perceptual trace evolves and is shaped into VSTM representations. The effects of Gestalt grouping principles on the precision and probability of VSTM maintenance would be interesting because grouped items may facilitate holistic processing of the memory array. One might expect a similar effect to that obtained by Lin and Luck (2009; see also Shapiro & Miller (2011)), where subtle differences within the manipulated dimension may promote precise coding strategies and facilitate performance.

If orientation similarity was specifically manipulated, then this could extend the non-spatial competitive feature dimensions explored in this thesis. Orientation similarity would be particularly interesting because the regular organisation of

orientation columns in early visual areas (e.g. Hubel & Wiesel, 1968) should make it possible to track the competitive inter-item dynamics through the visual processing hierarchy (e.g. fMRI or MEG; see Haynes & Rees, 2005). Orientation-based inter-item competition would extend the non-spatial competition effects presented in Chapter 6 and would provide further evidence to suggest that perception is an important determinant of the encoding strategies and successful maintenance of VSTM representations.

Future research could also shed light into continued inter-item dynamics during VSTM maintenance by using a combination of approaches from Chapters 4 and 6. The cueing benefit gained from orienting attention to items during maintenance can be used as an index of relief from the resolution of inter-item competition. If, for example, a cue is presented during maintenance to indicate the item which will be probed, then any inter-item competition should be resolved immediately. The degree of benefit gained from the cue should increase as the number of to-be-remembered items increases (see also Makovski et al., 2008). If, however, competition is resolved at encoding, then only a limited number of items will be maintained in VSTM, so the benefit gained from the cue will remain constant, regardless of the size of the initial memory array. As well as increasing the number of items, competition could be created by increasing the spatial proximity between items or the number of to-be-encoded perceptual groups (see Chapter 6); the greater the competition, the greater the retro-cueing benefit. The one advantage of this technique is that all items are equal upon encoding, so it is only competitive dynamics which will influence the survival of representations until the presentation of the cue.

It is also important for future research to concentrate on investigating the evolution of competition in VSTM maintenance over time. Like the current experiments in Chapter 6, it will be important to create competition conditions where there the differences in perceptual performance are minimised and there is sufficient encoding time for both conditions (see Experiments 2 and 3 from Chapter 6). Then, by manipulating the duration of the delay period, the evolution of competition between items can be examined during VSTM maintenance. If competition continues to affect performance throughout the delay period, then greater differences in performance would be observed at longer delays. In this way, the slopes of the decay functions over time for items in memory should be different for the two competition conditions. If the decay slope is indeed steeper in conditions of high competition, then this would suggest that inter-item competition does not only continue into VSTM maintenance but that this competition directly contributes to VSTM maintenance failure, i.e. forgetting.

It would also be interesting to extend the work of Chapter 6 to a neuroimaging setting. Using Multivariate Pattern Analysis (MVPA) in fMRI, Kuhl, Rissman, Chun and Wagner (2011) were able to decode whether there was competition (or interference) between memories of the same category in ventral occipitotemporal cortex during VSTM at retrieval. As an extension, MVPA could be applied at the sensor level in an MEG experiment to detect differential patterns of competition during VSTM maintenance at the site of competition as defined by the overlap of receptive fields. If a similar design was used to the current experiment, then differences in the pattern of activity resembling inter-item competition should be evident at different visual areas depending on the spatial separation between

stimuli. Previous research has used suppression of BOLD signal (see Section 2.5.2) to index the degree of inter-item competition (for a review see Shapiro & Miller, 2011). To my knowledge, this has yet to be transferred to an MEG or EEG setting. The superior temporal resolution of MEG compared to fMRI would mean that the competitive dynamics could be tracked from perception, encoding, maintenance and retrieval or comparison to the probe. The large number of sensors, furthermore also means that MEG data should be a suitable candidate for multivariate analyses across stimulus specific populations.

7.1.6 Why do we Have Capacity Limits?

Given the importance and ubiquity of VSTM in supporting both sensory and higher level processes, the existence of such a strict upper bound on capacity is of critical importance. The question then arises, why do we have such a capacity limited system? The functional reasons for this bottleneck could be a combination of the following: (1) there are unavoidable limitations on the populations of neurons which can simultaneously support different representations, (2) the computational cost of the active maintenance of information is high, (3) the ecological constraints on how humans can interact with the environment make representations of more than 3-4 items superfluous. These possibilities are not mutually exclusive.

Firstly, if an item-based account of VSTM capacity limitations is accepted, the severe limitation of the number of items may be the result of interactive dynamics between the neural populations representing each item. Mutual inhibition

processes may operate to segregate each concurrent representation to avoid confusion (Edin et al., 2009; Raffone & Wolters, 2001). Such a notion has been cast in terms of the organisation of neural representations according to oscillatory cycles of neuronal activity (Lisman & Idiart, 1995). For example, Siegel, Warden and Miller (2009) found improved VSTM performance was associated with spikes (Action Potentials: APs) occurring at particular phases of synchronised oscillatory activity. Naturally, there is a limit to the amount of information that can be coded by high frequency spike counts at a particular phase of an oscillatory cycle (see Fell & Axmacher, 2011). Beyond this critical amount, representations may no longer be disambiguated, leading to confusion and interference (Luck, 2008; Siegel et al., 2009). In order to prevent this interference, further information may be rejected from entering or being maintained (see also Buschman et al., 2011; Edin et al., 2009). This notion implies that there may be no theoretical limit to the number of possible representations *per se*; rather the modulation of the underlying neural circuitry is the limiting factor in creating and perpetuating robust and stable signals for each to-be-remembered item (see also Compte, Brunel, Goldman-Rakic, & Wang, 2000; Macoveanu, Klingberg, & Tegner, 2006).

Another potential reason for the severe capacity limitation is the high metabolic cost associated with action potentials (Attwell & Laughlin, 2001) which have been implicated with the active maintenance or rehearsal of information (e.g. Miller et al., 1996; Siegel et al., 2009)[29]. As such, we are physiologically limited to the amount of information the brain can simultaneously code and maintain. Current

[29] Recent evidence, suggests, however, that working memory may be maintained through more efficient calcium-mediated synaptic facilitation of relevant recurrent networks (see Mongillo, Barak, & Tsodyks, 2008). However, this still does incur significant metabolic cost.

estimates suggest that the brain already consumes 20% of the energy of the body, despite only weighing 2% of the total body mass (Aiello & Wheeler, 1995; Kety, 1957; Laughlin, Steveninck, & Anderson, 1998). Greater numbers of actively maintained representations may, therefore, prove too metabolically costly to be supported with the current anatomical support structures.

VSTM capacity limitations also make ecological sense. Humans are physically limited in the number of objects and entities with which they can interact. In a typical hunter/gatherer situation, there is a limited need to form a great number of mental representations. In addition, by having only two hands, humans are limited in the number of objects that can be manipulated simultaneously. It may be the case that there is no central capacity limit *per se*, just that humans are limited in the perceptual and sensory information that can be processed so the capacity limitations observed in attention and VSTM tasks is due to the scheduling and co-ordination of processing (Meyer & Kieras, 1997). Once again, this argument would lend itself to attention or executive type processes integrating information into a usable, coherent form.

7.2 Conclusions

Across four experimental Chapters, this thesis has described a series of experiments investigating the effects of attention and perception on the capacity limits of VSTM. Overall, the effects of attention were more evident in the probability of recall rather than the precision of representations. Subtle features in the design

of the tasks, however, mean that attentional effects on the precision of representations cannot be excluded. In Chapter 3, the individual differences of the electrophysiological signatures of anticipatory attention were able to predict the attentional cueing benefits in both sensitivity (d') and asymptote parameters. Similarly, the effect of orienting retrospective attention (Chapter 4) was evident in an increase in recall probability. In this case, attention serves to protect and consolidate the cued item into a robust, "probe-able" format, above and beyond effectively reducing the delay period. The different effects of attention on the precision and probability of recall of representations gives weight to the notion that these are two separate mechanisms, supported by dissociable neural resources.

Although this proposal is still highly speculative, there is an increasing amount of individual differences and neuroimaging evidence in the recent VSTM literature to add further credence that precision and number of representations are distinct. Across four experiments, there was a resounding lack of evidence to suggest that prior knowledge of the likely task demand was able to influence the trade-off between the number and quality of representations. It appears that this ability is not under flexible control.

In keeping with the continued contribution of perceptual attributes and codes to VSTM, it is likely that the competitive dynamics underlying perception also extend into VSTM maintenance. The results of the control experiments, moreover, suggest that competition in VSTM cannot be accounted for by the inter-item competition that occurred only during perceptual processing.

The experiments conducted in this thesis employed a wide range of psychophysical and electrophysiological methods to extend the understanding of capacity limits in VSTM. Unlike other studies to date, these experiments exploited the current knowledge of attention and perception to show how these can alleviate and constrain capacity limits. This combination brings forth new insights to the understanding of the correspondence between VSTM, attention and perception. Although this thesis does not answer the questions asked by Averbach and Coriell (1961) many years ago, it does bring us just a bit closer to understating the capacity and precision of VSTM.

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APPENDIX A

Control Areas for Retrospective Orienting of Attention

Using an activation likelihood estimation (ALE) software package GingerALE (The BrainMap Project, San Antonio, USA), a meta-analysis of the previous fMRI retro-cue studies was conducted. The ALE technique has a number of advantages in that it is based on foci which are weighted by the number of participants in each study and it calculates a quantitative estimate of the probability of activation which is thresholded in accordance with a false discovery rate (here 0.05; The BrainMap Project, San Antonio, USA). Furthermore, this version of the GingerALE procedure is based on random-effects inferences which allow greater generalisation of the results to the population of studies analysed (for more details see Eickhoff et al., 2009; Turkeltaub et al., 2011).

The analysis only included studies and conditions in which the retro-cues were presented more than 500ms after the offset of the memory array to ensure the results were associated with cueing VSTM rather than the iconic trace. Across the five studies, there were 79 foci and 65 participants (Lepsien et al., 2005; Lepsien & Nobre, 2007; Lepsien et al., 2011b; Nobre et al., 2004; Yeh et al., 2007). Co-ordinates from two studies (Nobre et al., 2004; Yeh et al., 2007) were converted from Talairach to MNI/SPM space using the GingerALE interface, based on the tal2icbm_spm Matlab function (Lancaster et al., 2007). The chosen minimum cluster size was the default 200mm^3*[30]The result of the procedure yielded 7

* Note that the number, weighting and significance of these clusters did not change if the minimum cluster size calculated by GingerALE, based on our data (240mm^3) was used.

significant clusters which indicate consistent activation across studies (see table A.1). All clusters had a minimum of two contributing foci.

Table A.1: Significant clusters reflecting the orienting of retro-spective attention calculated across five retro-cueing experiments: (Lepsien et al., 2005; Lepsien & Nobre, 2007; Lepsien et al., 2011b; Nobre et al., 2004; Yeh et al., 2007). Clusters are listed in order of significance and x,y,z, co-ordinates describe the approximate centre of each cluster. Both a location description and Broadmann Area are assigned to each cluster.

Cluster	x	y	z	Location Description	Broadmann Area
1	8	-54	54	Right Parietal Lobe: Precuneus	7
	6	-66	58	Right Parietal Lobe: Precuneus	7
2	22	-68	58	Right Parietal Lobe: Precuneus	7
3	-50	16	30	Left Frontal Lobe: Middle Frontal Gyrus	9
4	-32	-80	36	Left Occipital Lobe: Superior Occipital Gyrus	19
5	-34	-62	58	Left Parietal Lobe.Superior Parietal Lobule	7
6	38	-52	50	Right Parietal Lobe:.Inferior Parietal Lobule	40
7	32	12	58	Right Frontal Lobe: Sub-Gyral	6

Note: Co-ordinates given are in MNI space.

APPENDIX B

Supplementary Information to Chapter 5

B.1 Experiment 1: Trial-by-trial Top down Control over capacity limits in VSTM

Table B.1: Performance (proportion correct) for Experiment 1, low and high set size trials according to each set size and angle of rotation.

	Angle of Rotation		
	5° (*SEM*)	20° (*SEM*)	45° (*SEM*)
Low Set Size Trials			
2 Items	0.69 (0.03)	0.89 (0.01)	0.91 (0.02)
4 Items	0.58 (0.02)	0.71 (0.02)	0.77 (0.02)
High Set Size Trials			
4 Items	0.61 (0.03)	0.71 (0.02)	0.74 (0.03)
6 Items	0.56 (0.03)	0.67 (0.02)	0.66 (0.01)

B.2 Experiment 2: Allocation of Resources Blocked by Set size

Table B.2: Performance (proportion correct) for Experiment 2, low and high set size blocks according to each set size and angle of rotation.

	Angle of Rotation		
	5° (*SEM*)	20° (*SEM*)	45° (*SEM*)
Low Set Size Blocks			
2 Items	0.65 (0.02)	0.86 (0.02)	0.91 (0.02)
4 Items	0.55 (0.02)	0.70 (0.02)	0.74 (0.02)
High Set Size Blocks			
4 Items	0.57 (0.01)	0.68 (0.03)	0.73 (0.02)
6 Items	0.55 (0.02)	0.61 (0.02)	0.63 (0.02)

B.3 Experiment 3: Allocation of Resources Blocked by Precision

Table B.3: Performance (proportion correct) for Experiment 3, low and high precision blocks according to each angular change condition and set size.

	Set Size		
	2 Items (*SEM*)	4 Items (*SEM*)	6 Items (*SEM*)
Low Precision Blocks (° Change)			
45	0.90 (0.01)	0.72 (0.02)	0.61 (0.02)
20	0.85 (0.02)	0.69 (0.02)	0.62 (0.02)
High Precision Blocks (° Change)			
20	0.86 (0.02)	0.70 (0.02)	0.60 (0.02)
5	0.65 (0.02)	0.58 (0.02)	0.55 (0.02)

B.4 Calculation of Power to Detect Effects in Experiments 2 -4

When considering the difference between two sets of paired data (as in the current, repeated measures design), the critical comparison between Difficulty conditions can be thought of as the differences between the common condition (4 items or 20° Angle of Rotation), collapsed the other factor. In this way, it is possible to calculate the sample size required as if it is was a paired-samples t-test (Howell, 2002). The effect size, therefore can be calculated as follows:

$$\mathrm{d} = \frac{\mu_1 - \mu_2}{\sigma_{X_1 - X_2}}$$

Where d is the Cohen's effect size (Cohen, 1988, 1992), μ_1 is the mean for the one cue condition, μ_2 is the mean for the second cue condition and $\sigma_{X_1-X_2}$ is the standard deviation of the difference scores between the two populations X_1 and X_2.

According to Howell (2002), it is possible to calculate $\sigma_{X_1-X_2}$ based on a number of assumptions. Given the variance sum law:

$$\sigma^2_{X_1 \pm X_2} = \sigma^2_{X_1 +} \sigma^2_{X_2 \pm} 2\rho\sigma_{X_1 X_2}$$

assuming homogeneity of variance for the two cue conditions, $\sigma^2_{X_1 =} \sigma^2_{X_2 =} \sigma^2$ then:

$$\sigma^2_{X_1-X_2} = 2\sigma^2 - 2\rho\sigma^2 = 2\sigma^2(1-\rho)$$

$$\sigma_{X_1-X_2} = \sigma\sqrt{2(1-\rho)}$$

Where ρ is the correlation between X_1 and X_2. Based on previous experiments arising from this thesis, there was a moderately high test-retest reliability (on a comparable, neutral condition) in performance on 4items, and 20° angles of rotation conditions between different experiments (r=0.72, n=8[31]). Based on the accuracy data (proportion correct) from earlier experiments, σ is estimated to be approximately 0.096 and the expected difference between the cue conditions is approximately 0.045:

$$\mathrm{d} = \frac{\mu_1 - \mu_2}{\sigma\sqrt{2(1-\rho)}}$$

$$\mathrm{d} = \frac{0.045}{0.096\sqrt{2(1-0.72)}}$$

[31] It is noted that this n is low, however it was difficult to find large groups of participants who completed comparable experiments.

$$\mathrm{d} = 0.627$$

This equates to be a medium to large effect size (Cohen, 1988; Howell, 2002). Given:

$$\delta = \mathrm{d}\sqrt{n}$$

Where δ is the power statistic which combines information from the effect size and sample size (Howell, 2002). Based on standard 0.8 power (Cohen, 1992; Howell, 2002) for a two-tailed test at $\alpha = 0.05$, from the power tables, δ would need to be approximately 2.80. Hence:

$$2.8 = 0.627\sqrt{n}$$

Solving for n:

$$n = \left(\frac{2.8}{0.627}\right)^2$$

$$n = 19.94$$

From this, it appears that approximately 20 participants are needed to find a medium to large effect size in the current series of experiments. The effects presented in Chapter 5, therefore, should not be due to a lack of power.

APPENDIX C

Pilot to Control for Encoding Time

A pilot experiment was conducted in order to ensure that that 200ms was sufficient to allow the perceptual analysis and encoding of the memory array. This is important to eliminate the possibility that the effects of the experimental manipulations in this thesis were not due to perceptual differences in the encoding stage (see Bays et al., 2011; Eng et al., 2005). To establish that 200ms is sufficient encoding time for the demands of the current thesis, differences in performance when encoding time was 200, 300 and 500ms were tested and compared.

C.1 Method

C.1.1 Participants

Twelve participants aged between 21 and 34 (*M*=25.0, *SD*=3.77, 9 female) with normal or corrected-to-normal vision were recruited for the study. All participants were right handed as assessed by a handedness inventory (Oldfield, 1971). Participants gave informed written consent and were remunerated £7 for their time. This experiment was approved by the Central University Research Ethics Committee (CUREC).

C.1.2 Task and Stimuli

The task schematic is illustrated in Figure C.1, panel a. Participants attempted to encode either 2 or 4 arrows that were presented for 200, 300 or 500ms. On half the trials, masks were presented in the locations of the arrow stimuli

for 200ms immediately after the offset of memory array (*masked* trials). The other 50% of the time, an extra 200ms of fixation was presented to equate the retention intervals (*unmasked trials*). After a variable delay (800-1200ms), the probe arrow would appear in the same spatial location except it had rotated about its central axis (by 45 °, 20° or 5° in either a clockwise or anti-clockwise direction).

The tasks was programmed and presented using Presentation software (Neurobehavioral Systems v.13.0, 2009). All stimuli were presented against a light grey background [RGB: 192, 192, 192]. A black centrally presented fixation cross (0.86° by 0.86°) was presented throughout each trial, offsetting only when feedback was given. The arrow stimuli were constructed within the task programme on a trial-by-trial basis. The arrows were all the same colour, however, the colour for each trial was chosen at random from a selection of three colours (Blue [RGB: 0, 0, 255], Red [RGB: 255, 0, 0], Green [RGB: 0, 128, 0]. Each arrow subtended approximately 1.43° of visual angle from base to tip. Across trials, the arrows were equally distributed on both sides of the visual field. Masks were made of scrambled lines of all orientations with the same the colour as the arrows against the background (grey) colour. For each colour, there were four possible masks, the order of which was randomised on a trial-by-trial basis. Responses were made by turning the lever of a custom built response device according to the direction of orientation change. All Encoding Durations, Set Size, Mask Condition and Angles of Rotation were randomised across the entire experiment. Feedback about response accuracy was provided by replacing the fixation cross with either an “O” (correct) or an “X” (incorrect).

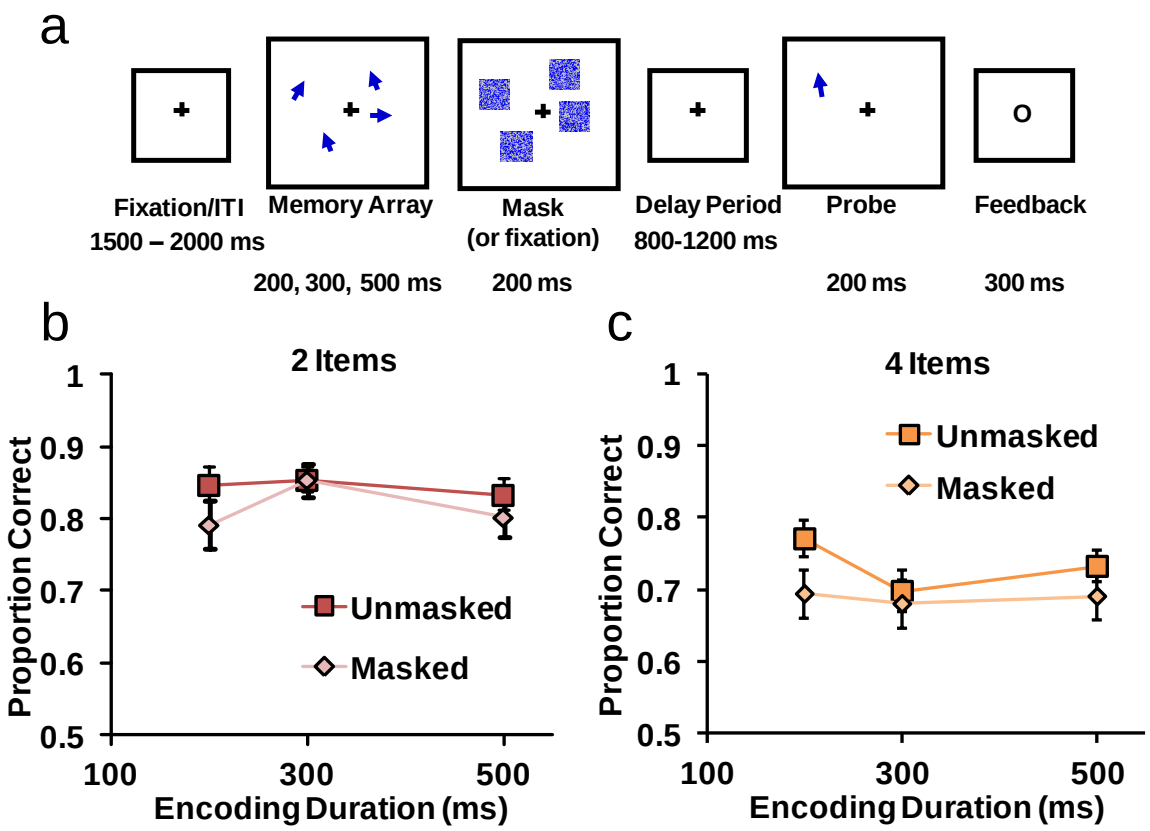


Figure C.1: Task schematic and main results for the experiment to control for encoding time. [a] Either two or four arrow stimuli were shown for 200, 300 or 500ms and, either an array of masks with the same colour and location as the arrows, or fixation was presented for 200ms. After a variable delay (800-1200ms), a probe arrow was presented in the same spatial location except it had rotated either clockwise or anti-clockwise by (45°, 20° or 5°). Participants attempted to discriminate in which direction the arrow had rotated. After response, feedback was presented for 300ms. [b] The average proportion correct for 2 items (left) or 4items (right) according to whether the displays were masked (diamond data points) or not (square data points). Error bars represent ±1 s.e.m.

C.1.3 Procedure

Participants performed the computerised task in a quiet, dimly lit room viewing a CRT monitor (refreshed at 60hz) at a distance of 90cm. Eye-movements were monitored to ensure participants maintained fixation. A 12-trial practice block familiarised participants with the task. In total, there were 576 trials which were presented across 10 blocks. In the experiment, encoding time durations of 50, 100, and 150ms were also included but are not of interest for the current experiment and thus will not be discussed further. For the analysis, therefore, there were 24 trials per sub condition of interest.

C.2 Results and Discussion

A 2 (Mask Condition: *mask* vs. *unmasked*) x 2 (Set Size: 2 vs. 4 items) x 3 (Encoding Duration: 200, 300 and 500ms) repeated measures Analysis of Variance (ANOVA) revealed a set of results in accordance with expectations. Critically, there was no significant main effect of Encoding Duration ($F(2,22) = 0.13$, $p=0.88$). In contrast, there was a significant main effect of Mask Condition ([mask<unmask]; $F(1,11) = 9.14$, $p=0.012$) and Set Size ([2 items>4 items]; $F(1,11) = 63.60$, $p<0.001$). There were no significant interaction terms ($ps>0.15$).

Overall, it appears that there was little effect of encoding time, by more than doubling the exposure duration from 200ms to 500ms, there is found no evidence to suggest that this resulted in any difference in performance. As such, it can be concluded that the use of 200ms encoding duration is sufficient in the current thesis. Unlike other research which suggests that encoding time can significantly

affect VSTM performance (e.g. Eng et al., 2005), the use of very simple stimuli in the current thesis reduces the perceptual demands in comparison to previous research. For the purposes of this thesis, therefore, 200ms should be sufficient encoding time.