The Role of Visual Short Term Memory Load in Visual Sensory Detection

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I, Nikos Konstantinou, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

In this thesis I established the role of Visual Short-Term Memory (VSTM) load in visual detection while comparing to the roles of perceptual load and Working Memory (WM) cognitive control load. Participants performed a short-term memory task combined with a visual detection task (as well as attention task, Chapter 2) during the memory delay. The level and type of load was varied (perceptual load, VSTM load or WM cognitive control load). Measures of detection sensitivity demonstrated that increased VSTM load and perceptual load have both resulted in impaired detection sensitivity that was of equivalent magnitude. In contrast, increased WM cognitive control load had either no effect on detection or under some conditions (when the detection task was combined with an attention task of higher priority) resulted in enhanced detection sensitivity, the opposite effect to VSTM load. The contrasting effects of different types of memory load rule out alternative accounts in terms of general task difficulty. Other interpretations in terms of changes in attention deployment, response bias, task priorities, verbal strategies, were also ruled out. These VSTM load effects lasted over delays of 4 seconds, were generalized to foveal, parafoveal and peripheral stimuli, and were shown to be predicted from estimates of the effects of load on VSTM capacity. fMRI results (Chapter 4) showed that high VSTM load reduces retinotopic V1 responses to the detection stimulus and psychophysics experiments (Chapter 5) showed that high VSTM load resulted in reduced effective contrast of the detection stimulus. These results in this thesis clarify the distinct roles of WM maintenance processes from those of WM cognitive control process in visual detection. These findings provide further support to the sensory recruitment hypothesis of VSTM, clarify previous discrepancies in WM research and extend load theory to account for the effects of VSTM load on visual detection.

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Chapter 1:

General Introduction

1.1 Preface

Centuries of magic-acts and more recent experimental phenomena of “inattentional blindness” and “change blindness” demonstrate the limits of visual perception. Unattended stimuli go unnoticed even when people wish to see them (e.g. when intending to “catch” the magician’s trick, or when attempting to detect the change in “change-blindness” tasks). Such perceptual failures are more likely when the attended task involves a high perceptual load (e.g. Cartwright-Finch & Lavie, 2007; Lavie, 2006; see Lavie, 2005; 2010 for reviews). In contrast, when tasks are carried under high load on cognitive control functions such as working memory (WM), irrelevant stimuli often intrude, despite the attempt to ignore them (e.g., De Fockert, Rees, Frith & Lavie, 2001; Lavie & De Fockert, 2005, Lavie, 2010 for review). These seemingly paradoxical results, whereby different types of load have opposite effects on perception, have been explained within load theory of attention and cognitive control (e.g. Lavie, 2000; Lavie, Hirst, De Fockert & Viding, 2004). When the attended information involves high perceptual load (e.g. many different stimuli or complex perceptual discriminations e.g. Lavie, 1995) its processing exhausts most of perceptual capacity and leaves little capacity to perceive any other stimuli that are either not directly relevant to the task (e.g. irrelevant distractors) or that appear to be of lower priority (e.g. due to their “marginal interest” e.g. Rensink, O’Regan & Clark, 1997). High perceptual load thus leads both to perceptual failures and better ignoring of irrelevant distractors. In contrast, performing a selective attention task under conditions of high WM load that tax cognitive control functions leads to the opposite effect: reduced capacity to exercise cognitive control over the current processing priorities thus leading to enhanced processing of low-priority and potentially distracting stimuli.

Working memory, however, is not unitary and a major distinction has been drawn between short-term maintenance and cognitive control WM processes (e.g. Baddeley, 1992;

Smith & Jonides, 1999), and their differential recruitment demands on posterior (maintenance) versus anterior (control) cortices. Indeed recent research indicates that visual maintenance involves the same sensory visual cortices as those involved in perception (Pasternak & Greenlee, 2005 for review; Harrison & Tong, 2009; Malecki, Stallforth, Heipertz, Lavie & Duzel, 2009; Munneke, Heslenfeld, & Theeuwes, 2010; Serences, Ester, Vogel & Awh, 2009 for recent demonstrations).

In this thesis, I aim to clarify the role of different types of working memory load in perception. Considering the evidence for the involvement of sensory brain areas in short term maintenance processes of WM within the framework of load theory led to the formulation of novel predictions. Specifically, loading visual maintenance processes of WM increases the demand on sensory representation capacities which are involved in visual perceptual processing and this is therefore predicted to result in reduced detection sensitivity for task-unrelated visual stimuli: a similar effect to that of perceptual load (Macdonald & Lavie, 2008; Schwartz et al., 2005). In contrast, loading WM cognitive control processes will lead to reduced control over stimulus processing priorities but will not affect the demand on visual sensory capacity. Thus WM cognitive control load will not result in reduced detection sensitivity. Instead the effects of WM cognitive control will depend on any potential conflicts in processing priorities between the visual detection task and another concurrent visual attention task: in the absence of any conflict in processing priorities, as when the visual detection task is the only priority, WM cognitive control load will not affect visual detection; however, when the visual detection task is performed with a concurrent visual attention task (e.g. visual search task) of higher priority, then loading WM cognitive control will result in better detection sensitivity due to inability to maintain processing priorities and the visual detection task gaining priority over the concurrent visual attention task.

In the next parts of this chapter I briefly review the empirical evidence that stimulated the questions addressed in this thesis. I begin by an outline of Load Theory and a description of the existing behavioural and neuroimaging evidence in support of the theory. Next, I concentrate on the empirical evidence from the psychophysics, non-human primate physiology and human neuroimaging literature demonstrating that sensory cortical areas are involved in the neural network that underlies short-term maintenance for visual information. Finally, I describe the empirical methodology I employed for testing my hypotheses.

1.2 Load Theory

Load theory (Lavie et al., 2004) dissociates between the effects of two mechanisms of selective attention on perception. The first is an early and rather passive perceptual selection mechanism. According to load theory, perception proceeds automatically on all stimuli, task-relevant as well as task-irrelevant, until all available capacity is exhausted. This leads to the prediction that high perceptual load, which engages full capacity in the relevant processing, would leave no spare capacity for perception of task-irrelevant distractors. In situations of low perceptual load, however, any capacity not taken up in perception of task-relevant stimuli would involuntarily ‘spill over’ to the perception of distractors.

The second is a more active cognitive control mechanism, such as verbal working memory, which is responsible for allocating attentional resources according to current task priorities, thus minimizing intrusions from task-irrelevant stimuli. This is a late selection mechanism, which actively rejects irrelevant information that has already been processed by sensory brain areas (e.g. in early visual cortex) from any further processing. Contrary to the effect of perceptual load, loading this cognitive control mechanism is predicted to lead to increased perception of irrelevant stimuli.

Next, I review the empirical evidence obtained for each of these mechanisms starting with the first early perceptual selection mechanism.

1.2.1 Behavioural and neuroimaging evidence for the effects of perceptual load

The effects of perceptual load on task-irrelevant distractors have been supported by various behavioural and neuroimaging studies. Behavioural studies have demonstrated response competition (Figure 1.1) and negative priming effects on target reaction times (RTs) from irrelevant distractors in situations of low perceptual load (e.g. using a letter search task with just one item or a simple feature detection task). However, these effects were eliminated in conditions of high perceptual load when the letter search task display was increased to six items or when subjects were asked to perform a complex feature-conjunction discrimination (e.g. Beck & Lavie, 2005; Lavie, 1995; Lavie & Cox, 1997; Lavie & Fox, 2000).

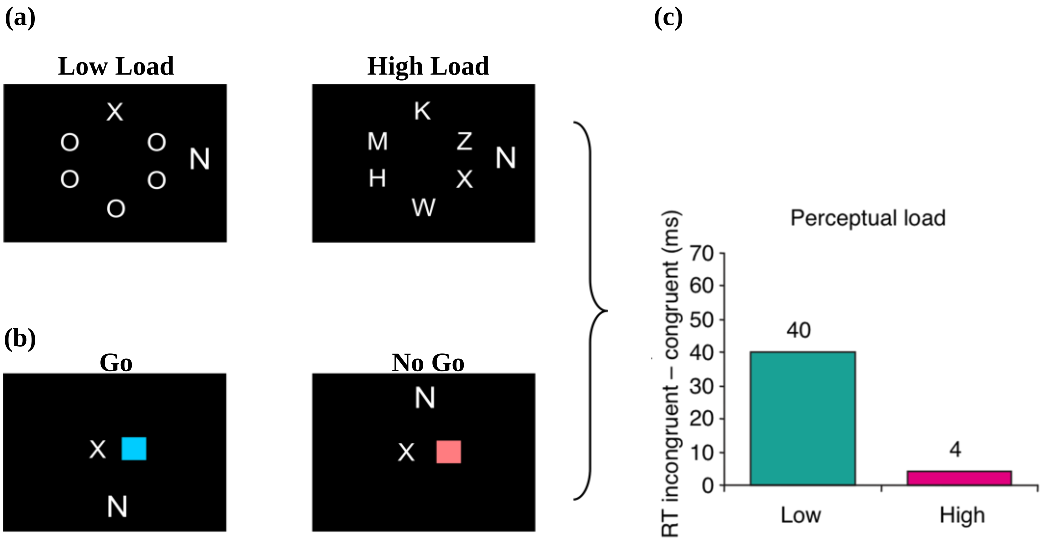

Figure 1.1. **Examples of stimuli and results obtained in perceptual load experiments, using the response competition paradigm.** **(a)** Perceptual load is manipulated by varying the number of items that are similar to the target (no similar in low load; five in high load). **(b)** Perceptual load is manipulated by varying task demands based on whether a specified color (e.g. blue) is detected in low load or a color-shape conjunction (e.g. red square) is detected in high load). **(c)** Typical results showing greater distractor interference in low than in high perceptual load conditions. Adapted from Lavie, 2005.

Neuroimaging studies testing predictions derived from Load Theory have demonstrated that visual cortex activity related to the presence of irrelevant distractor stimuli is attenuated under high perceptual load. For example, Rees, Frith, & Lavie (1997) used fMRI to test the prediction that high perceptual load reduces early visual cortex activity to task-irrelevant distractor stimuli. Specifically, irrelevant visual motion (dots moving radially toward the screen edge) was used as a distracting stimulus during the performance of a low or high load task of linguistic judgements on single words. Consistent with the prediction that early visual cortex activity related to irrelevant visual motion is reduced under conditions of high processing load (compared with low load), robust bilateral modulation of V5 activity, related to visual motion by load in the target task was observed. Later reports confirmed that the neural signature of irrelevant stimuli (e.g. parahippocampal activity related to images of places, and activity in retinotopic cortex related to the presence of flickering checkerboards) is reduced or even eliminated entirely with high perceptual load (e.g., Bahrami, Lavie, & Rees, 2007; O'Connor, Fukui, Pinsk, & Kastner, 2002; Pinsk, Doniger, & Kastner, 2003; Schwartz et al., 2005; Yi et al., 2004). For example, Schwartz et al. (2005) measured retinotopic visual cortex activity evoked by checkerboard patterns presented in the periphery while participants performed a task related to a rapid stream of stimuli presented at fixation. The task was performed under low or high perceptual load (Figure 1.2a). Visual cortex activity evoked by the task-irrelevant checkerboards was reduced under high load. This effect was found in areas V1, V2, V3 and ventral V4. Though the magnitude of the effect increased with successive visual areas, it was clearly present as early as V1 (see Figure 1.2b).

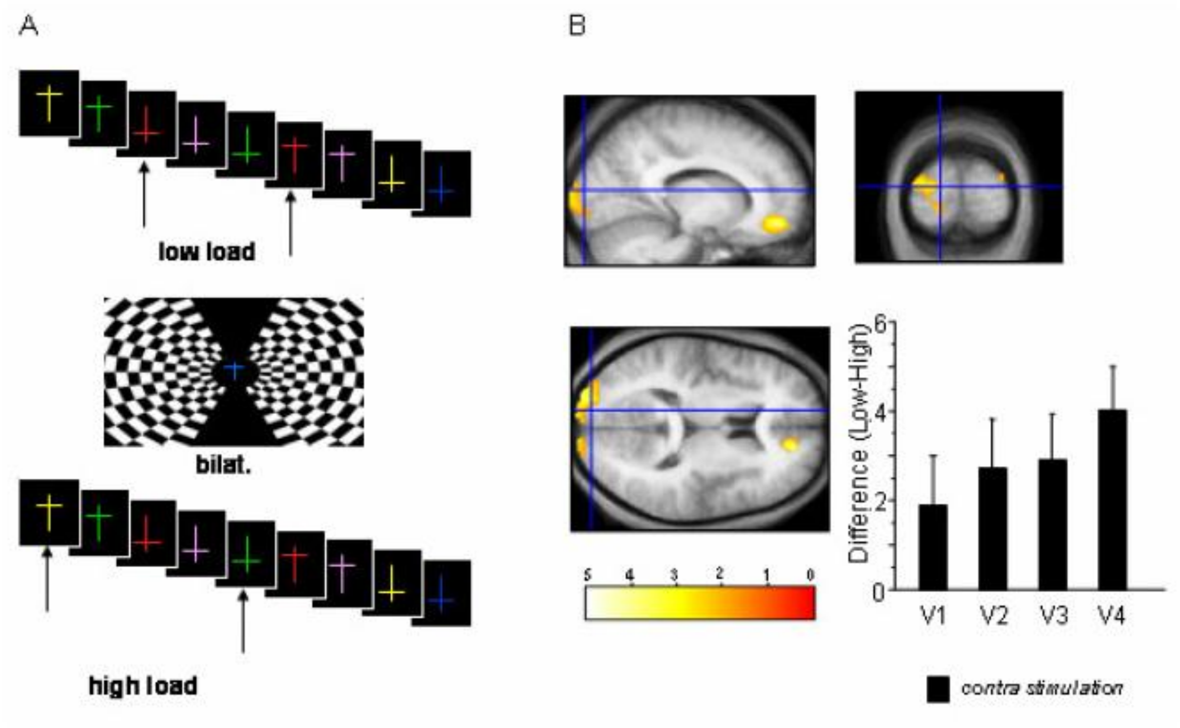

Figure 1.2. The effects of perceptual load on retinotopic visual cortex activity evoked by irrelevant stimuli. Stimuli and results in Schwartz et al. (2005). (A) Stimuli: A rapid stream of coloured crosses was presented at fixation, and participants monitored for targets defined at the beginning of each stream. Under low load, targets were defined by a single feature (colour, red crosses). Under high load, targets were defined by a conjunction of features (colour and orientation; upright yellow or inverted green crosses). Irrelevant contrast-reversing checkerboards were presented in the periphery either bilaterally (shown), on one side or on neither side. (B) Results: Visual cortex activity evoked by the checkerboards (pooled across unilateral and bilateral condition, contrasted with the no-checkerboard condition) is greater under low than under high perceptual load in the central task. The bar chart shows that the difference increases monotonically from visual area V1 to V4. Adapted from Schwartz et al., 2005.

1.2.2 Behavioural and neuroimaging evidence for the effects of cognitive control load

Evidence from behavioural and neuroimaging studies supported load theory's prediction that loading the active cognitive control mechanism, as in a verbal working memory task, increases interference by irrelevant distractors, an effect opposite to that of high perceptual load. Behavioural studies using the response competition (Figure 1.3) and attentional capture paradigms demonstrated that verbal working memory load increases distractor effects on RTs (e.g., Lavie, 2000; Lavie & De Fockert, 2005; Lavie et al., 2004). For example, Lavie et al. (2004) asked participants to perform a low perceptual load search task with a congruent or incongruent distractor presented on each trial, while manipulating the availability of cognitive control resources by varying the verbal working memory load. This was achieved by requiring that participants remember either a single digit (low working memory load) or a set of six digits (high working memory load), while performing the search task. Participants' memory for the set of digits was tested by asking whether a probe digit (presented after the search) had been a member of the memory set or not. By loading verbal working memory, the availability of cognitive control processes required to differentiate between competing relevant and irrelevant stimuli was reduced, resulting in an increase in the frequency of intrusions from irrelevant stimuli. In the high verbal working memory load condition, incongruent distractors produced a larger RT decrement and a larger increase in error rates compared to congruent distractors, than in the low verbal working memory load condition. Further evidence for these effects has come from studies demonstrating that in contrast with the reduction in distractor effects found in tasks of high perceptual load, high working memory load increases distractor effects, on both RTs (in the response competition and attentional capture paradigms, e.g. Lavie, 2000; Lavie & De Fockert, 2005; Lavie et al., 2004) and neural activity (related to irrelevant distractor faces in a Stroop- like paradigm, De Fockert, Rees, Frith & Lavie, 2001). Furthermore, functional neuroimaging studies assessing neural activity related to irrelevant distractor faces in a Stroop-like paradigm demonstrated increased visual cortex activity related to the presence of the distractor faces by high WM load (De Fockert et al., 2001).

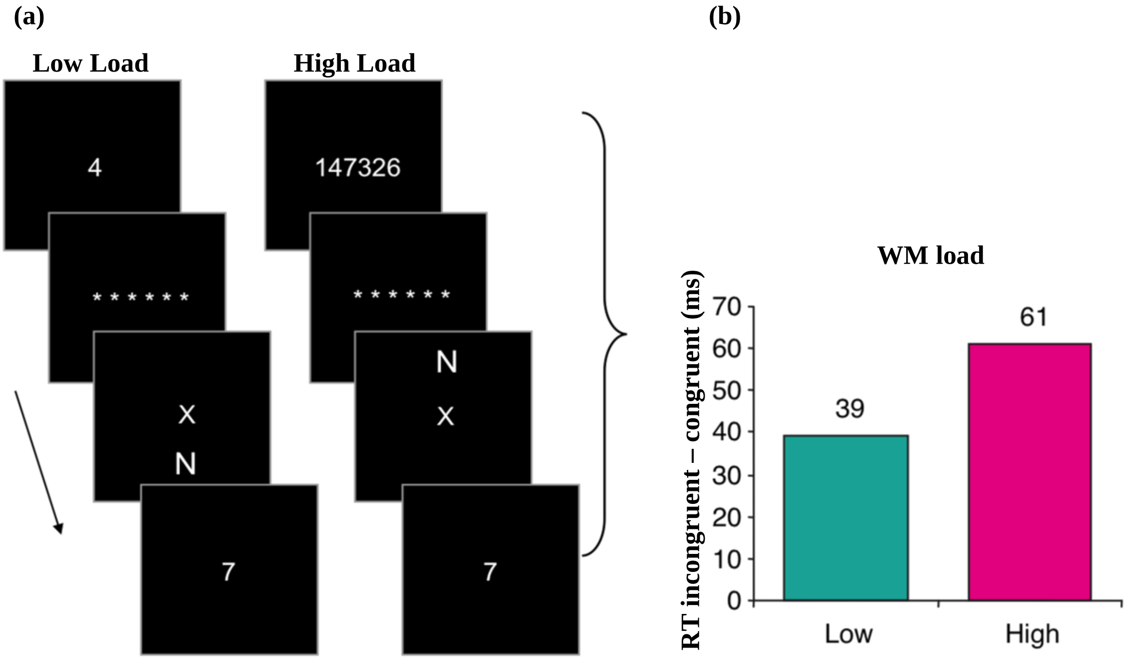

Figure 1.3. Examples of stimuli and behavioral results in WM load experiments. (a) WM load is manipulated during performance of a response competition task. Participants were asked to memorize either one (low load) or six (high load) digits and indicate whether a probe was present in the memory set. **(b)** Effects of distraction are greater in the high than the low WM load condition, an effect opposite to that of perceptual load. Adapted from Lavie, 2005.

The effect of working memory load is precisely the opposite to that of perceptual load (Lavie, 1995), i.e. under high perceptual load distractor effects are decreased, whereas under high working memory load, distractor effects increase. These two effects were demonstrated in the same experiment by Lavie et al. (2004), in which both perceptual load and working memory load were manipulated: under low perceptual load, there were large distractor effects on RTs in both conditions of working memory load, but they were larger under high working memory load than low (111 ms vs. 72 ms). Under high perceptual load, these distractor effects all disappeared, but were still larger under high working memory load (35 ms vs. -8 ms under low working memory load). Thus, the increase in interference caused by loading working memory can be seen to occur even under conditions of high perceptual load, and likewise, high perceptual load still drastically diminishes the processing of task-irrelevant information even when the ability of cognitive control to maintain the focus of selective attention on task priorities is impaired. The stark contrast between the opposing outcomes of loading the perceptual and working memory systems gives weight to Lavie's hypothesis that there exist two dissociable mechanisms by which selective attention can resist distraction: a passive form of control in which interference is eliminated when there is insufficient capacity remaining to process any information other than that specific to the task at hand, and an active form that engages working memory in maintaining current task processing priorities, thereby suppressing the processing of information not related to the task.

Loading working memory is not the only way to diminish the availability of cognitive control processes that would otherwise strive to prevent distraction. Indeed, a greater demand on such processes also occurs during multi-tasking (e.g., Della Sala, Baddeley, Papagano, & Spinnler, 1995; D'Esposito et al., 1995; Miller & Cohen, 2001; Shallice & Burgess, 1996). Lavie et al. (2004) demonstrated that exactly the same effect as that produced by loading working memory is achieved when executive control is required to coordinate two tasks simultaneously. Distractor interference effects exerted during the performance of a single, low perceptual load search task were compared with those produced while participants undertook the same search task immediately following the completion of a working memory task (the same stimuli and individual task procedures as those used in the aforementioned experiments by Lavie et al. were employed – the only difference being that the working memory task probe was presented and responded to before the search task display was presented). Two such experiments were run, one in which the working memory task was of low load, and another in which it was of high load. The results were the same regardless of the level of working memory load: distractor effects on RTs were increased by approximately 30 ms in both cases, a comparable increase to those produced by the change from low working memory load to high in Lavie et al.'s other experiments (including those reported here). Overall distractor effects were somewhat smaller in these single vs. dual task experiments (approx. 60 ms) than in the low vs. high working memory load experiments (between 100 and 200 ms), as would be expected, since the low vs. high working memory load experiments were all also dual-task situations, so the demand on cognitive control was compounded by the combination of working memory load and dual-task coordination.

The support for Lavie's cognitive control hypothesis has been broadened recently by the finding that the effects of attentional capture by singletons are increased under conditions of high working memory load, just as the effects of response competitive distractors are. Lavie and De Fockert (2005) reported that two different manipulations of working memory load each produced an approximately 40 ms increase in RT decrement in the presence of a singular green circle among a set of red circles compared with when there were only red circles, while a line orientation task was performed in which each line was contained within one coloured circle. The increased distraction that occurs when cognitive control processes are rendered less effective in preventing intrusions is therefore not limited to response-related distractors, but also occurs in the presence of perceptually salient singletons.

Lastly, the effects of working memory load on the processing of irrelevant information have been replicated in a neuroimaging study involving the response competitive distractor effects of pictures of faces (De Fockert et al., 2001). A working memory task involving the maintenance of the order of a sequence of digits (the numbers one to four in a random order in the high working memory load condition; in numerical order in the low working memory load condition) was interleaved with a name categorisation task, in which famous politicians' and pop stars' names had to be identified as such while congruent or incongruent pictures of the faces of the same celebrities were presented. Not only were face distractor interference effects greater in high working memory load than low, for both RTs (78 ms vs. 46 ms; note an increase of approximately 30 ms as per the aforementioned experiments) and error rates, but neural activity in the fusiform gyrus and other areas of extrastriate cortex known to be associated with the processing of faces (e.g. Kanwisher, McDermott & Chun, 1997) occurring when the distractor faces were presented, was greater under conditions of high working memory load than low. Taken together, the behavioural and neuroimaging findings reported by De Fockert et al. (2001) provide highly convincing evidence in support of the hypothesis that extraneous information is not so easily dismissed when processes of cognitive control are less readily available to maintain current task priorities due to the loading of working memory.

However, because this body of research used indirect measures of distractor interference, such as RTs and neural activity, it cannot offer conclusive evidence regarding conscious perception. Indeed Bahrami et al. (2007) recently showed that perceptual load can modulate V1 activity related to an irrelevant stimulus that the participants did not consciously perceive. Furthermore, the measures of distractor effects on target RTs in the behavioural experiments, despite their prevalent use as an index of distractor processing, cannot support any direct conclusions about conscious perception, since one cannot deduce whether a participant was or was not conscious of any stimulus on the basis of RT.

1.2.3 Evidence for the Effects of Load on Visual Awareness

Cartwright-Finch and Lavie (2007) addressed this issue testing the effect of perceptual load on conscious perception within the Inattentional Blindness (IB) paradigm. In a series of experiments, they found that the number of participants who reported being aware of a task-irrelevant stimulus presented unexpectedly on the last trial was strongly dependent on the level of perceptual load. The rate of awareness reports was considerably lower (around 40%–50% lower) in tasks of high perceptual load (involving either attention-demanding subtle perceptual discriminations or visual search for a letter among similar non-target letters) than in tasks of low perceptual load (involving either simple colour detection or visual search for a letter among very dissimilar non-target letters). This study conclusively demonstrated that high perceptual load is far more likely than low perceptual load to produce IB. However, the IB paradigm does not necessarily measure conscious perception since the unexpected critical stimulus (CS) might have been perceived but rapidly forgotten (Wolfe, 1999).

One recent study (Macdonald & Lavie, 2008), addressed this issue, by examining the effects of perceptual load using a direct measure of conscious perception (present/absent) in a modified Inattentional Blindness (IB) paradigm in which an expected CS was presented in multiple trials. The level of perceptual load was varied in a letter-search task, (target-letter search among dissimilar letters in low load and among similar letters in high load). The search-irrelevant CS appeared in the periphery and subjects responded to its presence or absence. The CS detection sensitivity was consistently reduced in the high (compared to low) perceptual load condition. Overall this study demonstrated a phenomenon of "load-induced blindness".

The studies reviewed so far demonstrate that whereas high perceptual load in the processing of task-relevant stimuli reduces perception of task-irrelevant stimuli or distractors, high load on cognitive control processes such as WM, leads to increased perception of task-irrelevant stimuli. These opposite effects highlight two dissociable mechanisms of perceptual selection: (a) a passive selection mechanism that rejects irrelevant stimuli when its capacity is exhausted and (b) an active cognitive control mechanism which rejects irrelevant stimuli by aligning the perceptual system with current stimulus priorities. This conclusion is supported by behavioural and neuroimaging studies using direct (present/absent reports) and indirect measures (RTs and neural activity).

I now turn to the evidence in support of my claim that VSTM maintenance shares common mechanisms with visual perception.

1.3. Visual Short Term Memory

Visual short term memory refers to the temporary maintenance (up to 30 s) of visual information (Baddeley, 1986; Baddeley and Hitch, 1974; Luck, 2008; Repovs & Baddeley, 2006). In addition to the well-established role of fronto-parietal cortices in VSTM (Funahashi, Bruce, & Goldman-Rakic, 1989, 1990; Fuster, 1973; Fuster and Alexander, 1971; Niki, 1974; Quintana, Yajeya, & Fuster, 1988; Watanabe, 1981) much recent research emphasizes the involvement of sensory cortices as well (Bisley Zaksas, & Pasternak, 2001; Bisley, Zaksas, Droll, & Pasternak, 2004; Harrison & Tong, 2009; Munneke, Heslenfeld & Theeuwes, 2010; Serences et al., 2009; Super, Spekreijse, & Lamme, 2001). Current formulations that integrate both anterior and posterior mechanisms suggest that the fronto-parietal activity is used to control visual cortex activity so that it remains active during the memory delay (e.g., Postle, 2006). Here, I focus on the evidence for the involvement of early visual cortex in VSTM maintenance as this is directly related to my claim that VSTM load would modulate the sensitivity of visual detection. Evidence for this has come from psychophysical studies, non-human primate electrophysiology, and human neuroimaging.

1.3.1 Psychophysics

Psychophysical studies have focused on the basic attributes (such as contrast or direction of motion; see Figure 1.4a, b) of stimuli that are maintained in VSTM. These studies provided evidence that VSTM maintenance involves similar sensory mechanisms as those involved in visual perception.

A number of studies have shown that retention of information in VSTM over periods of up to 30-s involves separate sensory feature-selective mechanisms. For example, different features can be retained in WM for different lengths of time (Figure 1.4b): spatial frequency (Magnussen & Greenlee, 1992), orientation (Vogels & Orban, 1986) or speed of motion can be retained for several seconds with little loss of precision, whereas the retention of luminance contrast (Lee & Harris, 1996), texture (Harvey, 1986), small spatial offsets (“Vernier Acuity”; Fahle & Harris, 1992) and direction of motion (Bisley & Pasternak, 2000) seem to be less robust. This selective decay of information indicates that there are separate maintenance processes for different stimulus features (Magnussen & Greenlee, 1999). However, because the procedures used to study the retention of various stimulus attributes were not matched, some of the differences in decay functions could be due to differences in the experimental paradigms used.

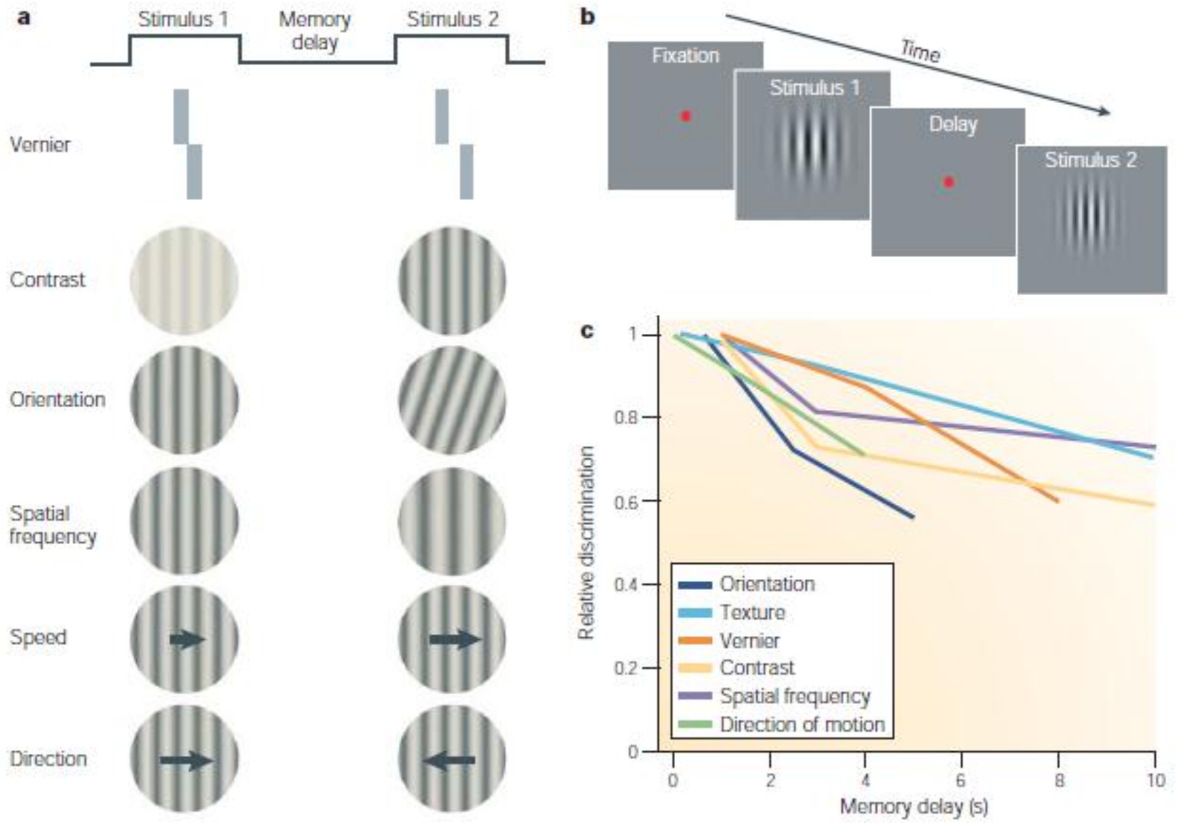

Figure 1.4: VSTM for selected stimulus attributes. **(a)** Delayed discrimination task and examples of visual stimuli that are commonly used to study the retention of stimulus attributes. **(b)** Typical behavioural paradigm. **(c)** Normalized discrimination sensitivity for various visual attributes plotted as a function of delay re-plotted from different studies.

More compelling evidence in support of feature-selective retention mechanisms comes from studies that used interference by an irrelevant distractor stimulus ("mask"), presented during the delay of the VSTM task (Figure 1.5). It has been found for example, that the ability of a masking grating to interfere with the delayed discrimination of spatial frequencies is greatest when the spatial frequency of the mask differs from that of the remembered stimulus by at least an octave (Magnussen, Greenlee, Asplund, & Dyrnes, 1991). The effect is specific to the spatial frequency of the remembered grating and is unaffected by changes in the orientation of the mask. This selective interference indicates that spatial frequency is preserved by specialized mechanisms that are closely associated with those involved in its encoding, and are distinct from mechanisms involved in stimulus orientation.

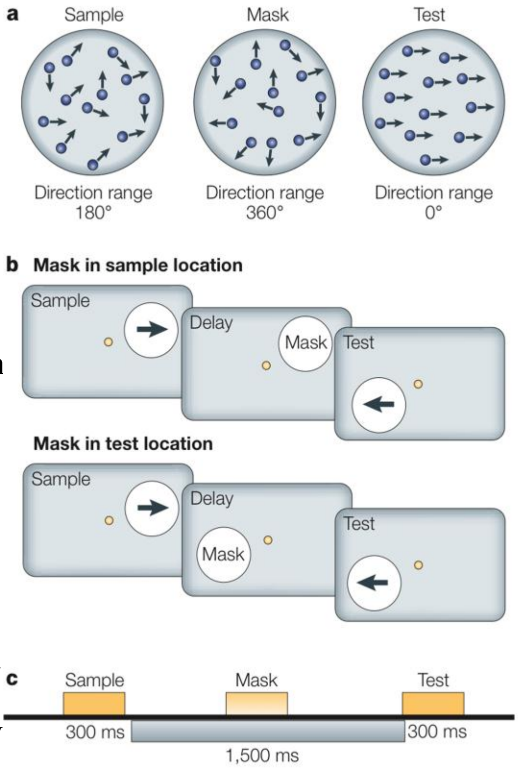

Figure 1.5. VSTM for stimulus direction. **(a)** Stimuli used to measure retention of motion direction in monkeys. **(b)** On each trial, the monkeys compared two directions of motion, sample and test. The sample consisted of random dots that moved in a variable range of directions; in the test stimulus, all the dots moved in the same direction. The monkeys reported whether the sample and test had the same mean direction of movement. The mask, consisting of dots moving in random directions, was introduced during the delay at the location of the preceding sample (upper row) or the upcoming test (lower row). **(c)** Temporal parameters of the task. Modified from Blake, Cepeda, & Hiris,1997.

Selective retention of motion direction has been shown in monkeys required to compare two random-dot moving stimuli separated by a delay. The monkeys remembered the direction of coherent motion with only a modest decrease over time and reliably retained the direction of motion of stimuli with relatively low levels of coherence for as long as 4–6 s (Bisley & Pasternak, 2000). In a separate study (Bisley, Zaksas, & Pasternak, 2001), the two comparison stimuli were spatially separated and a random-motion mask was introduced during the delay in either the sample location or the location of the upcoming test (Fig 4). The effect of the mask was specific to its properties and location. This selective interference indicates that the sensory attributes of visual motion are precisely preserved, which supports the idea that mechanisms that involved in the processing of visual motion are also involved in its storage. Furthermore, this selectivity of masking effects resembles the selectivity seen in studies of memory for spatial frequency and speed (Magnussen & Greenlee, 1992), indicating that these different memory networks might share a similar architecture.

Evidence that the storage of visual motion in these tasks is specific for the location of the stimulus comes from a study (Zaksas, Bisley, & Pasternak, 2001) that investigated the effect of spatial separation between the sample and test stimuli. The authors found that if the two comparison stimuli were spatially separated by more than a critical distance, the threshold for discrimination of motion was elevated. Moreover, the critical separation increased with retinal eccentricity, and its size coincided with the size of receptive fields in area MT, that is known to mediate sensory processing of motion. This suggests that MT might be involved in the VSTM task. Overall this study supports the idea that retinotopic visual cortex is involved in the storage of motion information.

In short-term memory for colour subjects retain information about hue with great precision (Nilsson & Nelson, 1981), indicating the involvement of brain regions concerned with sensory processing of colour. There is also evidence that the colour of an object can be retained separately from its location. In one study, colour or location distractors were introduced during the delay between two stimuli that differed in either colour or location (Vuontela et al., 1999). Location distractors interfered only with memory for location and not colour, whereas colour distractors interfered only with memory for colour, supporting the idea that memory for colour and spatial location are handled by separate systems.

Overall, the mechanisms that preserve basic attributes of visual stimuli in short-term memory can be characterized as narrowly tuned and spatially localized. These findings indicate that the sensory attributes of visual perception are precisely preserved in VSTM supporting the involvement of sensory cortical areas in short-term memory maintenance.

1.3.2 Non-Human Primate Electrophysiology

Until recently, much of the neurophysiological work on VSTM has focused on the inferotemporal (IT) cortex, a relatively advanced stage of the visual stream that is important for processing complex shapes (Ungerleider & Pasternak, 2004). This work has shown that IT neurons in monkeys trained to remember objects are active during the delay period after they have been shown the object, and that this activity is related to the remembered colour or shape (Fuster, 1990; Miller, Li, & Desimone, 1993).

However, two recent studies provided evidence for memory-related activity in area V5/MT. Bisley, Zaksas, Droll, & Pasternak (2004) recorded the activity of V5/MT neurons while two monkeys compared the direction of motion in two sequentially presented random-dot stimuli (a memory sample display and following a 1500-ms delay, a memory probe display) and reported them as the same or different by pressing one of two buttons. Findings showed that V5/MT neurons were active not only in response to the memory set and memory probe but also during the delay period that separated them. Using the same task, Bisley Zaksas, and Pasternak (2001) found that microstimulation of direction-specific cortical columns in area V5/MT of monkeys during the delay period of the task disrupted the animals’ accuracy in matching the memory set to the memory probe, dropping their performance to chance levels.

Perhaps the most direct evidence for the involvement of sensory visual cortex in VSTM comes from studies that implicate primary visual cortex (V1) in VSTM. Super, Spekreijse, & Lamme (2001) trained monkeys in a delayed-response figure-ground segregation task in which a motion- or an orientation-defined figure was presented and following a variable delay of up to 2000 ms (0 ms, 500 ms, 1000 ms, or 2000 ms) they were cued to make a saccade to the position where the figure was presented. Activity was recorded from V1 neurons with receptive fields that covered the figures presented during the task. Contextual modulation (CM) of each neuron was calculated by subtracting the neuron's response when background noise dots covered its receptive field (RF) from its response when the motion- or orientation-defined figure covered its RF. Results showed that CM related to figure perception during the first 250-ms of the delay period was equally strong in correct and incorrect trials (when the animal failed to make a saccade within 500-ms from cue onset) but memory-related CM in the last 250-ms of the delay period was stronger in correct than incorrect trials, indicating stronger persistence of activity for correct than incorrect trials. By introducing a second stimulus during the delay, which was either relevant or irrelevant to the task, the authors found that delay period CM to the figure continued when it was a target and decreased when it was a distractor. Therefore, primary visual cortex activity related to the figure-ground segregation continues throughout the delay period of a VSTM task. The persistence of figure-ground modulation is stronger when the task is performed correctly and when the figure evoking the modulation is relevant to the task.

1.3.3 Human Neuroimaging

Human neuroimaging has also been used to study the neural correlates of VSTM. Early fMRI studies failed to find evidence for sustained activity over memory delays in early visual cortex and focused on prefrontal and parietal cortices instead. For example, Courtney et al. (1997), measured brain activity during a short-term memory task in which subjects matched a sample-face with a test-face shown after an 8 s delay. Occipito-temporal areas exhibited mostly transient responses to stimuli, indicating their role in perceptual processing, whereas only prefrontal areas demonstrated sustained activity during memory delays (see also Todd & Marois (2004) for a recent demonstration that brain activity at intra-parietal sulcus (IPS) during the delay period (1200 ms) of a conjunction (colour and spatial location) VSTM task correlates with the number of items stored in VSTM (calculated using Cowan's K).

However, later fMRI studies have highlighted the role of visual cortex in VSTM, as I describe next. Some studies investigating the neural substrates of short-term memory for faces and places provided evidence for the importance of the fusiform face area (FFA) in the retention of faces and parahippocampal place area (PPA) in the retention of places – the very brain areas responsible for the perception of faces and places respectively. For example, Ranganath, DeGutis, and D'Esposito (2004) using event-related fMRI identified category specific FFA and PPA neural activity during the encoding and maintenance periods of a delayed match-to-sample task. On each trial, subjects were shown a sequence of three images for 1 s each. Based on a cue, participants encoded and rehearsed only one of these items across a 12 s delay. Findings showed that FFA and PPA exhibit greater encoding and maintenance related activity when its preferred stimulus was relevant to the upcoming test stimulus. In another study with faces used as stimuli in a delayed-recognition task, Postle, Druzgal, and D'Esposito (2003) traced neural activity during the retention interval (7 s) interposed between the serial presentation of four face stimuli. Subjects were cued which of the first three faces to remember and match as same or different (by button press) with the fourth one. Findings showed that FFA was the only brain area demonstrating reliable retention of target-specific activity across the delay period.

Recently, Harrison and Tong (2009) used fMRI with a pattern-classification analysis while participants performed a delayed orientation discrimination task. Two sample orientation gratings were presented successively, followed by a numerical cue indicating whether to remember the first or the second grating. After an 11 s delay, a test grating was presented and subjects indicated which way it was tilted relative to the cued grating. The pattern-classification analysis indicated that sustained activity patterns throughout the delay period in areas V1–V4 were predictive (with over 80% accuracy) of the orientation grating held in memory. The similarity of these activity patterns to those evoked during "passive viewing" of the oriented gratings was evaluated by training the classifier on one data set and testing it on the other. Generalization performance for activity pooled across V1-V4 was still significantly above chance, indicating that retaining an orientation in VSTM recruits many of the same orientation-selective sub-populations as those that are activated under stimulus-driven conditions. In a similar demonstration, Serences et al. (2009) used multivoxel pattern analysis of the 10-s delay period of either a colour- or an orientation-discrimination task. Results revealed sustained pattern of activation in V1 during the delay that was specific for the feature stored in memory (colour or orientation) and qualitatively similar to that observed during the discrimination of sensory stimuli.

Although both Harrison and Tong (2009) and Serences et al. (2009) provide strong evidence for the involvement of early visual cortex in VSTM, both studies failed to find increased BOLD responses during the delay period in early visual cortex related to the maintained stimulus. A recent neuroimaging study demonstrated for the first time increased BOLD sensory visual cortex activity during the delay period of a visual short-term memory task (Munneke, Heslenfeld & Theeuwes, 2010). In this study, participants had to remember for a short period (5 s) the exact location of a cued coloured circle within an array of four circles (each of a different colour). Following the delay period, a set of four white circles with a left or right opening was shown. The maintained circle served as the memory set item in a delayed match-to-sample task (visual short-term memory condition) or as the location cue for an upcoming target stimulus (spatial attention condition). The trial sequence of the two conditions was identical except for an instruction word at the beginning of each trial indicating which task participants had to perform. In the working memory condition participants indicated whether a white circle was present in the memorized location. In the spatial attention condition participants indicated which side of the white circle in the maintained location contained a gap (left or right). Keeping a spatial location in visual short-term memory resulted in increased BOLD signal (compared to the ipsilateral location) in early visual cortex (V1, V2 and V3). These increased BOLD responses were observed during the delay period of the working memory condition and were retinotopically-specific, indicating increased activity in sensory visual cortex during a visual short-term memory task.

In summary, the evidence reviewed above demonstrates that the neural network underlying the maintenance of information in VSTM includes visual cortical areas devoted to the sensory encoding of this information. As reviewed, this conclusion is supported by a range of studies, from purely psychophysical measures to single-cell recordings and functional neuroimaging. This conclusion, taken together with load theory’s demonstrations that drawing on sensory perceptual resources (i.e. perceptual load) in one task leads to reduced sensory response (e.g. Schwartz et al., 2005) and the related perceptual sensitivity to task-irrelevant stimuli (Macdonald & Lavie, 2008) led me to the hypothesize that VSTM load will also lead to reduced early visual cortex response and related detection sensitivity to visual stimuli unrelated to the VSTM task. However, WM cognitive control load manipulations that do not vary demands on sensory perceptual resources but vary instead demands on cognitive control over task processing priorities were predicted to either not affect detection sensitivity or increase detection sensitivity in cases of a concurrent (to the visual detection) high priority attention task.

Next I describe the methodological approach used in this thesis to test these predictions

1.4 General methodological approach and overview

The tasks employed in the experiments reported in this thesis required participants to make “present” or “absent” reports to a target stimulus in a visual detection task that allowed for estimation of detection sensitivity (*d’*) and response bias measures (β). During performance of the visual detection task the level of information load (VSTM load, perceptual load or cognitive control WM load) was manipulated in a concurrent task.

In Chapter 2, the effects of these three types of information load were contrasted in a modified experimental paradigm that has been established recently by Macdonald and Lavie (2008). As discussed above, Macdonald and Lavie (2008) manipulated perceptual load in a visual letter search task by varying the number of non-target items in the search array (1 item in low load vs. 6 items in high load), establishing a phenomenon of load-induced blindness: high, compared with low, perceptual load in the letter search task led to a consistent reduction of participants’ sensitivity for detecting a peripheral visual stimulus that was unrelated to the search task. Here, in Chapter 2 participants performed the visual detection and concurrent visual search task employed by Macdonald and Lavie (2008) but now during the delay period of a VSTM task or a WM cognitive control task, as described below. In Chapters 3 and 4, during the delay period of either a VSTM task or a WM cognitive control task, participants performed a visual contrast-increment detection task that was adjusted on each participant’s contrast threshold using a staircase method. In Chapter 5, I employed an orientation discrimination task on a tilted Gabor patch of various contrast levels that participants performed at orientation threshold (obtained using a staircase method) during the delay period of a VSTM task.

In typical VSTM tasks, observers view a brief memory set, which consists of one or more objects (e.g. coloured squares) that the participants are asked to remember. After a brief retention interval, a memory probe is presented, and the participants compare the memory set with the memory probe (for a classic example, see Phillips, 1974). In most experiments, the memory set and memory probe displays are identical on 50% of trials and differ in some subtle way on the remaining trials, and participants simply make an unspeeded same-different response to indicate whether they noticed a difference (for more recent examples see also Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). For example, in the study by Luck and Vogel (1997) each memory set contained between 1 and 12 coloured squares, and the memory probe was either identical to the memory set or differed in the colour of one of the squares. VSTM task accuracy is typically near perfect for arrays with a small number of items and then decreases systematically as the number of items increases.

This VSTM task offers several advantages that make it ideally suited for the purposes of this thesis, as I describe next. First, this VSTM task closely resembles the way in which our visual short term memory system is used in the natural environment. For example, our visual input is frequently interrupted by periods of suppressed visual processing caused by blinks and eye movements, and VSTM presumably plays an important role in comparing a memory representation of the visual input formed before the interruption with the new input that is visible after the interruption.

A second advantage is that this paradigm has been broadly used in the literature for estimating the amount of information that people hold in their VSTM. Obtaining such an estimate was of particular importance here because the main hypothesis tested in this thesis is that sensitivity for visual detection depends on the amount of information people hold in visual short term memory. Since accuracy rates are uninformative regarding this, I therefore used Cowan's K formula (Cowan et al., 2005). The general logic of the formula used for these memory estimates has been first develop by Pashler (1988), who developed an equation for memory estimates from the hit rate (H) and false alarm rate (FA) in the VSTM task described above. Pashler's equation was further improved by Cowan et al. (2005), and the resulting equation is simply: $K = N (H - FA)$, where K is the memory estimate and N is the number of items presented in the memory set. For example, Luck and Vogel (1997) demonstrated that participants performing the VSTM task I describe above are nearly 100% correct when the memory set contained one or two items, and most participants were close to 100% accuracy for the memory set of three items. Almost all participants made errors at a set size of four, and accuracy declined systematically as the set size increased from 3 to 12 items. However, studies employing Cowan's K formula (e.g. Todd & Marois, 2004) suggested that people's memory capacity can be approached with set sizes of approximately 3-4 items (for a similar argument, see Bays & Husain, 2008, 2011). It should be noted here that although the above formula has been mostly used in the literature to estimate the number of discreet items held in memory, in this thesis it is simply employed as a measure of the amount of information (and not discreet items) currently held in visual short term memory.

However, perhaps the main advantage of this VSTM paradigm is that it involves only relatively simple non-maintenance processes, making task performance sensitive primarily to the nature of the visual short term maintenance. The role of encoding processes is minimized by using of very simple and highly discriminable stimuli (e.g. of different colour each), whereas the role of verbal strategies can be minimized by using difficult-to-label stimuli (e.g. spatial location) or by using concurrent articulatory suppression tasks (such as repeating aloud a set of digits; see Chapter 3) that interfere with verbal rehearsal (Besner, Davies, & Daniels, 1981; Murray, 1968). The role of response systems can also be minimized by using simple, unspeeded "change" or ”no-change" responses.

Importantly, increasing the set size in this task does not involve increased load on cognitive control processes, as for example is the case with tasks that require participants to maintain the serial order of the items held in memory. For example, in the "successor naming" task (employed in Experiments 3 and 6 in this thesis), participants are asked to maintain via verbal rehearsal a set of digits in either fixed order (e.g. 1-9) or a random order that is different on every trial. Upon presentation of the memory probe that consists of a single digit, participants are requested to report the digit that followed this probe in the memory set. Maintenance of serial-order via verbal rehearsal has been shown to recruit on cognitive control (e.g. D'Esposito, Postle, Ballard, & Lease, 1999; Marshuetz, 2005) and high load in this task has been shown to result in enhanced distractor processing (e.g. De Fockert et al., 2001; Lavie et al., 2004). These two tasks were therefore suited for contrasting the effects of load on visual maintenance (VSTM task) to those of cognitive control (successor naming task) resources on visual perception (detection sensitivity; *d'*) in Chapters 2 and 3.

In experiment 10 presented in Chapter 4, I employed fMRI to investigate the effects of VSTM load on sensory visual cortex. As discussed in section 1.3 above, sensory visual cortex is involved in both, encoding as well as short term maintenance of incoming visual information. In light of this evidence, I used retinotopic mapping to investigate whether the response of primary visual cortex (V1) to incoming information is reduced with higher VSTM load. If VSTM load draws on resources that are employed in visual perception (i.e. sensory visual cortex) then the sensory response to incoming visual information should be reduced with higher VSTM load.

Finally, Chapter 5 examines the mechanisms by which load on visual perceptual resources (i.e. VSTM load and perceptual load) affects visual perception. It is well-known from single unit electrophysiology studies that neural responses in visual sensory cortex increase their response with increasing contrast of a visual stimulus (Albrecht & Hamilton, 1982; Sclar, Maunsell & Lennie, 1990). Here, I examined the effects of perceptual load (Experiment 11) and VSTM load (Experiment 12) on the function that relates the contrast of a visual stimulus to the neural response to the same stimulus (i.e. the contrast response function). Specifically, I considered whether load on perceptual resources affects the contrast response function by applying a fixed multiplicative response gain factor (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999) or by changing the sensitivity of the contrast response function (i.e. contrast gain; Li & Basso, 2008; Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000).

Chapter 2:

The Effects of Different Types of Working Memory Load on Visual Detection

2.1 Chapter Introduction

The experiments in Chapter 2 sought to establish the effects of VSTM load on detection sensitivity for a task-unrelated visual stimulus while contrasting these effects to those of perceptual load and WM cognitive control load. Perceptual load theory proposes that perception of such a visual stimulus depends upon whether capacity is exhausted by the perceptual demands of a concurrent task: the stimulus is perceived if task demands on perceptual resources are minimal but it will not be perceived if attending to the concurrent task fully exhausts capacity. Relating load theory with recent evidence that visual maintenance involves the same sensory visual cortices as those involved in perception (e.g. Munneke et al., 2010) led me to predict a novel dissociation between the effects of loading different WM processes on detection sensitivity. Specifically, I predicted that loading visual short term memory (VSTM) maintenance processes will increase the demand on sensory representation capacities which are involved in perceptual processing and this should result in reduced perception of any low-priority stimuli: a similar effect to that of perceptual load (Macdonald & Lavie, 2008). In contrast, loading WM cognitive control processes will lead to reduced control over stimulus processing priorities and thus result in enhanced processing of lower priority stimuli.

In the present chapter, participants performed a visual search task (searching for one of two pre-specified target letters among other letters) during the delay period of a short-term memory task. During half of the search displays a meaningless shape that was unrelated (e.g. in location, shape and identity) to the letter search task was presented in the periphery. Participants were requested to detect the presence of this shape but this was set as their lowest task priority. Participants were informed that the memory and search tasks were their primary tasks and performance accuracy in the memory and search task (but not the detection assignment) was emphasized.

The level and type of load involved in the tasks was varied. In Experiment 1, participants performed a VSTM task (requiring recognition of color and location for a colored-squares array). VSTM maintenance load was manipulated (Experiment 1) by varying the set size of the memory sample of colored squares. Perceptual load of the visual search task was manipulated (Experiment 2) by varying the search set size. Both manipulations were expected to draw on sensory visual representations and thus lead to reduced detection sensitivity.

In Experiment 3 participants performed a WM “successor naming” task (requiring recall of digit order) and load was manipulated by presenting the memory sample digits either in a fixed order (low load) or in a random order (high load). The successor naming task is known to recruit on WM cognitive control (e.g. D’Esposito, Postle, Ballard, & Lease, 1999; Marshuetz, 2005) and high load in this task has been shown to result in enhanced distractor processing (e.g. De Fockert et al., 2001; Lavie et al., 2004). Here I predicted that reduced control over the task processing priorities under high WM cognitive control load would lead to enhanced detection sensitivity of the low priority peripheral-detection stimulus.

2.2 Experiment 1

2.2.1 Introduction

In Experiment 1 participants searched for target letter X or N presented alone in one of six locations arranged in a circle around fixation. They were also asked to detect a small, meaningless grey figure that was presented outside of the letter circle. This task was performed during the maintenance interval of a delayed match-to-sample VSTM task. VSTM load was manipulated by varying the number of items in the memory set. In the low VSTM load condition only one item was presented in the memory set, and in the high VSTM load condition the memory set contained six items. I predicted that the high VSTM load condition would lead to reduced detection sensitivity for the peripheral figure that was presented together with the letter-search task during the maintenance period.

2.2.2 Method

Participants. All participants in this experiment (as in all the rest of the experiments reported in this thesis) were recruited from the UCL subject pool, provided informed consent, had normal colour vision, normal visual acuity, were naïve to the purpose of the experiment, provided informed consent, and were compensated for their participation. Sixteen participants took part in Experiment 1. Two participants who missed the detection stimulus on more than 90% of trials, and one participant who failed to make any response on 50% of trials were replaced by three new participants. The age range was 18 to 32 years (M = 23.25 years, SD = 3.84 years) and 10 were females.

Stimuli & Procedure. This experiment (and all the remaining experiments reported in this chapter) was controlled using E-Prime (Psychology Software Tools, Inc., 2003) running on a PC attached to a 19-inch CRT monitor (resolution = 800×600; refresh rate: 60Hz; mean background luminance: ~ 70Cd/m^2). A viewing distance of 60cm was maintained with a chin rest.

Figure 2.1 illustrates the trial sequence and display durations. Trials started with a fixation cross followed by a memory set of one (low load) or six (high load) colored squares (0.38°x0.38°) randomly placed on a 3x3 grid (1.38°×1.38°) centered at fixation. Each square was of a different color, chosen randomly from black (< 0.01cd/m^2), blue (x = .15, y = .07; 29.05 cd/m^2), cyan (x = .20, y = .27; 69 cd/m^2), green (x = .27, y = .59; 65.84 cd/m^2), magenta (x = .28, y = .14; 48.20 cd/m^2), pink (x = .32, y = .30; 69.14 cd/m^2), red (x = .62, y = .33; 39.56 cd/m^2), white (77 cd/m^2), and yellow (x = .40, y = .49; 73.61 cd/m^2). Following a 2 s interval, a black letter (X or N; 0.6°×0.4°) appeared in one of six locations (with small black dots in the five empty positions that extended 0.05° × 0.05°) arranged in a circle (1.7° in radius) around fixation. Participants identified which of the two target letters was presented by pressing 0 for X and 2 for N on the numerical keypad using their right hand. Participants were asked to also detect a small (0.3°x0.3°) gray ($x = .27$, $y = .31$; 49.81 cd/m^2) shape that was presented at 5.4° eccentricity on 50% of the trials (randomly selected) and press ‘S’ for present or ‘A’ for absent upon presentation of a question mark.

Display backgrounds were mid-gray ($x = .27$, $y = .29$; 64.11 cd/m^2). The memory probe was a single square presented in one of the occupied memory-set positions. Participants used their left hand to pressed ‘S’ indicating that this was a match to the memory set in colour and position or ‘A’ to indicate “different”. The memory probe was a match on half of the trials, and had a different colour on the other half. In all tasks, responses were not speeded and no response feedback was given.

The condition of VSTM load was blocked (as in all the remaining experiments reported in this thesis). Following a 48-trial practice block participants completed four blocks of 72 trials each alternating between low and high load blocks. Block order was counterbalanced across participants. The same procedure was followed in the rest of the experiments in this chapter (Experiments 2 and 3).

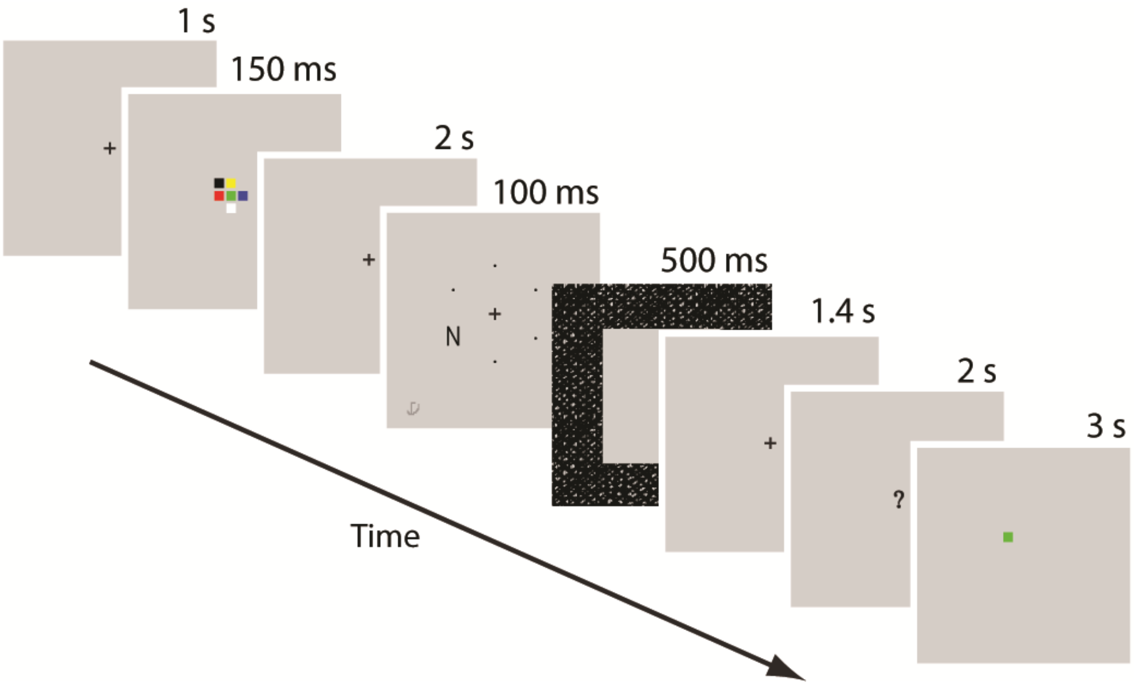

Figure 2.1. An example trial sequence and timing in Experiment 1. A trial from the high VSTM load condition with a detection stimulus present (bottom left corner of the search task display) is shown (displays not drawn to scale). The correct memory probe response here is ‘different’. In the low VSTM load condition the memory set had only one square.

2.2.3 Results

VSTM. Table 2.1 shows mean percentage accuracy rates and mean memory estimates (Cowan’s K = (hit rate – 0.5 + correct rejection – 0.5) * N, where K is the memory estimate and N is the number of items presented in the memory set).

Table 2.1. Mean Percentage Accuracy Rates in the VSTM Task and the Letter Search Task and Mean Memory Estimates in the VSTM Task as a Function of VSTM Load in Experiment 1.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Search Accuracy (%)
Low	85 (13)	0.68 (0.26)	95 (5)
High	58 (11)	0.99 (1.28)	95 (5)

SDs are listed in parenthesis.

As the table shows, VSTM task accuracy was significantly decreased from the low to the high VSTM load condition, t(15) = 5.66, p = .006, d = 1.47 (Cohen effect size). Although the memory estimates (K) were increased with higher VSTM load, this trend did not reach statistical significance, t(15) = 0.93, p = .369, d = 0.34. This trend for increased memory estimates with higher load and more importantly the effect of load on the mean accuracy rates clearly indicate that VSTM load was manipulated effectively in Experiment 1.

Letter Search. As shown in Table 2.1, search task accuracy was the same in the low and high VSTM load conditions, *t* < 1.

Detection. In all experiments in this chapter, analyses of the detection task performance were made on trials with correct performance on the search and memory tasks. Importantly, consistent with my predictions, detection sensitivity was significantly reduced from the low to the high VSTM load condition, t(15) = 3.29, p = .005, d = 0.62 (see Figure 2.2). There was no effect of VSTM load on response bias (β; *t* < 1).

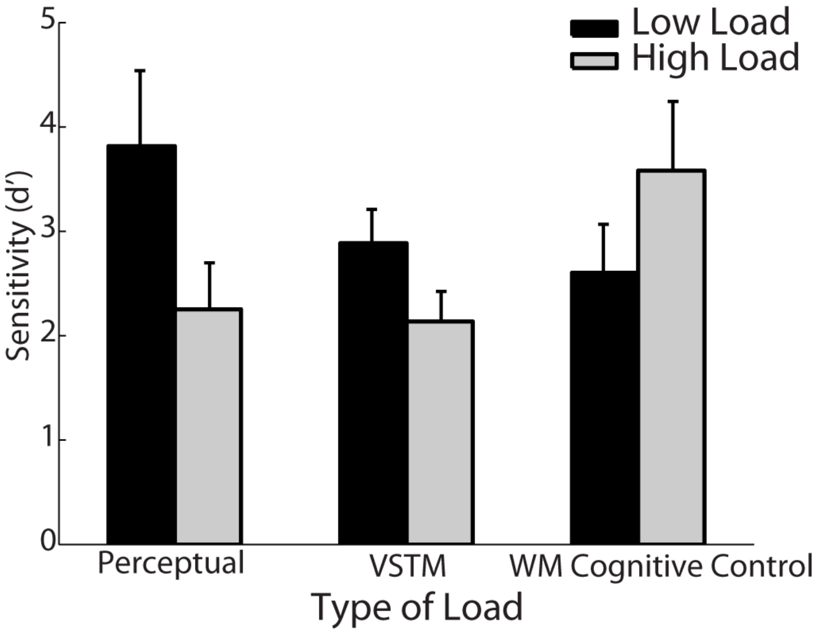

Figure 2.2. Experiments 1-3 results. Mean detection sensitivity (d') is plotted as a function of the level and type of load. Error bars represent +1 SEM.

Moreover, Figure 2.3 shows that the reduction in detection sensitivity with higher load could be predicted from the extent to which VSTM was occupied under high load. A negative correlation between the increase in memory estimates (K) and the reduction in *d'* with high load indicated that individuals who held more items in memory under high (vs. low) VSTM load also showed a greater reduction of detection sensitivity with higher load (b = -.28, t(13) = 2.74, p = .02). This effect was found after the data of one outlier participant with a detection sensitivity reduction of more than 2 SDs under high VSTM load were excluded from the linear regression analysis. The finding of a trade-off between detection sensitivity and the extent to which VSTM capacity was filled under load strongly suggests shared capacity between VSTM and perception.

The findings of Experiment 1 confirm my prediction that detection sensitivity depends on the amount of visual information maintained in short-term memory.

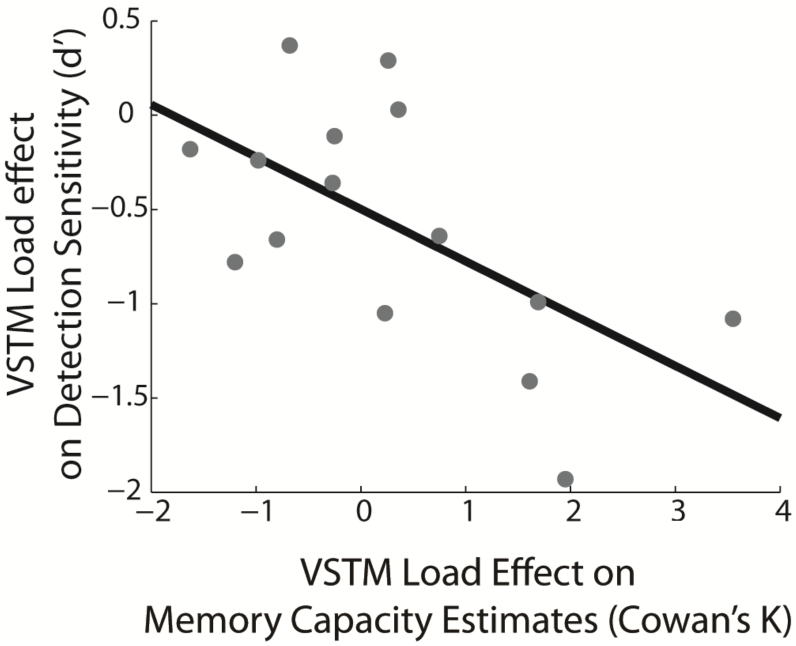

Figure 2.3. Scatter plot showing the effects of VSTM load on detection sensitivity (high load d' minus low load d', y axis) and on memory capacity estimates (calculated using Cowan's (2005) formula, x axis). The line represents the best linear fit. The increase in K with high load explained a significant proportion of variance in the reduction of detection sensitivity scores ($R^2 = .37$), $F(1,13) = 7.51$, p = .02.

2.3 Experiment 2

2.3.1 Introduction

Experiment 2 sought to replicate the effects of perceptual load on detection sensitivity (Macdonald & Lavie, 2008) with this new experimental paradigm. Whereas in Experiment 1 VSTM load was varied and perceptual load in the search task was always low load, in Experiment 2 I manipulated perceptual load by varying the number of non-target items in the letter-search task and VSTM load was kept always of low load.

2.3.2 Method

Participants. Eight participants took part in Experiment 1. One participant whose search accuracy was below 50% was replaced by a new participant. The age range was 19 to 35 years (M = 23.63 years, SD = 5.34 years) and 4 were females.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 1 except that VSTM load was not varied and always the low VSTM load condition was employed. Instead, in Experiment 2 perceptual load was varied by manipulating the number of non-target letters in the letter-search task. In the low perceptual load condition the target letter (either X or N) was presented alone (with small black dots in the empty positions). In the high perceptual load condition letters H, K, M, W, and Z were presented together with the target letter in the rest of the empty positions.

2.3.3 Results

VSTM. Mean percentage accuracy rates and mean memory estimates as a function of VSTM load are presented in Table 2.2.

Table 2.2. Mean Percentage Accuracy Rates in the VSTM Task and the Letter Search Task and Mean Memory Estimates in the VSTM Task as a Function of Perceptual Load in Experiment 2.

Perceptual load	VSTM Accuracy (%)	Memory estimates (K)	Search Accuracy (%)
Low	95 (2)	0.90 (0.05)	96 (4)
High	94 (5)	0.85 (0.13)	78 (11)

SDs are listed in parenthesis.

As shown in Table 2.2, VSTM task accuracy rates ($t < 1$) and memory estimates, t(7) = 1.17, p =.28, d = 0.50, were not different between the low and the high perceptual load conditions.

Letter Search. The mean accuracy rates are presented in Table 2.2. As the table shows, the letter-search task accuracy was reduced from the low to the high perceptual load condition, t(7) = 5.51, p =.001, d = 1.49. Thus perceptual load was manipulated effectively (Lavie, 1995).

Detection. Importantly, detection sensitivity was again significantly reduced from the low to the high perceptual load condition, t(7) = 2.38, p = .049, d =.86 (see Figure 2.2). There was no effect of load on response bias (β).

Finally a mixed ANOVA between-experiment comparison on detection sensitivity scores between Experiments 1 and 2 with load as the within-subject factor (low, high) revealed no difference between the effects of VSTM load and perceptual load on detection, $F(1, 22) = 2.12$, p = .16, $\eta^2 = .09$.

Overall, the findings of Experiment 2 replicate Macdonald and Lavie's (2008) findings within this new interleaved memory and perception tasks paradigm and confirm my prediction that the effects of perceptual load on detection would be akin to those of VSTM maintenance load.

2.4 Experiment 3

2.4.1 Introduction

In Experiment 3 I examined the effects of loading WM cognitive control processes on detection using the same paradigm as in Experiment 1 but replacing the VSTM task with a WM "successor naming" task requiring order-recall for digits (e.g. De Fockert et al., 2001).

2.4.2 Method

Participants. 10 new participants (aged 19-38) took part in Experiment 3. The age range was 19 to 38 years (M = 24.50 years, SD = 5.40 years) and 6 were females.

Stimuli & Procedure. The search and detection task was identical to that used in the low load condition of Experiment 1. A “successor naming” WM task required participants to indicate which digit followed the memory probe digit in the memory set. The memory set consisted of nine black digits (1–9, each subtending 0.7° by 0.5°) presented in a row, in fixed numerical order for 500 ms (low load condition) or in random order for 2000 ms (high load condition). Following the detection response, a single memory probe digit (that was equally likely to be any of the first eight digits of the trial’s set) was presented at fixation until a response was made (or 4 s elapsed).

2.4.3 Results

WM. Mean percentage accuracy rates as a function of WM load are presented in Table 2.3.

Table 2.3. Mean Percentage Accuracy Rates in the WM Successor-Naming Task and the Letter Search Task as a Function of WM Load in Experiment 3.

WM load	WM Accuracy (%)	Search Accuracy (%*)*
Low	98 (2)	98 (2)
High	59 (21)	98 (2)

SDs are listed in parenthesis.

As the table shows, WM task accuracy was significantly reduced from the low to the high WM load condition, $t(9) = 6.16$, $p < .001$, $d = 1.59$, confirming the efficacy of the WM cognitive control load manipulation in Experiment 3.

Letter Search. As shown in Table 2.3, search task accuracy was the same in both the low and high load conditions WM load conditions, $t(9) = 1.85$, $p = .10$, $d = .26$.

Detection. Importantly, detection sensitivity was now significantly increased from the low to the high WM load condition, $t(9) = 2.53$, $p = .03$, $d = .53$. As in the previous experiments, load had no effect on response bias (β).

The opposite effects on detection of WM load in the present experiment versus VSTM load (Experiment 1) and perceptual load (Experiment 2) were confirmed in mixed-model ANOVAs with the between-subject factor of load type (WM vs. VSTM; or WM vs. perceptual load) and the within-subject factor of level (low, high) that revealed significant interactions (for WM vs. VSTM, $F(1,24) = 17$, $p < .001$, $\eta^2 = .42$; for WM vs. perceptual load, $F(1,16) = 12.24$, $p = .003$, $\eta^2 = .43$).

2.5 Chapter Conclusions

The results of Chapter 2 demonstrate contrasting effects of loading different WM processes on visual detection. During performance of a search task, detection sensitivity for a low priority search-unrelated stimulus in the periphery was reduced with high visual maintenance load, an effect that was equivalent to that of perceptual load. However, detection sensitivity was enhanced with high load on WM cognitive control processes. The findings that different types of load have opposite effects on stimulus detection cannot be explained in terms of a general effect of increased task-difficulty under higher load. All high load conditions were more difficult but the effect on detection sensitivity critically depended on the type of process loaded.

The findings presented in this chapter therefore support the hypothesis that visual short term maintenance processes utilize the same perceptual representation resources as those used in visual detection, and extend load theory to accommodate for competitive interactions between representation in VSTM and incoming visual information.

Chapter 3:

Establishing the Effects of Visual Short Term Memory Load on Visual Detection

3.1 Chapter Introduction

The purpose of Chapter 3 was to compare the effects of different types of processing load (VSTM, perceptual, WM cognitive control) on visual detection using an improved experimental paradigm that allows addressing several potential alternative accounts for these effects. In the experiments described so far in Chapter 2, participants performed a letter-search task that was presented concurrently with the visual detection task. Participants were questioned about the target-stimulus in the visual detection task only after their response to the visual search task (i.e. after at least 2 seconds have elapsed from the stimulus offset; see Figure 2.1, Chapter 2). This design raises various alternative accounts for the effects of load on detection sensitivity in terms of an interaction of load with attention employed in the search task, memory failures and task priorities.

The first concern regarding the design of the experimental paradigm of Chapter 2 is that the effects of the various types of load on visual detection might have depended on some form of interaction with the deployment of attention in the search task. In other words, the previous effects of reduced detection sensitivity with higher perceptual and VSTM load, as well as the opposite effects with higher WM cognitive control load, could have been indirectly due to load affecting the ability to perform the search task, rather than the demands on perceptual representational capacity (with perceptual and VSTM load) or WM cognitive control placed directly on sensory detection. Although no effects were seen on the search task performance in the experiments reported in Chapter 2, this may simply be due to ceiling effects in the performance of the search task (e.g. a pop-out effect of the search task angular target letter in low as well as high VSTM load conditions). It was therefore important to assess whether the effects of load generalize to tasks that preclude an interaction of load with attention. The visual letter-search task was therefore eliminated from the task and participants responded to the visual detection task immediately following the stimulus presentation.

As well as addressing the effects of a possible interaction of load with attention, the elimination of the search task also serves to examine and potentially rule out memory-based accounts as well as task-priority based accounts of the results of reduced detection sensitivity with higher perceptual load and VSTM load. Regarding memory-based accounts, recall that participants were questioned about the visual detection only after their response to the search task and at least 2 s have elapsed since the stimulus offset. Thus, because participants are questioned a relatively long time after the offset of the stimulus, it is possible that high load led to higher rates of forgetting: rather than having not seen the target stimulus participants may have simply forgotten it had been there. Alternatively, the detection stimulus may have generated a weak signal that was easily wiped out of memory by the interleaved search task response.

A further concern regarding the effects of the search task is that of giving greater priority to the detection task in the low load compared to the high load conditions of the perceptual load and VSTM load manipulations (Experiments 1 and 2). In the experiments of Chapter 2, participants were instructed to prioritize the search task over the detection task. However, because the low load condition was easier to perform than the high load condition, participants may have equally prioritized the search and detection tasks in the low load condition but gave higher priority to the search task in the high load condition as instructed. That is, the search task may have been prioritized over the detection task to a greater extent in the high load than low load condition. If this were the case, it could explain the better detection performance in the low load than high load in the experiments of perceptual load and VSTM load manipulations (Experiments 1 and 2). Eliminating the search task and questioning participants about the visual detection task immediately following the stimulus presentation directly addresses these memory-failure and task-priorities concerns.

An additional concern with the experimental design employed in Chapter 2 is that the detection task was not of equivalent difficulty across all participants. Because the same stimulus figure was used as the detection target for all participants in the experiments of Chapter 2, differences in contrast sensitivity threshold between participants might have affected the results. For example, if for some participants the detection of the visual stimulus was near ceiling it might have underestimated the effect. A further aim of this chapter was therefore to establish a detection task of equivalent difficulty across participants. For this reason, I replaced the stimulus figure used as the target in the detection task of Chapter 2 with a contrast-increment target in one of four peripheral gratings (one in each quadrant of the screen), that was adjusted based on each participant's individually assessed contrast-threshold. Prior to the experiment, each participant's contrast threshold was assessed using a staircase method, and the amount of contrast-increment in the target was then set to 120% of each participant's threshold. This same procedure was followed in all subsequent experiments in this thesis, thus ensuring that the detection task was of equivalent difficulty across participants in different experiments.

In this chapter I first set out to assess the effects of VSTM load (Experiment 4), perceptual load (Experiment 5), and WM cognitive control load (Experiment 6) on detection sensitivity after implementing the methodological changes described above. Eliminating the letter-search component and establishing a detection task of equal difficulty across participants allowed me next to address various alternative factors such as the effects of verbal maintenance strategies and longer intervals between the memory set and the detection stimulus (Experiment 7) as well as effects of the spatial extent of visual processing during the VSTM task delay period by eliminating the spatial separation between the central VSTM task displays and the peripheral detection task stimuli (Experiment 8). Furthermore, I aimed to directly assess an important implication of the suggestion of shared resources between VSTM and visual perception. Specifically, I examined whether there is a trade-off between the amount of information maintained in VSTM and sensitivity for detection (Experiment 9).

3.2 Experiment 4

3.2.1 Introduction

The purpose of Experiment 4 was to examine the effects of VSTM load on detection sensitivity using the modified experimental paradigm that excluded the visual search component and replaced the detection target stimulus with a contrast-increment target of equivalent difficulty across participants. In this paradigm, participants were asked to perform the same VSTM task as the one employed in Chapter 2. During the memory delay only the detection task was presented that comprised of the contrast-increment target presented (in 50% of the trials) on one of four peripheral gratings. Participants reported whether the target was present or absent immediately after the stimulus presentation, thus eliminating the 2 s delay between the stimulus presentation and the detection response in the experiments of Chapter 2. The experiment was preceded by a staircase procedure for determining each participant's contrast threshold as described in the method.

3.2.2 Method

Participants. Fifteen new healthy volunteers were recruited from the UCL Psychology subject pool. The age range was 19 to 36 years (M = 24.13 years, SD = 4.56 years) and 10 were females.

Stimuli & Procedure. This experiment (and all the remaining experiments reported in this thesis) was controlled using Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent.php) for MATLAB (Mathworks, Inc.) running on a PC attached to a 19-inch CRT monitor (resolution = 800×600; refresh rate: 60Hz; mean background luminance: ~ 70Cd/m^2). A viewing distance of 60cm was maintained with a chin rest.

The timings and procedure of Experiment 4 are presented in Figure 3.1. Each trial begun with a fixation cross display presented for 1000 ms and following a 500 ms blank interval the VSTM set was presented for 150 ms. The memory set contained one (low VSTM load) or six different colored squares (high VSTM load) subtending 0.6°, randomly chosen on each trial from the same set of nine colors as Experiment 1 (Chapter 2) and were randomly placed among nine possible locations in a 3 × 3 matrix that extended 2.4°.

After a 1000 ms blank interval, four achromatic vertical square-wave gratings (4.2° × 4.2°; 2.5 cpd; non-target contrast: 10%) were presented for 100 ms in each of the four quadrants at a distance of 6° from fixation. Participants were asked to detect the presence of a contrast increment (target), present in one of the gratings on 50% of the trials. The presence and location of the target were counterbalanced across each block of trials. The target contrast-increment was individually assessed for each participant using a staircase procedure prior to the experiment, with an accelerated stochastic approximation method (Kesten, 1958) for obtaining target-contrast estimate of approximately 75% hit rate. Following presentation of the detection stimuli, a “?” appeared at fixation for 1900 ms serving as a 2000ms response window and contributing to the 3000 ms memory delay period (offset of memory set until onset of memory probe). Participants made a left hand “present” (middle finger) or “absent” (index finger) button press response. After the response window for the detection task, the memory probe (one colored square) appeared for up to 3000 ms at one of the positions occupied in the memory set. Participants indicated whether the color of the memory probe matched the color of the memory set square at the same location. Participants responded with a right hand button press using index finger for “same” or middle finger for “different”. In half of the trials the color of the memory probe matched that of the memory set. In the unmatched trials, the memory probe had a different color that was equally likely to have been selected from the other colors of the memory set or the remaining color set. None of the responses were speeded, and no feedback was given in any of the tasks.

Participants first participated in the staircase threshold procedure for determining the target contrast. After 32 practice trials, participants completed 256 trials in 8 blocks (4 low and 4 high VSTM load blocks) of 32 trials each in an ABBABAAB counterbalanced order.

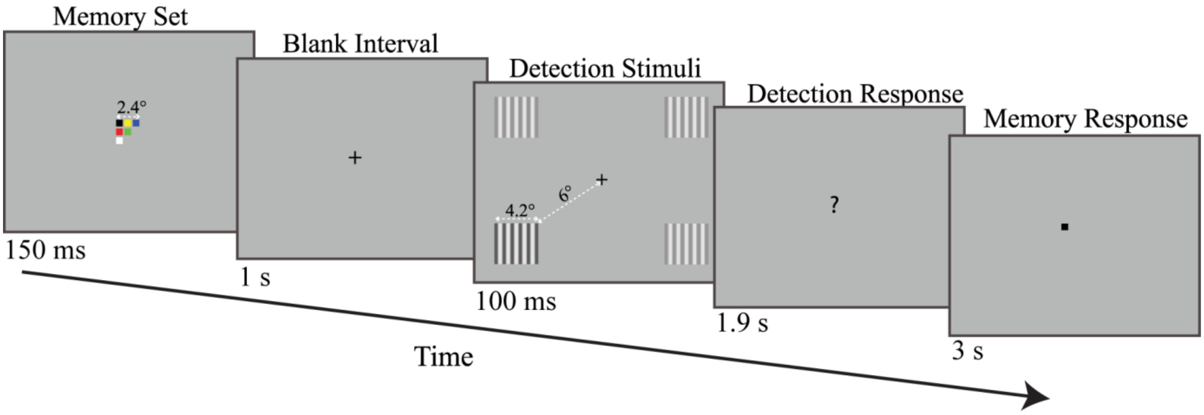

Figure 3.1. An example trial sequence and timing in Experiment 4. A trial from the high VSTM load condition with the contrast-increment target present (bottom left corner of the “detection stimulus” display) is shown (displays not drawn to scale). The correct memory probe response here is ‘same’. In the low VSTM load condition the memory set had only one square.

3.2.3 Results & Discussion

VSTM. Mean percentage accuracy rates and mean memory estimates (Cowan’s K) are presented in Table 3.1.

Table 3.1. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task and Mean Detection Sensitivity as a Function of VSTM Load in Experiment 4.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Detection Sensitivity *(d')*
Low	94 (4)	0.88 (0.09)	2.07 (0.79)
High	61 (6)	1.36 (0.76)	1.57 (0.70)

SDs are listed in parenthesis.

As the table shows, VSTM task accuracy decreased significantly from the low to the high VSTM load condition, t(14) = 16.06, p < .001, d = 1.87. The memory estimates were significantly increased from the low to the high VSTM load condition, t(14) = 2.41, p = 0.03, d = 0.82. These results indicate that in Experiment 4 VSTM load was manipulated effectively.

Removing the search task that was presented together with the detection task in Experiment 1 resulted in improved VSTM task performance in this experiment (M = 78%, SD = 17%) compared to Experiment 1 (M = 71%, SD = 17%) as indicated by a mixed ANOVA between experiment comparison on the accuracy rates with experiment as the between subjects factor (Experiment 1, Experiment 4) and with the level of load as the within subject factor (low, high) that revealed a main effect of experiment, *F*(1, 29) = 9.04, p = .005, $\eta^2 = .24$. A similar between experiment comparison (Experiment 1, Experiment 4) with load as the within subjects factor (low, high) on memory estimates did not reveal any differences between this experiment (K = 1.12, SD = 0.59) and Experiment 1 (K = 0.84, SD = 0.92), *F*(1, 29) = 2.22, p = .15, $\eta^2 = .07$. No significant interactions between experiment and load were observed on either accuracy rates, *F*(1, 29) = 1.79, p = .19, $\eta^2 = .06$, or memory estimates, *F* < 1.

Detection. As shown in Table 3.1, consistent with the findings of Experiment 1, detection sensitivity was again significantly reduced from the low to the high VSTM load condition, t(14) = 4.74, p = 0.003, d = 0.65. As was the case in the experiments reported in Chapter 2 no effects of VSTM load on response bias (beta) were found ($t < 1$).

A mixed ANOVA between experiment comparison on detection sensitivity scores with experiment (Experiment 1, Experiment 4) as the between-subject factor and load (low, high) as the within-subject factor indicated better overall sensitivity for the detection target stimulus in Experiment 1 (d' = 2.51, SD = 1.26) compared to Experiment 4 (d' = 1.82, SD = 0.78), $F(1, 29) = 4.05$, p = .05, $\eta^2 = .12$. These differences possibly reflect that fact that in Experiment 4 I used the contrast-increment target for the detection task that was individually adjusted based on each participant's contrast threshold, whereas in Experiment 1 all participants attempted to detect the same stimulus figure. It is therefore likely that the perceived contrast of the stimulus figure used as target in the detection task of Experiment 1 was higher than 120% of participants' contrast-threshold as was the case with the detection target stimulus in this experiment. This analysis did not reveal any interaction effects between the factor of experiment and the factor of VSTM load, $F < 1$. Indeed, VSTM load affected detection sensitivity similarly in Experiments 1 and 4 (in Experiment 1 d' reduced by 0.75 and Cohen's d effect size was 0.62; in Experiment 4 d' reduced by 0.50 and Cohen's d was 0.65).

Overall, Experiment 4 replicated the effects of VSTM load on detection sensitivity found in Experiment 1 and extended these effects over a range of lower detection sensitivity scores. Importantly, because the search task component was now eliminated, these findings rule out an alternative account in terms of an interaction of load with the employment of attention in the search task. Moreover, the fact that in this experiment participants did not have to delay their detection response until after they had made their search response (as was the case in Chapter 2) rules out an alternative account in terms of a VSTM load effect on memory rather than on detection sensitivity. Furthermore, the fact that the detection task was now the only priority during the memory delay period rules out a further alternative account regarding differences in the priority of the detection task over the search task between low load and high load.

3.3 Experiment 5

3.3.1 Introduction

Experiments 1 and 2 in Chapter 2 provided preliminary support for the hypothesis that the effects of VSTM load are akin to those of perceptual load. However, so far the evidence relied on comparisons between different experimental methods. Specifically, previously VSTM load was manipulated in a visual delayed match-to-sample task whereas perceptual load was manipulated in a visual letter-search task. Differences in the methods of the experimental paradigms employed thus preclude any direct comparisons between the effects of perceptual load and VSTM load.

In Experiment 5 I assessed whether the effects of VSTM load are more directly equivalent to those of perceptual load (Macdonald & Lavie, 2008) by manipulating perceptual load in closely matched experimental conditions to those of manipulating VSTM load. Specifically, in this experiment perceptual load was manipulated with an identical task to that used manipulating VSTM load in Experiment 4. The detection stimulus now appeared on the same display as the memory set instead of 1 s after the memory set in Experiment 4. Because the detection stimulus was presented on the same display as the memory set, the requirement to encode a memory set with a greater number of items in high (6 items) compared with low (1 item) VSTM load (Lavie, 1995) now placed a larger perceptual load during the detection task.

3.3.2 Method

Participants. Ten new healthy volunteers were recruited from the UCL Psychology Subject pool. The age range was 20 to 29 years (M = 23.6 years, SD = 3.27 years) and 6 were females.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 4 except that the detection stimuli now appeared on the same display as the memory set with duration of 100 ms (see Figure 3.2). The stimulus display was followed by a 2 s question mark display during which participants made their detection response. This was followed by a 1 s blank display contributing to a 3 s memory delay. Like in Experiment 4, the memory probe appeared next (with one colored square), for up to 3 s during which participants made their VSTM task response.

Participants completed 256 trials in 8 blocks of 32 trials each in the counterbalanced order of ABBABAAB. Prior to the experiment, each participant completed 32 practice trials as well as the staircase threshold procedure for determining the target contrast as described in Experiment 4.

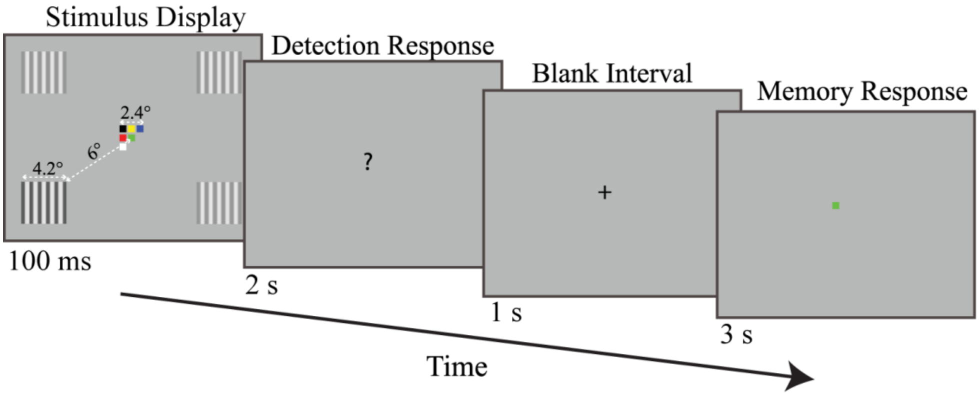

Figure 3.2. An example trial sequence and timing of Experiment 5. Here a trial from the high VSTM load condition is shown. The contrast-increment target (here present at bottom

left corner of the stimulus display) is presented on the same display as the memory set. In the low VSTM load condition the memory set had only one square.

3.3.3 Results & Discussion

VSTM. Mean percentage accuracy rates and mean memory estimates as a function of VSTM load are presented in Table 3.2.

Table 3.2. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task and Mean Detection Sensitivity as a Function of VSTM Load in Experiment 5.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Detection Sensitivity *(d')*
Low	92 (5)	0.84 (0.10)	1.60 (0.67)
High	61 (6)	1.33 (0.72)	1.05 (0.65)

SDs are listed in parenthesis.

As shown in the table, VSTM task accuracy decreased significantly from the low to the high VSTM load condition, t(10) = 13.69, p < .001, d = 1.85. The memory estimates (Cowan's K) were significantly increased from the low to the high VSTM load condition, t(10) = 2.29, p < 0.05, d = 0.88. These results indicate that in Experiment 5 VSTM load was manipulated effectively.

The effect of load on VSTM task performance was similar in this experiment (mean accuracy rate reduced by 31% and K increased by 0.49) to that of Experiment 4 (mean accuracy rate reduced by 33% and K increased by 0.48). A mixed ANOVA between-experiment comparison with experiment as the between-subject factor (Experiment 4, Experiment 5) and with load as the within-subject factor (low, high) performed on accuracy rates and on memory estimates (K) of the VSTM task revealed no effect of the type of load both for the accuracy rates and for the memory estimates (both $F < 1$). No significant interactions between the type of load and the level of load were found either, both for the accuracy rates and for the memory estimates (both $F < 1$). Thus presenting the detection stimulus together with the memory set did not affect performance on the VSTM task.

A further mixed ANOVA comparison between Experiments 2 and 5 with type of perceptual load task as the between-subject factor (search task in Experiment 2, VSTM task in Experiment 5) and the level of load as the within-subject factor (low, high) performed on accuracy rates revealed a main effect of experiment, $F(1, 17) = 16.87$, $p = .001$, $\eta^2 = .50$, indicating that the VSTM task in this experiment (M = 76%, SD = 17%) was more demanding than the search task in Experiment 2 (M = 87%, SD = 12%), $t(17) = 4.35$, $p < 0.001$, $d = 1.43$. The same comparison also revealed an interaction between experiment and load, $F(1, 17) = 9.89$, $p = .006$, $\eta^2 = .37$. This interaction reflects the fact that the effect of load was greater in the VSTM task of this experiment (accuracy reduced by 30%, Cohen's d = 1.85) than the search task of Experiment 2 (accuracy reduced by 18%, Cohen's d = 1.49).

Detection. Importantly, as shown in Table 4, detection sensitivity was significantly reduced from the low to the high perceptual load condition, $t(10) = 4.55$, $p = 0.001$, $d = 0.78$. Consistent with the findings of VSTM load, no effects of perceptual load on response bias were found ($t < 1$).

A mixed ANOVA between experiment comparison with type of load (VSTM, perceptual) as the between subject factor and level of load (low, high) as the within subject factor on detection sensitivity scores did not reveal a main effect of the type of processing load on detection sensitivity, $F(1, 24) = 3.03$, $p = .10$, $\eta^2 = .12$. Importantly, no interaction effects between the level and the type of processing load was found either, $F < 1$. Indeed, the reduction in detection sensitivity with higher perceptual load in this experiment (d' reduced by 0.55; Cohen's d effect size was 0.78) was equivalent to that of higher VSTM load in

Experiment 4 (*d'* reduced by 0.50; Cohen's d effect size was 0.65). Thus, the effects of perceptual load on detection sensitivity were equivalent to those of VSTM load.

A further mixed ANOVA comparison on detection sensitivity scores between this experiment and Experiment 2 (that manipulated perceptual load with the letter-search task) with experiment (Experiment 2, Experiment 5) as the between-subject factor and with the level of load (low, high) as the within-subject factor revealed a main effect of experiment, $F(1, 17) = 12.74$, p = .002, $\eta^2 = .43$, indicating that the manipulation of perceptual load with the VSTM task in this experiment resulted in lower detection sensitivity scores (*d'* = 1.32, SD = 0.63) than the manipulation of perceptual load with the letter-search task in Experiment 2 (*d'* = 3.04, SD = 1.42), t(17) = 3.56, p = 0.002, d = 1.29. Importantly, however, there was no significant interaction effect between experiment and the level of load, $F(1, 17) = 3.19$, p = .092, $\eta^2 = .16$.

The results of Experiments 5 thus demonstrated, within the same experimental paradigm and closely matched experimental conditions that the effects of VSTM load on detection sensitivity are akin to those of perceptual load. This finding provides further support for the suggestion that visual perception and visual short-term memory utilize common (capacity limited) sensory brain resources (Pasternak & Greenlee, 2005).

3.4 Experiment 6

3.4.1 Introduction

The aim of Experiment 6 was to examine the effects of loading WM cognitive control processes on detection sensitivity using the modified detection task that eliminated the visual search component and replaced the detection target with the contrast-increment target. WM cognitive control was manipulated using the same WM "successor naming" task as the one used in Experiment 3 that required serial order-recall for digits (De Fockert et al., 2001).

With the exclusion of the search task I no longer predicted that WM cognitive control load will enhance detection sensitivity. Recall that according to load theory, detection sensitivity was enhanced in Experiment 3 because reduced control over task priorities with higher WM load led to the failure to maintain the higher priority of the search task over the concurrent detection task leading to enhanced detection sensitivity compared to low load. In this new design, that eliminated the search task, the detection task was now the only priority during the memory delay and there was therefore no potential conflict in task priorities as was the case in Experiment 3. Because in this experiment cognitive control is no longer needed to maintain priorities between one attention task (visual letter-search task) and another (visual detection task) during the memory delay, no such effects of WM cognitive control load on detection sensitivity were predicted. Yet, it remained important to ensure that the effects of VSTM load and perceptual load observed with this new improved paradigm (Experiments 4 and 5) are due to load on visual representation capacity and not due to task difficulty.

3.4.2 Method

Participants. Sixteen new healthy volunteers took part in Experiment 6. The age range was 20 to 37 years (M = 26.44 years, SD = 5.81 years) and 6 were females.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 4 except that the VSTM task was now replaced by a WM successor-naming task identical to that used in Experiment 3.

Participants completed 256 trials in 8 blocks of 32 trials each. The condition of load was blocked in counterbalanced order (ABBABAAB). Before the experiment participants completed 32 practice trials and the staircase threshold procedure for determining the target contrast as described in Experiment 4.

3.4.3 Results & Discussion

WM. Mean percentage accuracy rates as a function of WM load are presented in Table 3.3.

Table 3.3. Mean Percentage Accuracy Rates in the WM Successor-Naming Task and Mean Detection Sensitivity as a Function of WM Load in Experiment 6.

WM load	WM Accuracy (%)	Detection Sensitivity (*d'*)
Low	97 (3)	2.29 (1.10)
High	54 (20)	2.26 (1.27)

SDs are listed in parenthesis.

As shown Table 3.3, WM task accuracy decreased significantly from the low to the high WM load condition, $t(15) = 8.39$, $p < .001$, $d = 1.67$. These results indicate that in Experiment 6 WM cognitive control load was manipulated effectively.

A mixed ANOVA between experiment comparison with experiment (Experiment 3, Experiment 6) as the between-subject factor and with level of load (low, high) as the within-subject factor on the WM accuracy rates did not reveal an effect of experiment or an interaction between experiment and load (both $F < 1$). Indeed, the effect of load on WM task performance was similar in this experiment (mean accuracy rate reduced by 43%) to that of Experiment 3 (mean accuracy rate reduced by 40%).

A further mixed ANOVA comparison with experiment (Experiment 4, Experiment 6) as the between-subject factor and with level of load (low, high) as the within-subject factor on the accuracy rates of this successor-naming WM task and accuracy on the VSTM task of Experiment 4 did not reveal a main effect of experiment ($F < 1$) or an interaction between experiment and load, $F(1, 29) = 3.72$, $p = .064$, $\eta^2 = .11$. The effect of load was similar in the successor-naming WM task in this experiment (mean accuracy rate reduced by 43% with load) compared to the VSTM task (mean accuracy rate reduced by 33% with load). Thus the difficulty of the WM task in this experiment was equivalent to the difficulty of the VSTM task in Experiment 4. This finding is important for addressing the effects of task difficulty on the effects of VSTM load observed in Experiment 4. If indeed task difficulty contributes significantly to the VSTM load effects, then this experiment with an equally difficult WM manipulation should lead to similar effects on detection sensitivity to the VSTM load effects in Experiment 4.

Detection. Only results from trials with a correct response in the successor-naming WM task are reported here. As shown in Table 4, despite the consistent reduction of detection sensitivity with higher VSTM load and perceptual load in previous experiments (Experiments 1, 2, 4, and 5), and even though the WM load manipulation in this experiment was at least as strong as that of VSTM load in Experiment 4, detection sensitivity was unaffected by higher WM cognitive control load in the successor-naming WM task, $t(15) = 0.096$, $p = 0.925$, $d = 0.03$. Response bias (β) was also not significantly different between the two WM cognitive control load conditions ($p = .12$).

Notice also that whereas detection sensitivity was enhanced with higher WM cognitive control load in Experiment 3, it was unaffected by load in the same successor-naming WM task in this experiment. This suggests, as I predicted, that the visual letter-search task might have played a critical role in the effects of WM cognitive control load on detection sensitivity in Experiment 3. Performing two tasks concurrently in Experiment 3 (search task plus detection task) higher WM cognitive control load resulted in participants failing to maintain a higher priority on the search task versus the detection task leading to enhanced detection sensitivity. Eliminating the search task in this experiment also eliminated any potential task priority conflicts, thus also eliminating any effects of WM cognitive control on detection sensitivity. However, because the main focus of this thesis was on the effects of VSTM load on detection sensitivity, this finding was not pursued further in the following chapters.

The results of Experiment 6 demonstrated that although the successor-naming WM task in this experiment was at least as difficult as (with a trend for being more difficult than) the VSTM task in Experiment 4, detection sensitivity was unaffected by WM cognitive control load, thus establishing the specificity of the effects of perceptual load and VSTM load on detection sensitivity. This finding convincingly rules out an alternative account of the effects of perceptual load and VSTM load in terms of an increase in the demand on general cognitive capacity resources instead of a specific demand on perceptual representational resources as claimed in this thesis. Furthermore, the contrast between the findings of this experiment and those of Experiment 3, that high WM cognitive control load enhanced detection sensitivity when a concurrent visual search task was also performed, allows for a more detailed understanding of the role that working memory plays in the control of selective attention. Specifically, cognitive control appears to be involved in resolving any potential conflicts in task priorities when an additional concurrent attentional task of higher priority is performed together with the visual detection task. In such situations, where cognitive control resources are rendered unavailable by loading working memory results in a failure to maintain task priorities between the two concurrent tasks. Because the visual detection task gains priority when WM cognitive control resources are loaded, detection sensitivity is thus enhanced.

3.5 Experiment 7

3.5.1 Introduction

The aim of Experiment 7 was to examine whether the effects of VSTM load on detection sensitivity are found in a task that precludes verbal rehearsal. This is of particular importance because verbal rehearsal of the memory set during the VSTM task might have exerted effects of WM cognitive control load. As discussed in Chapter 1, when participants are engaged in a verbal working memory task, their ability for cognitive control is reduced leading to increased distractor effects (Lavie et al., 2004) and enhanced sensitivity for perception of irrelevant (to the attention task) stimuli (e.g. Experiment 3, Chapter 2). It was therefore important to examine whether any differences in WM cognitive control load between the low and the high VSTM load conditions exert any significant contributions to the VSTM load effects on detection sensitivity. If participants encoded and maintained the low VSTM load memory set (where the memory set location was irrelevant) via verbal rehearsal but relied less on verbal rehearsal for the high VSTM load memory set (where maintenance of the spatial location of the memory set was required), then it is possible that the involvement of these verbal strategies in the low VSTM load condition led to higher levels of demand on cognitive control. Thus, according to load theory, the higher detection sensitivity in low VSTM load (compared with high load) might simply reflect effects of the higher demand on cognitive control.

In Experiment 7 I thus modified the experimental design used in Experiment 4 by adding a concurrent verbal working memory task. Specifically, participants were presented with two digits before each memory set and were required to rehearse them aloud throughout each trial. Rehearsing aloud causes articulatory suppression which discourages the use of verbal rehearsal mechanisms and verbal/abstract recoding of the visual information. This task is well-known to produce dramatic impairments in verbal encoding and maintenance (e.g.

Vogel, Woodman & Luck, 2001) but produce minimal effects on memory for objects and colours (Luck & Vogel, 1997; Todd & Marois, 2004), and it was thus suited to the purposes of the current experiment for causing articulatory suppression without affecting performance on the VSTM task. If verbal rehearsal of the memory set is contributing to the VSTM load effects on detection sensitivity, then when minimizing verbal strategies with this articulatory suppression task, these effects should be reduced or even eliminated.

An additional purpose of Experiment 7 was to address the effects of longer temporal intervals between the memory set and the detection task. In all previous experiments so far, only a 1 s temporal interval has been used. It was therefore important to address whether the VSTM load effects can extend to longer temporal intervals between the memory set and the detection task. In Experiment 7 I therefore increased the interval between the VSTM set (coloured squares) and the detection task to 4 s (instead of 1 s in Experiment 4). Importantly, the articulatory suppression task was employed together with the longer interval given previous evidence that verbal strategies are more encouraged by such longer memory intervals (Coltheart, 1972).

3.5.2 Method

Participants. Eighteen new healthy volunteers participated in Experiment 7 (5 females, M = 25.22 years, SD = 4.73 years, age rage 20-36,). One participant was replaced because of detection sensitivity rate that was lower than 2 SDs than the group average in the low VSTM load condition. Another participant was excluded because his VSTM task performance in the low VSTM load condition was 2 SD below the group average.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 4 except of the following changes: (a) each trial begun with a set of two black digits (chosen randomly between digits 1–9, each subtending 0.7° by 0.5°) that was presented for 1000 ms in a row centred at fixation. Participants were instructed to rehearse the digits aloud throughout the duration of the trial. The experimenter remained in the testing room together with the participants in order to ensure that participants articulated aloud the two digits. (b) The interval between the memory set and detection stimuli was now increased to 4 s (instead of 1 s in Experiment 4). This also resulted in a longer delay period (6 s) compared to the delay period of all the previous experiments (3 s).

Participants completed 256 trials in 8 blocks of 32 trials each with load blocked in the counterbalanced order of ABBABAAB. Prior to the experiment, each participant completed a short (32 trials) practice as well as the staircase threshold procedure for determining the target contrast as described above.

3.5.3 Results & Discussion

VSTM. Mean percentage accuracy rates and mean memory estimates as a function of VSTM load are presented in Table 3.4.

Table 3.4. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task and Mean Detection Sensitivity as a Function of VSTM Load in Experiment 7.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Detection Sensitivity (*d’)*
Low	89 (11)	0.78 (0.20)	2.06 (1.30)
High	63 (15)	1.59 (1.73)	1.50 (1.07)

SDs are listed in parenthesis.

As shown in the table, mean accuracy rates in the VSTM task were significantly reduced from the low to the high VSTM load condition, t(17) = 8.52, p < .001, d = 1.41. The estimated number of items held in VSTM (Cowan’s K) increased significantly from the low to the high VSTM load condition, $t(17) = 2.13$, $p < 0.05$ $d = 0.64$. These results confirmed that in Experiment 7 VSTM load was manipulated effectively.

Increasing the delay period of the VSTM task and engaging participants in an articulatory suppression task did not impair memory performance in Experiment 7 ($M = 83\%$, $SD = 14\%$) compared to Experiment 4 ($M = 78\%$, $SD = 17\%$) as indicated by a mixed ANOVA between-experiment comparisons with load as the within-subjects factor (low, high) on mean accuracy rates and memory estimates (both $F < 1$). No interaction effects were found on either accuracy rates, $F(1, 31) = 3.42$, $p = .074$, $\eta^2 = .099$, or memory estimates, $F < 1$. Thus, performance on the VSTM task was not impaired by the addition of a longer delay period and the suppression of verbal maintenance strategies.

Detection. As shown in Table 3.4, consistent with the findings of the previous experiments, and despite suppressing verbal articulation and increasing the temporal separation between the memory set and the detection stimuli, detection sensitivity was still significantly reduced from the low to the high VSTM load condition, $t(17) = 2.28$, $p =.036$, $d = 0.46$. As in all the previous experiments, no effects of VSTM load on response bias (beta) were found ($p = .43$).

Detection sensitivity was similarly reduced in this experiment (*d'* reduced by 0.56; Cohen's d effect size was 0.46) as Experiment 4 (*d'* reduced by 0.50; Cohen's d effect size was 0.65). A mixed ANOVA between-experiment comparison on detection sensitivity scores between Experiments 4 and 7, with load as the within-subject factor (low, high) revealed no significant effect of experiment and importantly no interaction, both $F < 1$. Thus, verbal strategies did not contribute to the effects of VSTM load on detection sensitivity. Moreover, these effects did not vary as a function of the temporal separation between the memory set and the detection stimuli.

As participants were now engaged in an additional concurrent articulatory suppression task, Experiment 7 clearly demonstrates that the VSTM load-induced reduction in detection sensitivity accurately reflects greater demands imposed on visual representational resources with no significant contributions from the employment of verbal strategies. In addition, as these effects were found with an extended temporal separation between memory set and detection task, Experiment 7 generalizes these findings to longer intervals (up to 4 s) than those used in previous experiments (1 s). As there were no effects of verbal maintenance strategies or longer interval, in the sake of simplicity of the experimental design, these were not added to the methods of the next experiments.

3.6 Experiment 8

3.6.1 Introduction

In the experiments in Chapter 2, the VSTM displays occupied a small area around fixation (furthest eccentricity was approximately 1.7^{o}) whereas the detection stimulus was presented in the periphery (at 5.4^{o} eccentricity). In Experiment 8 I attempted to establish whether the effects of VSTM load can extend to cases where the VSTM displays and the detection stimulus overlap in the same spatial foveal and parafoveal locations.

In addition, the spatial separation between the VSTM and the detection stimuli raises an important concern regarding shifts of spatial attention between the foveal locations of the memory set and the peripheral locations of the gratings. This concern is particularly important because maintenance of the spatial location of the memory set is only required in the high VSTM load condition. Recall that in low VSTM load, the memory probe always appears in the same location as the memory set item (that only contains one item) and participants need to report whether they match in colour, thus maintenance of its location is not required. But in high VSTM load participants need to maintain the location of each colour square: the memory probe appears in one of the six locations of the memory set items and can have one of the colours of squares in the same or different locations (or a colour that was not in the memory set at all). During the delay period, spatial attention might thus split between the foveal locations of the memory set items and the peripheral locations of the detection stimuli only in the high (but not in the low) VSTM load condition. The reduced detection sensitivity scores observed in the high (vs. the low) VSTM load condition might thus be due to effects of spatial attention.

In Experiment 8 I thus eliminated the spatial separation between the detection stimuli and the VSTM task displays by presenting the detection stimuli on the very same central locations as those of the memory set items. The four peripheral gratings of the detection task employed in Experiment 4 were now replaced with nine gratings (same size as the memory set items) presented on the very same spatial locations as the memory set items. Participants were asked to detect the presence of a contrast increment (present in 50% of the trials) in one of the nine gratings. The spatial separation between each of the nine possible locations was also increased (compared to Experiment 4) in order to aid discrimination of the detection task gratings (see Figure 3.3). If different demands on spatial attention between low and high VSTM load are indeed causing the VSTM load effects on detection sensitivity, then when the spatial separation between the memory set and the detection stimuli is removed these effects should be reduced or even eliminated.

3.6.2 Method

Participants. Thirteen new healthy volunteers participated in Experiment 6. The age range was 19 to 35 years (M = 24.31 years, SD = 4.54 years) and 11 were females.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 4 except of the following changes: (a) The four peripheral gratings (one in each quadrant of the screen) of Experiment 4 were now replaced by nine achromatic vertical square-wave gratings (10 cpd; non-target contrast: 10%) of the same size as the VSTM set stimuli (0.6°), and presented after a 1 s blank interval in each of the nine possible locations of the memory set. Participants were asked to detect the presence of a contrast increment (target) that was present in one of the nine gratings on 50% of the trials. (b) The colored squares in the memory set and the detection gratings were presented in a 3 × 3 matrix that now subtended 5.2° (instead of 2.4° in Experiment 5) with nearest contours 1.7°.

Participants completed a total of 256 trials in 8 blocks of 32 trials each, with VSTM load counterbalanced in the order of ABBABAAB. Prior to the experiment, each participant completed a short (32 trials) practice as well as the staircase threshold procedure for determining the target contrast as described in Experiment 4.

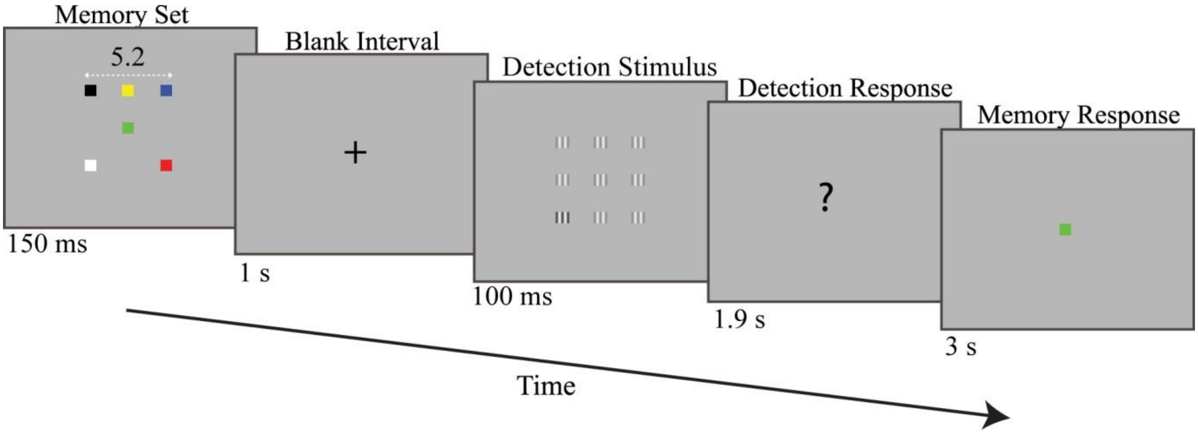

Figure 3.3. An example (high VSTM load) trial sequence and timing in Experiment 8. A trial from the high VSTM load condition is shown here. The detection task in Experiment 8 consisted of 9 gratings presented on the same spatial locations as the memory set items. The contrast-increment target was presented on 50% in one of the nine gratings (here present at bottom left corner of the "detection stimulus" display).

3.6.3 Results & Discussion

VSTM. Table 3.5 shows the mean percentage accuracy rates and mean memory estimates (Cowan's K).

Table 3.5. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task and Mean Detection Sensitivity as a Function of VSTM Load in Experiment 8.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Detection Sensitivity *(d')*
Low	93 (5)	0.87 (0.11)	1.57 (0.79)
High	73 (13)	2.72 (1.56)	1.17 (0.82)

SDs are listed in parenthesis.

As can be seen in Table 3.5, mean accuracy rates in the VSTM task were significantly reduced from the low to the high VSTM load condition, t(12) = 6.27, p < .001, d = 1.44. The memory estimates (K) increased significantly from the low to the high VSTM load condition, t(12) = 4.39, p < .001, d = 1.29. These results confirmed the effectiveness of the VSTM load manipulation in Experiment 8.

A mixed ANOVA comparison with experiment (Experiment 4, Experiment 8) as the between subject factor and the level of load (low, high) as the within subject factor, indicated that increasing the spatial separation between the memory set items and eliminating the need for spatial shifts of attention between fovea and periphery in this experiment resulted in better VSTM task performance (M = 83%, SD = 14%, for accuracy; K = 1.80, SD = 1.44, for memory estimates) compared to Experiment 4 (M = 78%, SD = 17%, for accuracy; K = 1.12, SD = 0.59, for memory estimates), in both accuracy rates, *F*(1, 26) = 5.59, p = .026, $\eta^2 = .18$, and memory estimates (K), *F*(1, 26) = 8.47, p = .007, $\eta^2 = .25$. A significant interaction between experiment and the level of VSTM load was also found both for accuracy rates, *F*(1, 26) = 9.99, p = .004, $\eta^2 = .28$, and for memory estimates, *F*(1, 26) = 8.47, p = .007, $\eta^2 = .25$.

This interaction reflects the fact that the effect of load on VSTM task performance was smaller in this experiment compared to Experiment 4. In this experiment, accuracy rates reduced by 20% (from 93% in low load to 73% in high load), t(12) = 6.27, p = .001, d = 1.44, whereas in Experiment 4 a greater reduction of 33% in accuracy rates (from 94% in low load to 61% in high load) was observed, t(14) = 16.06, p < .001, d = 1.87. The fact that under high load participants performed better in this experiment resulted in a robust increase by 1.87 in memory estimates (from 0.87 in low load to 2.72 in high load), t(12) = 4.39, p = .001, d = 1.29, compared to Experiment 4 where memory estimates increased only by 0.48 (from 0.88 in low load to 1.36 in high load), t(14) = 2.41, p = .03, d = 0.59.

Detection. Importantly, as Table 2 shows, although the detection stimuli were now presented on the same foveal and parafoveal locations as the memory set items thus eliminating the need for peripheral shifts of spatial attention during the delay period, detection sensitivity was still significantly reduced from the low to the high VSTM load condition, t(12) = 2.64, p =.021, d = .49. As in all the previous experiments no effects of VSTM load on response bias (beta) were found (*t* < 1).

A mixed ANOVA between experiment comparison on detection sensitivity rates with experiment (Experiment 4, Experiment 8) as the between-subject factor and level of load (low, high) as the within-subject factor revealed no effect of experiment, *F*(1, 20) = 1.92, p = .18, η^2 = .09, and importantly no interaction between experiment and load, *F* < 1. Indeed, the reduction in detection sensitivity in this experiment (*d'* reduced by 0.40; Cohen's d effect size was 0.49) was equivalent to that of Experiment 4 (*d'* reduced by 0.50; Cohen's d effect size was 0.65). Hence, the effects of VSTM load on detection sensitivity did not vary as a function of the spatial separation between the VSTM and detection task displays or as a function of spatial attention shifts.

Experiment 8 therefore extends the effects of VSTM load on detection sensitivity found in the previous experiments to cases where the location of detection stimuli overlap with the foveal and parafoveal locations of the VSTM task stimuli. Moreover, these findings were demonstrated using an experimental design that eliminated differences in shifts of spatial attention between low and high VSTM load conditions. This finding strengthens the claim that the load induced reduction in detection sensitivity is specifically due to increased demands on representational capacity with higher VSTM load, rather than any differences on the demands for spatial attention between the various load conditions.

3.7 Experiment 9

3.7.1 Introduction

The suggestion of shared resources between VSTM and perception has been a central tenet of this thesis and is indeed critical for the explanation of the findings of reduced detection sensitivity with higher VSTM load. An important assumption of the shared resources hypothesis that has not been as yet directly tested is that sensitivity for detection of a visual target-stimulus depends on the amount of information held in visual short term memory. In other words, because both mechanisms (visual short term memory and visual perception) rely on common sensory resources with limited capacity, it is assumed that visual perception can only utilize resources that are not currently occupied in the short-term maintenance of visual information. Preliminary support for the prediction of a trade-off between visual perception and VSTM was provided in Experiment 1 by demonstrating that the magnitude of the reduction in detection sensitivity from VSTM set size 1 to set size 6 depends on the magnitude of the increase in memory estimates (using Cowan's K) from set size 1 to set size 6. In Experiment 9 I set out to establish this trade-off between memory estimates and detection sensitivity across all set sizes from 1 through 6 items. I therefore employed the combined delayed match-to-sample and detection task from Experiment 4 while VSTM load was now parametrically increased using set sizes of 1 through 6 items. I assessed the psychometric function of detection sensitivity and of memory estimates as a function of VSTM set size (see Figure 3.4). I predicted that the function of detection sensitivity would be negatively correlated with the function of the estimated amount of information maintained in visual short term memory (Cowan's K memory estimates).

3.7.2 Method

Participants. Nine new healthy paid volunteers (four females, M = 25.67 years, SD = 5.39 years, age range 19-34) participated in Experiment 9.

Stimuli and Procedure. The task stimuli and trial procedure were identical to Experiment 4 except that the VSTM set size was now randomly varied between set sizes of one, two, three, four, five or six items. Following one practice block of 32 trials, each participant completed 4 experimental blocks of 192 trials each, for a total of 768 trials.

3.7.3 Results & Discussion

Mean VSTM task accuracy was reduced as VSTM load was increased (set size: one, M = 83%, SD =16%; two, M = 73%, SD = 14%; three, M = 68%, SD = 11%; four, M = 65%, SD = 10%; five, M = 60%, SD = 7%; six, M = 55%, SD = 7%), $F(5,40) = 23.41$, $p < .001$, $\eta^2 = 0.75$. The memory estimates (Cowan's K), shown in Figure 3.4, exhibited a significant quadratic trend, $F(1,8)$, = 31.71, $p < .001$, $\eta^2 = 0.80$ (linear trend $F < 1$). These results confirm that the manipulation of VSTM load was effective: increased memory set size filled up more VSTM capacity up to set size four which is consistent with previous reports indicating that capacity is typically approached with set sizes of 4 items (Todd & Marois, 2004). Importantly, the behavioral function of the group-average memory estimates (Cowan's

K) under each set size exhibited a strong negative correlation with the corresponding detection sensitivity function (*d'*; Figure 3.4), r = -.87, n = 6, p = .024 (see Figure 3.5).

Although the trade-off between VSTM and perception was clearly demonstrated with the significant negative correlation between memory estimates and detection sensitivity scores, I note that performance under set size of 6 items in this experimental design (accuracy rate M = 55%, memory estimate K = .56) was lower than what has been found in Experiment 4 (accuracy rate M = 61%, memory estimate K = 1.36) using the same set size of six items but a somewhat different experimental design, t(22) = 2.39, p = 0.026, d = 0.92. This result likely reflects differences between the design of Experiments 4 and 9: whereas in Experiment 4 (as in all previous VSTM load manipulations in this thesis) only two levels of VSTM load were used (low load set size 1 vs. high load set size 6) that were blocked, Experiment 9 included six levels of VSTM load that were randomly intermixed within each block. It is therefore possible that the intermixed design with various levels of VSTM load in Experiment 9 led participants to adopt a strategy that was suboptimal for the highest set size in the experiment (i.e. set size 6).

The results of Experiment 9 indicate a trade-off between detection sensitivity and the extent to which VSTM was filled under load, suggesting shared resources between VSTM and visual detection providing further support for the hypothesis I advance in this thesis.

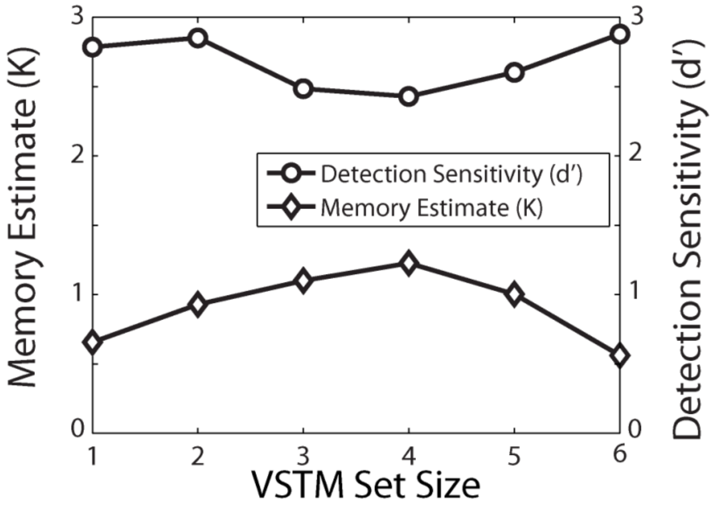

Figure 3.4. Mean memory estimates (Cowan's K) and mean detection sensitivity scores (*d'*) as a function of memory set size in Experiment 9.

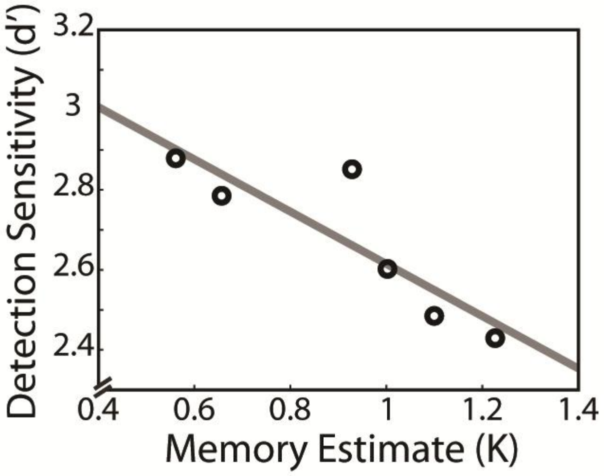

Figure 3.5. Scatter plot showing the relationship between the mean memory estimates (Cowan's K; x axis) and mean detection sensitivity (*d'*; y axis) under the various levels of VSTM load in Experiment 9. The line represents the least-square linear fit.

3.8 Chapter Conclusions

The findings of this chapter replicate the effects of VSTM load on detection sensitivity after ruling out various alternative accounts for the effects of VSTM load. Most importantly, these effects were replicated in a detection task of equivalent difficulty across participants while the letter-search component of the task was eliminated. This finding indicates that these effects are not due to an indirect effect of load on the employment of attention during the search task. Neither are these effects due to an interaction of load with the search response (that preceded the detection response in Chapter 1) on the encoding or remembering the detection target stimulus. This finding also rules out an alternative account for the results in terms of differences in the priority of the search task over the detection task between low load and high load.

The effects of VSTM load on detection sensitivity were confirmed to be equivalent to the effects of perceptual load (Experiment 5) without any significant contributions from verbal strategies since these effects persisted during conditions of articulatory suppression (Experiment 7). Experiment 8 also ruled out an alternative account in terms of differences in shifts of spatial attention between the low and the high VSTM load conditions as the effect of VSTM load was demonstrated when the detection stimuli shared the same spatial locations as those of the VSTM task. Furthermore, these VSTM load effects were extended to longer temporal intervals up to at least 4 s (Experiment 7) and to conditions where the spatial locations of the VSTM displays and the detection stimuli overlap on the same foveal and parafoveal spatial locations (Experiment 8).

Importantly, despite the consistent reduction of detection sensitivity with higher VSTM load (Experiment 4) and perceptual load (Experiment 5), an equally difficult WM cognitive control load manipulation did not affect detection sensitivity (Experiment 6). Because detection sensitivity was enhanced when the visual detection task was performed concurrently with the visual search task in Chapter 2 (Experiment 3) but it was unaffected when the search task component was eliminated in this chapter (Experiment 6), these findings clarify that WM cognitive control is required in the maintenance of processing priorities only during the performance of a concurrent task of higher task priorities. Furthermore, this difference between the effects of load on maintenance processes of WM and load on WM cognitive control processes rules out an alternative account for the effects of VSTM load in terms of general task difficulty or in terms of load on general cognitive capacity resources thus confirming the specificity of the effect. Indeed, the finding of a trade-off between visual perception and the amount of information held in VSTM that allows prediction of detection sensitivity from the extent to which VSTM capacity is loaded (Experiment 9) confirmed that these effects accurately reflect limitations in perceptual capacity occupied during short-term visual maintenance. The present findings thus demonstrate that the effects of reduced detection sensitivity reflect effects of load on perceptual representational resources.

Chapter 4:

The Effects of Visual Short Term Memory Load on the Retinotopic Primary Cortex Response to Contrast

4.1 Chapter Introduction

As discussed in Chapter 1, a growing body of work indicates that VSTM maintenance involves the same sensory brain areas as those involved in the perceptual encoding of the maintained information (e.g. Pasternak & Greenlee, 2005; Postle, 2006 for reviews), including even primary visual cortex (e.g., Harrison & Tong; 2009; Munneke, Heslenfeld & Theeuwes, 2010; Serences, Ester, Vogel & Awh, 2009), in support of a sensory recruitment hypothesis of VSTM (e.g. Ester, Serences & Awh, 2009; Postle, 2006; Serences et al. 2009).

As also reviewed in Chapter 1, the critical role of the level and type of information load in determining visual processing has been extensively studied within the framework of Load Theory. Load Theory suggests that competition for capacity-limited sensory neural resources results in reduced sensory cortex responses to stimuli that are not directly relevant to tasks involving high perceptual load (for review see Lavie, 2005; 2010). These effects are found throughout visual cortex, as early as primary visual cortex (e.g. O’Connor, Fukui, Pinsk & Kastner, 2002; Schwartz et al., 2005) and are associated with failures to detect the mere presence of competing stimuli during tasks of high perceptual load: a phenomenon of “load induced blindness” (e.g. Macdonald & Lavie, 2008).

Consideration of the sensory recruitment hypothesis within the framework of Load Theory leads to a novel hypothesis concerning the effects of VSTM load on the sensory visual processing of incoming stimuli. I hypothesized that high (compared to low) VSTM load would impose a larger demand on the sensory visual cortices involved in memory maintenance and this should reduce their capacity for sensory processing involved in visual detection. This hypothesis leads to the prediction that increased VSTM load will result in reduced sensory visual cortical responses to visual stimuli presented during the maintenance delay, resulting in failure to detect them. To ask whether the effect of VSTM load can be found as early as the retinotopic V1 responses related to the fundamental process of contrast detection I used fMRI and assessed the retinotopic responses to contrast increment targets presented in the periphery during the maintenance interval of the VSTM task under varied levels of VSTM load.

4.2 Experiment 10

The experimental paradigm employed in Experiment 10 was identical to that used in Experiment 4 (Chapter 3).

4.2.1 Method

Participants. Eight healthy volunteers participated in the imaging experiment. The age range was 20 to 30 years (M = 23.88 years, SD = 3.44 years) and 4 were females. The experiment was approved by the UCL ethics committee.

Stimuli & Procedure. The apparatus, stimuli, and procedure were identical to Experiment 4 (see Figure 3.1, Chapter 3) except that stimuli were here projected onto a screen mounted at the back of the scanner bore through an LCD projector (display resolution: 800x600). Participants viewed the stimuli through a mirror mounted on the head coil.

Each run consisted of 8-trial blocks within each 64-trial run in the order of an ABBABAAB design (counterbalanced across participants). Trials were separated by a variable inter-trial-interval (ITI) of 10.8 – 11.3s. Each participant completed four or five runs (325 volumes per run). Prior to the experiment, each participant completed a short (32 trials) practice of the behavioural task outside the scanner. While in the scanner, participants performed the staircase threshold procedure for determining the target contrast as described in Experiment 4.

In a second session, two runs (165 volumes) of retinotopic mapping and two runs (165 volumes) of functional localizer were acquired for each participant, used to identify the regions of retinotopic cortex most responsive to the four gratings in early visual cortex (V1, V2, V3). The retinotopic mapping runs consisted of checkerboard wedges presented alternately at the horizontal and vertical meridians. Each run consisted of 5 repetitions of each meridian (duration = 10 volumes) separated by 6 volumes of rest. During the functional localizer scans, participants viewed flashing black and white disks (of the same diameter as the pedestal gratings) presented at the same area as the pedestal gratings, while maintaining fixation.

fMRI Data Acquisition and Analysis. Imaging data were collected at the Wellcome Trust Centre for Neuroimaging (London, UK) using a 3T Allegra Siemens MRI scanner. I used gradient-echo echoplanar T2*-weighted imaging (TE 65ms; TR 2210 ms; 34 axial slices; voxel size 3mm isotropic) to acquire Blood Oxygenation Level Dependent (BOLD) contrast functional images covering the cortex. A T1-weighted MPRAGE structural image volume was also acquired for each participant.

Data were analyzed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). The first five volumes of each run were discarded to allow for magnetic saturation effects. The remaining images were slice time corrected, realigned and unwarped, coregistered (without reslice) to the individual participant's structural scan, spatially smoothed with a narrow Gaussian kernel of 8mm full-width half-maximum, and spatially normalized (only for the whole-brain analysis). A high-pass filter (cutoff 128 s) was applied to the data for removing low-frequency signal drifts.

Each participant's early visual cortex (V1, V2, and V3) was defined using data from the retinotopic mapping scans (Figure 4.1A). Data from the localizer scans were used to define regions-of-interest (ROIs) of the retinotopic locations within each participant's V1, V2 and V3 that responded most strongly to the locations of the gratings (Figure 4.1B). Responses to each of the four grating-locations were contrasted with responses to the other grating-location in the same hemisphere. Statistical parametric maps of those contrasts (t-contrasts, $p<.001$, uncorrected) were overlaid on flattened representations of each subject's anatomy and voxels most responsive to each of the grating locations were selected for each ROI using the Freesurfer package (http://surfer.nmr.mgh.harvard.edu/). These surface-based ROIs were then converted to volumes within SPM8, allowing the analysis of the response to the different detection task events (present/absent) under the two VSTM load conditions (low/high). The separate events representing target present (separately for each of the four visual quadrants) and target absent, under low and high VSTM load, were modeled using different regressors in a within-subject analysis with a voxel-wise general linear model (GLM). The design matrix also included separate regressors for the events of memory set, memory probe (separately for low and high VSTM load), and memory and detection response as well as motion parameters. Each of these events was modeled using a finite impulse response approach and was convolved with a canonical hemodynamic response function (HRF).

For the whole brain analysis, the GLM employed a separate regressor for each of the two load conditions (low/high VSTM load) with duration of 6.15 s capturing the whole trial period. The motion parameters were also included in the model to capture any motion-related artifacts. Statistical parametric maps were obtained using a t-contrast testing the main effect of VSTM load for each participant. In a second stage a random-effects analysis was performed on these individual parameter estimates using one-sample t-test on the contrast images obtained from each subject for the condition of interest. Random-effect SPMs for each comparison of interest were obtained using a cluster-defining voxelwise threshold of $p < .001$ (uncorrected), and whole brain FDR-correction using cluster extent, $p < .05$ (FWHM = 11.7 mm × 11.9 mm × 12.4 mm, resels = 794.13).

4.2.2 Results

VSTM. Table 4.1 shows the mean percentage accuracy rates and mean memory estimates (Cowan's K).

Table 4.1. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task and Mean Detection Sensitivity as a Function of VSTM Load in Experiment 10.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)	Detection Sensitivity (*d'*)
Low	97 (2)	0.95 (0.04)	3.11 (1.36)
High	73 (8)	2.71 (1.00)	2.63 (1.34)

SDs are listed in parenthesis.

As shown in the table, mean VSTM accuracy rates were significantly reduced from the low load to the high VSTM load condition, t(7) = 7.41, p <.001, d = 1.76. Memory estimates (Cowan's K) increased significantly from the low to the high VSTM load condition, t(7) = 8.52, p <.001, d = 1.78, confirming that the behavioral manipulation was effective and high load condition occupied more VSTM capacity than the low load condition.

A mixed ANOVA between experiment comparison with experiment (Experiment 4, Experiment 10) as the between subject factor and the level of VSTM load (low, high) as the within subject factor indicated better VSTM task performance in this experiment (accuracy, M = 85%, SD = 14%; Cowan's K = 2.23, SD = 1.45) compared to Experiment 4 (accuracy M = 78%, SD = 17%; Cowan's K = 1.12, SD = 0.59), $F(1, 21) = 20.41$, $p < .001$, $\eta^2 = .49$, for accuracy, and $F(1, 21) = 41.91$, $p < .001$, $\eta^2 = .67$, for memory estimates. A significant interaction between load and experiment was also found, $F(1, 21) = 4.39$, $p < .05$, $\eta^2 = .17$, for accuracy, and $F(1, 21) = 35.54$, $p < .001$, $\eta^2 = .63$, for memory estimates.

This interaction reflects the fact that the effect of load on VSTM task performance was smaller in this experiment compared to Experiment 4. In this experiment, accuracy rates were reduced by 24% (from 97% in low load to 73% in high load), whereas in Experiment 4 a greater reduction of 33% in accuracy rates (from 94% in low load to 61% in high load) was observed, t(14) = 16.06, p < .001, d = 1.87. Because participants performed better under high VSTM load in this experiment, this resulted in a robust increase by 1.76 in memory estimates (from 0.95 in low load to 2.71 in high load), compared to Experiment 4 where memory estimates increased only by 0.48 (from 0.88 in low load to 1.36 in high load), t(14) = 2.41, p = .03, d = 0.59.

These differences between Experiments 4 and 9 possibly reflect general practice effects of the participants in Experiment 9. These participants had previously taken part in numerous neuroimaging and other psychophysical studies and as a result were very well practiced in similar psychophysical tasks as well as very experienced in the conditions under which such experiments are conducted.

Detection. Importantly, consistent with the findings of previous experiments in Chapters 2 and 3, stimulus detection sensitivity (*d'*) was again significantly reduced from the low to the high VSTM load condition, t(7) = 4.13, p =.004, d = 0.37 (Figure 4.1C) . As was also the case in the experiments reported in Chapters 2 and 3 no effects of VSTM load on response bias (beta) were found (p = .23).

A further mixed ANOVA between experiment comparison with experiment as the between subject factor (Experiment 4, Experiment 10) and with level of load (low, high) as the within subject factor on detection sensitivity scores indicated significantly better sensitivity in this experiment (*d'* = 2.87, SD = 1.33) compared to Experiment 4 (*d'* = 1.82, SD = 0.78) , *F*(1, 21) = 6.07, p = .02, η^2 = .22. No interaction between experiment and load was observed, *F* < 1, thus the effect of load on detection sensitivity in this experiment was similar to that of Experiment 4.

Imaging results. A whole brain contrast of activity in the high versus low load conditions revealed that similar parietal areas (e.g. intra-parietal sulcus (IPS), MNI coordinates (x,y,z): right/left, +24/-21, -61/-67, +52/+58 ; see Table 4.2) as those previously implicated in VSTM maintenance (e.g. Mitchell & Cusack, 2007; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Todd & Marois, 2004) also showed greater activity in the high compared to the low VSTM load condition in the task used here.

Table 4.2. List of active regions in whole-brain contrast high > low VSTM load

Brain Region	Z score	MNI coordinates (x,y,z in mm)
R Middle Cingulate Cortex	4.85	3,20,40
L Middle Frontal Gyrus	4.82	-24,14,58
R Precuneus	4.76	21,-61,31
R Superior Frontal Gyrus	4.70	24,8,58
R Middle Occipital Gyrus	4.58	33,-73,28
R Intraparietal Sulcus	4.44	24,-61,52
L Precuneus	4.44	-6,-52,67
R Middle Frontal Gyrus	4.33	33,32,34
R Precuneus	4.18	3,-46,67
L Intraparietal Sulcus	4.17	-21,-67,58
R Superior Frontal Gyrus	4.15	21,14,64
R Postcentral Gyrus	4.11	45,-34,58
R Inferior Parietal Lobule	4.03	36,-46,46

R Inferior Parietal Lobule	3.84	42,-40,46

L, left; R, right.

More importantly, retinotopic analysis confirmed that as I predicted, retinotopic V1 activity related to the presence (versus absence) of the contrast increment (i.e. the detection target) in one of the retinotopic stimulus locations during the memory delay was significantly reduced under high (compared to low) VSTM load, $t(7) = 2.49$, $p < .05$ (see Figure 4.2C). The same comparisons for V2 and V3 showed similar trends but these were not statistically significant (V2, $t(7) = 1.61$, $p = .15$; V3, $t(7) = 1.69$, $p = .14$). VSTM load had no effect on peripheral V1 activity in the detection target locations during the foveal presentation of the VSTM set, $t(7) = .37$, $p = .72$. Thus the effect of VSTM load on V1 does not reflect effects of general task difficulty but rather a specific suppression of the retinotopic V1 response to the detection target during memory maintenance.

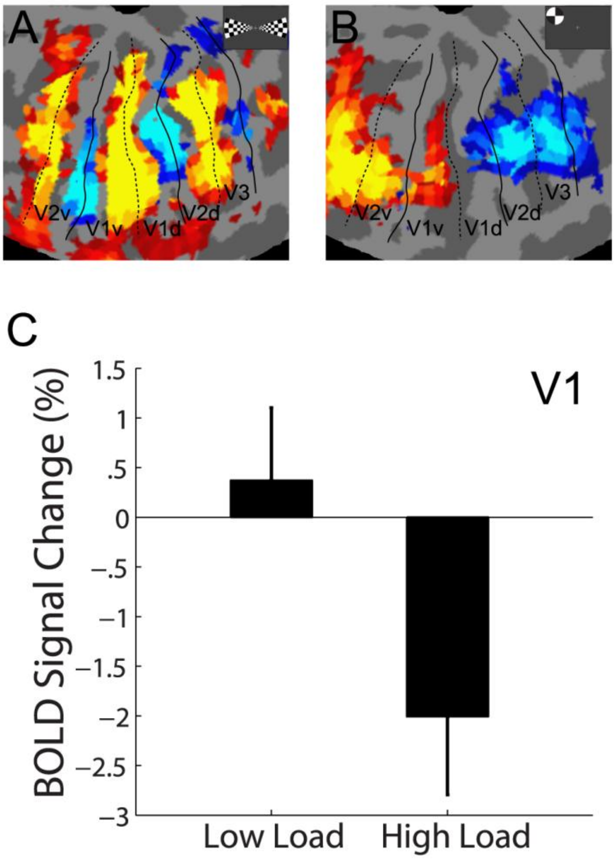

Figure 4.1. Retinotopic mapping and imaging data for V1. Retinotopic meridian mapping stimulus example (top right corner) and data (A) and functional localizer stimulus example (top right corner) and data (B) from a representative subject overlaid on an inflated surface of the right occipital pole. (C) Mean differential retinotopic V1 BOLD responses to contrast target (present > absent) as a function of VSTM load. Error bars represent +1 SEM.

4.3 Chapter Conclusions

The results of Experiment 10 demonstrate that V1 responses to incoming visual information and associated visual detection performance critically depend on the extent to which VSTM is loaded. In support of my prediction, high VSTM load led to reduced retinotopic V1 responses to a contrast increment target presented during the maintenance delay and this effect was associated with reduced detection sensitivity (Experiment 4). These results provide firm support for the hypothesis that sensory recruitment during VSTM maintenance would result in an effect of VSTM load on elemental visual processing in primary visual cortex akin to the effect of perceptual load (e.g. O'Connor, Fukui, Pinsk & Kastner, 2002; Schwartz et al., 2005; Lavie, 2005, for review). Like perceptual load, VSTM load has led to reduced sensory cortical responses to incoming stimuli. The results of Experiment 10 suggest that competitive interactions in sensory visual processing under load include not just stimulus competition (c.f. Torralbo & Beck, 2008) but also competition with visual representations held in memory.

Chapter 5:

The Effects of Visual Short Term Memory Load and Perceptual Load on the Contrast Response Function

5.1 Chapter Introduction

Chapters 2 and 3 demonstrated an effect of VSTM load on detection sensitivity akin to that of perceptual load. In addition, the neuroimaging experiment in Chapter 4 demonstrated that recruitment of sensory brain areas during VSTM maintenance resulted in an effect of VSTM load on sensory visual processing akin to that of perceptual load (Schwartz et al., 2005). Retinotopic primary cortex responses to contrast and the associated detection sensitivity measures were reduced when participants maintained in visual short-term memory a visual-spatial pattern of high (vs. low) load. These findings indicate that loading visual sensory resources, in common to perception and VSTM, reduces perception of contrast.

However, the means by which load on perceptual representation resources affects the perception of contrast has not as yet been addressed directly. Here I considered two theories that have dominated the literature investigating the mechanisms by which attention affects neural responses. The first is the appealingly simple proposal that attention modulates neural responses multiplicatively by a fixed gain factor (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999). According to this “response gain” model, attention and the contrast of a visual stimulus exert independent effects on neural responses. When attention is directed towards a visual stimulus of a given contrast, the neural response is a fixed multiplicative increase of the response to the same stimulus in the absence of attention. Because neural response to a visual stimulus increases with higher contrast, attention exerts an increasing effect with higher contrast: that is, the higher the contrast of a visual stimulus, the greater the effect of attention on neural responses. Thus, attention is akin to turning up (when directing attention towards a stimulus) or turning down (when directing attention away from a stimulus) the gain of the neural response.

An interesting alternative is that of a more specific interaction between attention and the contrast of a visual stimulus. According to this account, the “contrast gain” model, the neural response to an attended stimulus of a given contrast is the same as the response to an unattended stimulus of higher contrast (Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak & Desimone, 2000). Thus, attention is effectively increasing the contrast of a visual stimulus when attention is directed towards it or decreasing it when attention is directed away from the visual stimulus.

These two theories have been contrasted previously in psychophysical and electrophysiology studies examining how attention affects the function that relates the neural response to a visual stimulus with the contrast of the same stimulus, i.e. the contrast response function. As can be seen in Figure 5.1, neurons in visual cortex exhibit a systematic non-linear increase in firing rate with increasing stimulus contrast (Albrecht & Hamilton, 1982; Sclar, Maunsell & Lennie, 1990). Contrast response functions exhibit a sigmoid shape: an expansive non-linear shape at low contrasts, a relative linearity at an intermediate range of contrasts, and a compressive (saturating) non-linear shape at higher contrasts. Effects of response gain are manifested via scaling of the entire contrast response function by a fixed multiplicative factor (Figure 5.1a). According to the response gain account, the combination of neural responses to contrast and the additive effects of attention result in weak responses increasing slightly and strong responses increasing more. As seen in Figure 5.1a, the characteristic effect of response gain on the contrast response function is a change in the slope (e.g. it becomes steeper with attention) and in the upper asymptote (e.g. it increases with attention) of the function. Notice that the dynamic range of both contrast response functions of Figure 5.1a (attended and unattended) is ideally suited to detect differences in contrast between 2% and about 25%. Critically, response gain does not shift the sensitivity (i.e. the dynamic range) of the function but it rather modulates the gain of the response. For example, although with contrasts above 25% both functions in Figure 5.1a respond at their maximal level, attention changes the peak response of the unattended (red) function from about 80% to about 90% (blue function).

On the other hand, contrast gain increases the sensitivity of the function by shifting the dynamic range horizontally without affecting the shape (i.e. no change in the slope or the asymptote) of the function (Figure 5.1b). For example, in Figure 5.1b the dynamic range of the unattended (red) function is sensitive to changes in contrast between 5% and about 50%. However, with attention the dynamic range of the function is shifted horizontally to the left (blue function) now sensitive to differences in a lower and much narrower range of contrasts between 2% and about 25%. Notice that unlike the effects of response gain, the peak response for both functions in Figure 5.1b is the same at about 90%. Contrast gain effects thus render the neural response equivalent to an actual change in the physical contrast of the visual stimulus.

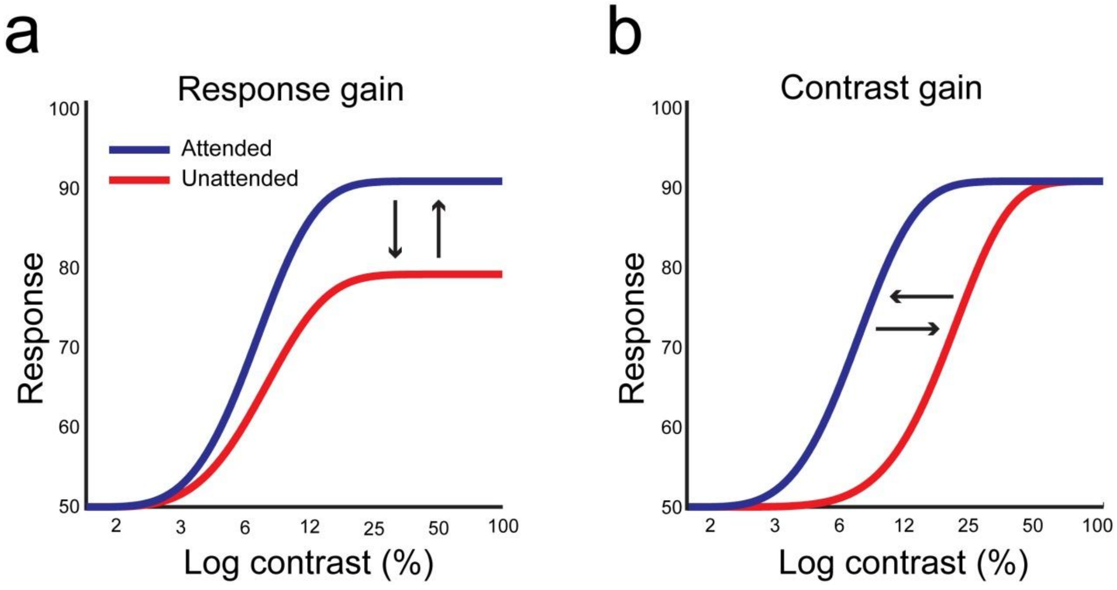

Figure 5.1. Possible effects of attention on the contrast response function. (a) The response gain model predicts that attention will result in an increase in firing rate for a

neuron, which is characterized by a change in the slope (steeper) and asymptote (higher) of the contrast response function. (b) The contrast gain account predicts that attention will increase the sensitivity of a neuron resulting in an increase of the effective contrast of a visual stimulus. This effect is characterized by a leftward shift of the contrast response function in the attended (red curve) versus the unattended condition (blue curve) without any change in the shape (slope) or the asymptote of the curve.

These two accounts can thus be compared on the basis of their distinct predictions for the effects of attention (or any other factor) on the contrast response function. Specifically, in the case of effects of attention, whereas response gain predicts that (a) attention will amplify neural responses in a multiplicative manner that will lead to a steeper slope of the contrast response function, and (b) the peak response to a stimulus (i.e. the upper asymptote of the function) can be increased with attention, contrast gain does not allow for either of those effects. Thus any such changes would constitute evidence for response gain. On the other hand, a change in the sensitivity (i.e. horizontal shift of the dynamic range) of the contrast response function in the absence of an effect on the slope and the upper asymptote of the function would constitute evidence for effects of contrast gain.

Most psychophysical studies that tested which of those two theories best describes the effects of attention on neural responses have used the spatial cueing paradigm with contradictory results. Some results are consistent with contrast gain effects of attention (Cameron, Tai & Carrasco, 2002; Carrasco, Ling, & Read, 2004; Barbot, Landy & Carrasco, 2011), while others are more in keeping with effects that are intermediate between response gain and contrast gain changes (Ling & Carrasco, 2006; Pestilli, Ling, & Carrasco, 2009; Pestilli, Vierra & Carrasco, 2007). Apart from two factors which will be dealt with in Experiment 13 (the stimulus size and the attention field size) these differences are due to factors that appear to be irrelevant for the concerns of this thesis. For example, one such factor that has been suggested to be important for explaining these differences appears to be the amount of time observers are given to deploy their spatial attention (Cheal & Lyon, 1991). In a recent psychophysical study, Ling and Carrasco (2006) investigated the effects of attention on the contrast response function using spatial cues of various durations and various inter-stimulus-intervals (ISI). In this study, participants performed a 2AFC orientation discrimination task on a slightly tilted peripheral Gabor patch of various contrast levels. In each trial, the Gabor was preceded by one of two types of spatial cues that differed in duration and ISI between the cue and the Gabor patch. The first spatial cue was presented for 150 ms with an ISI of 150 ms. The second type of spatial cue was presented for a shorter period of 40 ms and with a shorter ISI of 60 ms. The contrast response function of the orientation discrimination task under each of the two spatial cue conditions was compared to a neutral condition that consisted of just a fixation spot in the absence of a spatial cue. As predicted by the contrast gain account, the spatial cue with the long duration (150 ms) and long ISI (150 ms) led to a consistent horizontal (leftward) shift of the contrast response function (compared to the neutral condition) without changing the asymptote of the function. The spatial cue with the short duration (40 ms) and short ISI (60 ms) also led to a consistent leftward shift of the function, but importantly, it also led to a consistent increase of the asymptote of the function as predicted by response gain. Based on these findings, the authors suggested that these differences highlight two distinct components of spatial attention: ‘sustained’ attention, that is employed when a spatial cue of longer durations and ISI instructs observers to wilfully deploy their attention to the upcoming target location, and ‘transient’ attention which is involved when a spatial cue of shorter duration and ISI reflexively captures attention to an upcoming target location.

More relevant to the purposes of this thesis than the spatial cueing studies are the studies that have used the single- vs. dual-task paradigm since these studies varied the level of processing load, i.e., the dual-task condition placed a higher level of processing load than the single-task condition. In one such study, evidence for pure response gain effects under the dual (vs. the single) task condition has been reported (Morrone, Denti & Spinelli, 2002). In the single task condition of this study, participants performed a contrast discrimination task on two peripheral gratings presented left and right from fixation. In the dual task condition, the contrast discrimination task on the peripheral gratings was performed concurrently with an additional contrast discrimination task presented at fixation. The stimuli in both tasks were either all the same colour (equichromatic yellow) and the contrast oddball item differed in luminance or the stimuli were all the same luminance (equiluminant red-green) and the contrast oddball item differed in colour. Consistent with response gain effects, the dual task condition changed (reduced) the asymptote of the contrast response function, compared with the single task condition, only when the central task stimuli and the peripheral gratings were both varied in luminance or both varied in colour. That is, when attention was split between two tasks of the same modality, response gain was reduced, without any effects on the threshold of the contrast response function.

However, using a similar dual task paradigm, a subsequent study challenged these findings suggesting that in such dual task conditions attention operates via a mixed model that involves effects of both response gain and contrast gain (Huang & Dobkins, 2005). In this study, participants performed a contrast discrimination task on two peripheral gratings in the single task condition (similar to Morrone et al., 2002), whereas in the dual task condition the peripheral contrast discrimination task was performed together with a central RSVP task that required colour discrimination. Similar to the findings of Morrone et al. (2002), the dual task condition, compared with single task, led to a change (reduction) in the asymptote of the function indicating effects of response gain. However, an additional horizontal (rightward) shift of the dual (vs. single) task function was also found indicating effects of contrast gain in addition to the response gain effects. Huang and Dobkins (2005) attributed the differences of their findings to those of Morrone et al. (2002) to experimental parameters suggesting that the contrasts of their stimuli captured the entire contrast response function better than those of Morrone et al. (2002). Whereas the stimuli used by Huang and Dobkins (2005) employed contrasts up to 64%, Morrone et al. (2002) used stimuli of contrasts only up to 30%, and thus they might have missed any effects at higher contrasts.

In addition to testing different ranges of contrasts, these two studies also manipulated attention in the dual-task condition using two different types of central tasks. Whereas Morrone et al. used a luminance or colour pop-out task (i.e., is an oddball present or absent?), Huang and Dobkins (2005) used a colour discrimination RSVP task that required participants to report whether the letter ‘T’ presented in a stream of other letters was red or orange. The additional contrast gain effects found by Huang and Dobkins (2005) are suggestive that their RSVP task was more demanding than the central contrast discrimination task used by Morrone et al. (2002). According to this suggestion, studies showing only response gain effects may have employed a central task that was not demanding enough to produce contrast gain effects. By extension of this argument, the strongest contrast gain effects would be produced when a central task consumes all available resources or when an observer is instructed to completely ignore a peripheral stimulus. Although such effects on ignored stimuli cannot be measured psychophysically (an observer cannot respond to an ignored stimulus), consistent with this suggestion, monkey electrophysiology studies that reported contrast gain effects in areas V4 and MT obtained these results when the animal directed attention away (i.e. completely ignored) the visual stimulus (Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000).

Considering this suggestion that a highly demanding central task exerts effects of contrast gain on a concurrent peripheral task within the framework of Load Theory led to a novel prediction concerning the effects of perceptual and VSTM load on the contrast response function. Specifically, I hypothesized that high load on a central task that exhausts perceptual representational capacity would decrease the sensitivity of the contrast response function, compared with low load, as predicted by the contrast gain account. With respect to any possible effects of response gain, these might depend on whether the effects observed by Morrone et al. (2002) and by Huang and Dobkins (2005) are due to load or whether they are due to any other confounding variables of the single- versus dual-task paradigm. Such dual-task designs make it particularly hard to isolate the source of any possible effects that could simply be due, for example, to effects of general task difficulty from performing an additional task. Moreover, because in these studies participants are responding to the primary task (e.g. peripheral contrast discrimination in Morrone et al., 2002, and in Huang & Dobkins, 2005) following their response to the additional task (e.g. central disk contrast discrimination in Morrone et al, 2002, and RSVP in Huang & Dobkins, 2005), any effects might have simply be due to forgetting the relevant attribute (e.g. contrast level) of the visual stimulus.

In Experiment 11 I investigated the effects of perceptual load on the contrast response function. Participants performed a peripheral orientation discrimination task on a tilted Gabor of various contrast levels while perceptual load was manipulated in a similar task to that used in Chapter 3 (Experiment 5). Specifically, the orientation discrimination task appeared on the same display as the memory set of the VSTM task, thus the requirement to encode a set of a greater number of items in high (6 items) compared with low (1 item) VSTM load now placed a larger perceptual load on the orientation discrimination task (Lavie, 1995). In Experiment 12 I assessed the effects of VSTM load on the contrast response function under closely matched experimental conditions to those used to investigate effects of perceptual load. The paradigm of Experiment 12 was identical to that of Experiment 11 except that now the orientation discrimination stimulus appeared during the delay period of the VSTM task (1 s after the memory set) instead of being presented on the same display as the memory set in Experiment 11. Furthermore, in Experiment 13 I assessed whether the effects of VSTM load on the contrast response function observed in Experiment 12 are due to specifically loading perceptual representational resources or it is rather due to an increase in the demand on general cognitive capacity resources.

The performance of each participant on the orientation discrimination task (mean accuracy) for each of several contrasts was fit to the Weibull function (see Method). The parameters of the psychometric function (contrast threshold, slope, and asymptote) were estimated separately for the low and the high load conditions. Differences on the estimated contrast threshold (the stimulus contrast at half the maximum performance) between the two load conditions determined effects of contrast gain. Differences on the shape (slope) and asymptote (response saturation level) of the contrast response function between the various conditions determined effects of response gain.

5.2 Experiment 11

5.2.1 Introduction

The aim of Experiment 11 was to evaluate whether perceptual load affects the contrast psychometric function via response gain or contrast gain. The average orientation discrimination accuracy of each participant at each of several contrast levels was fitted to the Weibull function. The parameters (contrast threshold, slope, and asymptote) of the psychometric function were estimated separately for the low and the high VSTM load conditions for each participant. Effects of perceptual load on contrast threshold would indicate contrast gain whereas effects on the slope and the asymptote would indicate response gain.

5.2.2 Method

Participants. Eight individuals (6 males; age range: 20 – 32 years; mean age: 26.22 years) took part in Experiment 11.

Stimuli and Apparatus. The experiment was presented on an IBM-compatible PC attached to a 20-inch CRT monitor (resolution = 800×600; refresh rate: 60Hz; mean background luminance: ~70Cd.m^2) and a standard QWERTY keyboard.

The stimuli, and procedure used in the VSTM task were identical to Experiment 4. For the orientation-discrimination task a Gabor patch was presented (sinusoidal grating of 3cpd enveloped in a Gaussian window, tilted left or right) within a left or right columnar bar (vertical length: 12.4°; horizontal eccentricity from midline: 6.2°) in a counterbalanced fashion with the exact location within the columnar bar randomly assigned. The tilt angle of the Gabor patch was individually assessed for each participant with a staircase procedure prior to the main experiment. Previous electrophysiology studies that evaluated effects of attention on the contrast response function avoided levels at which response saturation occurs. Similarly, in order to properly compare response gain and contrast gain psychophysically, the psychometric functions should arise from a demanding task that ensures that performance on the low load condition does not asymptote at 100%, leaving room to test for effects of response gain. For this reason, the orientation discrimination threshold of each participant was assessed using an accelerated stochastic approximation method obtaining target-contrast estimates that resulted in approximately 75% accuracy rate (Kesten, 1958). Moreover, in order to capture the full psychometric function the method of constant stimuli was used; the Gabor contrast was randomly chosen in each trial from a set of eight contrasts (0.1%, 7.3%, 14.4%, 21.6%, 35.9%, 43.1%, 66.5%, 90%).

Procedure. The procedure used is illustrated in Figure 5.2. Trials were initiated by the participant. A fixation mark appeared first for 1000 ms followed by the stimulus display for 100 ms. The stimulus display contained the VSTM set (one coloured square for low load and six for high load) at fovea, and the tilted Gabor for the orientation-discrimination task in the periphery. Participants were then given up to 2500 ms to respond with their left hand as to whether the Gabor was tilted clockwise or counter-clockwise (index finger indicated clockwise and middle finger counter-clockwise), followed by a blank screen comprising a 3 s delay period. Next, the memory probe appeared for 3000 ms (or until response) comprised of one coloured square in one of the memory set items' location. Participants indicated with a right-hand response whether the location and colour of the memory probe matched that of the memory set (index finger indicated "same", middle finger indicated "different"). The memory probe matched the memory set in half of the trials, whereas it changed colour during the other, unmatched, half.

Feedback was given only on incorrect memory responses with words "WRONG memory response" above fixation. Responses to the two tasks were not speeded. Participants completed six 64-trial runs (following one practice run). The VSTM load condition was blocked in 8-trial blocks (counterbalanced in an ABBABAAB fashion) within each run.

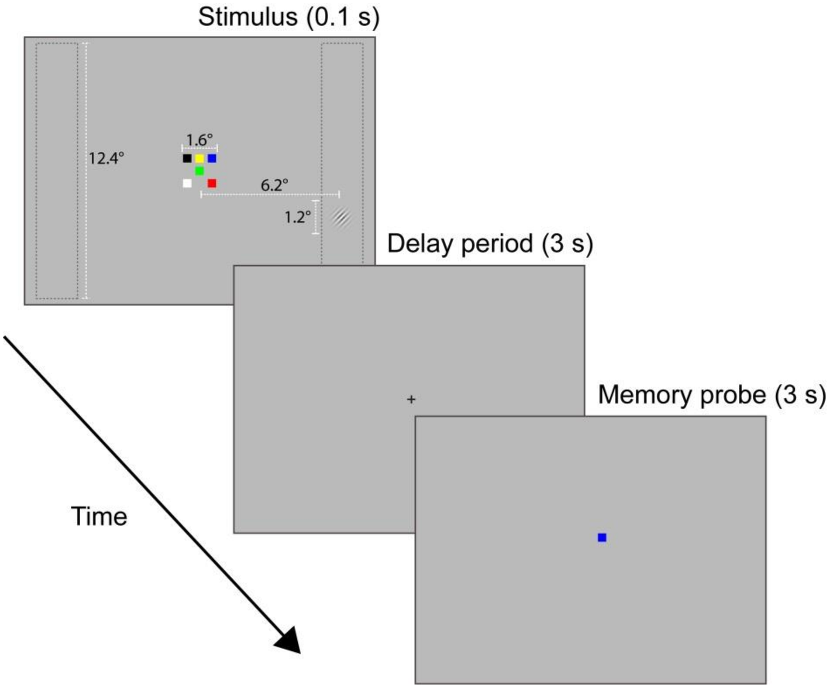

Figure 5.2. Sequence of events for an example high perceptual load trial in Experiment 11. Six squares in high load (or one square in low load) were presented at fixation. In the periphery, a tilted target Gabor patch appeared within a left or right columnar bar (shown in grey dashed lines here, but not presented during the experiment). Participants maintained the memory set while responding (during the delay period) as to the orientation (clockwise vs. counter-clockwise) of the peripheral Gabor patch. The memory probe appeared next for 3 seconds or until response. Participants indicated with a button press whether the location and colour of the memory probe matched that of the memory set.

5.2.3 Results & Discussion

VSTM. Mean percentage accuracy rates and mean memory estimates (Cowan's K) are presented in Table 5.1.

Table 5.1. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task in Experiment 11.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)
Low	95 (3)	0.90 (0.07)
High	63 (6)	1.46 (0.68)

SDs are listed in parenthesis.

As the table shows, VSTM task accuracy decreased significantly from the low to the high VSTM load condition, t(7) = 21.69, p <.001, d = 1.87. The memory estimates were significantly increased from the low to the high VSTM load condition, t(7) = 2.65, p = .03, d = 1.03. These results demonstrate that the VSTM load manipulation in Experiment 11was effective.

Contrast gain vs. response gain. To assess whether the effects of perceptual load on visual detection are consistent with contrast gain or response gain, the data from each participant were fitted to the Weibull contrast response model.

$$\psi(x;\ \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda)\, F(x; \alpha, \beta),$$

where x is the stimulus contrast, $\alpha, \beta, \gamma, \lambda$ are the fitted model parameters which determine the shape of the psychometric function, and F is the Weibull function:

$$F(x; \alpha, \beta) = 1 - \exp(-(x/\alpha)^{\beta}), \text{ with } x \in (-\infty, +\infty), \alpha \in (-\infty, +\infty), \beta \in (-\infty, +\infty).$$

The contrast threshold (alpha), the slope (beta) and the asymptote (lambda) of the contrast response function were left to vary freely and estimated separately for the low and the high load conditions.

Fits were performed using maximum likelihood estimation, and the errors of the parameters were estimated by parametric bootstrap analysis. Goodness-of-fit was assessed with deviance scores, which were calculated as the log-likelihood ratio between a fully saturated model and the data model. This analysis confirmed good fits in all participants as indicated by cumulative probability estimates of the obtained deviance scores (all p-values > .05).

Figure 5.3a shows the group-average psychometric functions and their Weibull fits, for the low and the high perceptual load conditions. Importantly, although performance in the low perceptual load condition asymptotes at a high level, it does not reach ceiling levels (100% accuracy). Rather, because each participant's orientation threshold was assessed through a staircase procedure, the task was rendered difficult enough such that observers' performance asymptotes at ~80% accuracy, thus leaving room for response gain (if any) to manifest itself in the high load condition.

Compared with low load, the contrast response function of the high perceptual load condition is shifted to the right, as predicted by the contrast gain account. A comparison of the estimated individual contrast thresholds (alpha) between low and high perceptual load confirmed a significant increase of the contrast-threshold from the low (M = 17%, SD = 8%) to the high perceptual load condition (M = 29%, SD = 14%), t(7) = -2.40, p <.05, d = .88 (see Figure 5.3b). Importantly, the same analysis did not reveal any significant differences on the estimated asymptotes (low load, M = 80%, SD = 7%; high load, M = 80%, SD = 10%, t(7) = -0.18, p =.86, d = .11) or the slope (low load, M = 5.71, SD = 5.40; high load, M = 16.56, SD = 36.83), t(7) = -0.74, p =.48, d = .39) of the psychometric function between the two conditions.

The results of Experiment 11 demonstrate that high perceptual load shifts the contrast response function to the right without affecting the slope and/or the asymptote of the psychometric function. This finding is consistent with the predictions of the contrast gain model and indicates that perceptual load interacts interchangeably with contrast. Specifically, the rightward shift of the contrast response function, in the absence of any effects on the slope and/or the asymptote, indicates that load does not decrease the strength of neural responses to contrast. Instead, high perceptual load reduces the neural sensitivity to contrast, an effect equivalent to a reduction in the effective contrast of a visual stimulus.

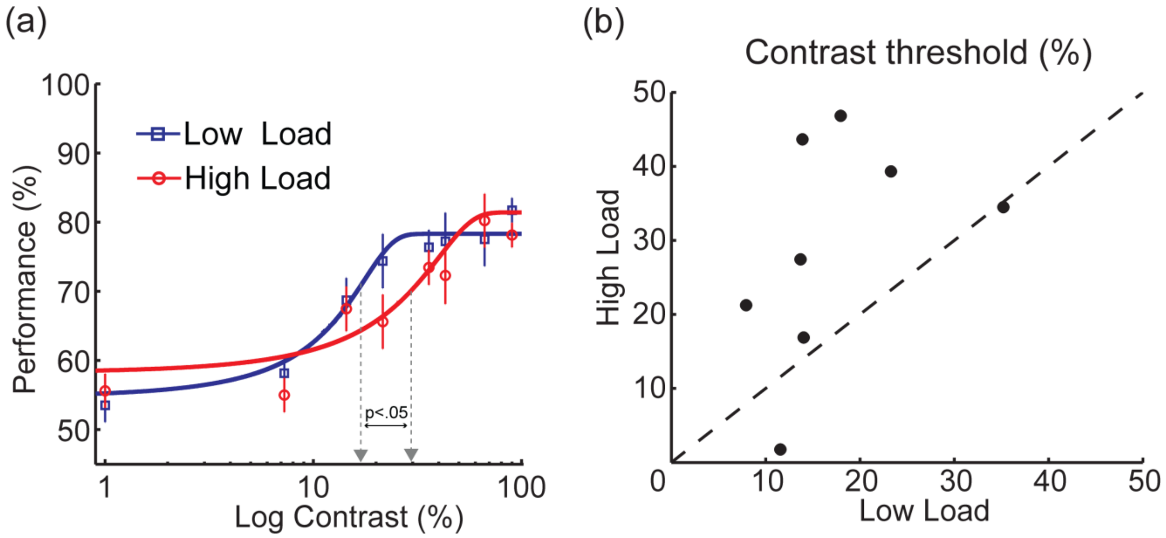

Figure 5.3. Perceptual load effects on discrimination accuracy performance in Experiment 11. (a) Psychometric functions for low (blue curve) and high (red curve) perceptual load. The estimated contrast threshold parameter for each psychometric function is also shown (contrast threshold yielding half-maximum performance). Each data point represents the mean across participants. Error bars are +/-1 SEM. (b) The estimated contrast threshold of individual participants plotted for high versus low VSTM load.

5.3 Experiment 12

5.3.1 Introduction

In Experiment 11 I employed a perceptual load manipulation by presenting the orientation discrimination task on the same display as the memory set. The finding of a rightward shift of the contrast response function with higher perceptual load in the absence of any effects on the slope and the asymptote of the psychometric function indicated that perceptual load exerts effects of contrast (but not response) gain.

So far, the effects of perceptual load on sensitivity for detecting a contrast increment (e.g. Experiment 5, Chapter 3) established in the previous chapters were shown to be akin to those of VSTM load. For example, a between experiment comparison of Experiment 4 (VSTM load) and Experiment 5 (perceptual load) of Chapter 3 showed that the load-induced reduction in detection sensitivity was in the same direction and of similar magnitude in both, the VSTM and the perceptual load manipulations. These findings are consistent with the recent evidence that short-term maintenance utilizes the same resources as those used in perception (e.g. Munneke et al., 2010; also see Chapter 2). As predicted by load theory, because the capacity for perceptual representations in early visual cortex is occupied in both types of load (VSTM and perceptual), similar effects on detection sensitivity are observed.

In Experiment 12 I thus asked whether VSTM load affects the contrast of a stimulus via contrast gain, like was the case for perceptual load, or via response gain. The experimental paradigm used in Experiment 11 was modified by presenting the orientation discrimination task during the delay period of the VSTM task (see Method). Similar to Experiment 11, each participant's orientation discrimination accuracy at each level of contrast was fitted to the Weibull function, and the parameters of the psychometric function were estimated separately for the low and the high VSTM load conditions. A change in the contrast threshold of the function would indicate effects of contrast gain whereas a change in the slope and the asymptote would indicate effects of response gain.

5.3.2 Method

Participants. Seven right-handed individuals (4 males; mean age 24.9; age range: 18-33) participated in Experiment 12. Three participants were replaced because of poor memory performance (all three memory estimates in high load (Cowan's K) < 1.2). Another participant was excluded because a software failure resulted in the loss of the participant's responses during the experiment.

Stimuli Procedure. The apparatus, stimuli, and procedure were identical to Experiment 11 except that the orientation-discrimination stimulus now appeared 1000 ms following the offset of the memory set for 100ms, during the memory delay. Moreover, following preliminary pilot testing, the high load memory set now contained four items (instead of six items in Experiment 11).

5.3.3 Results & Discussion

VSTM. Mean percentage accuracy rates and mean memory estimates (Cowan's K) are presented in Table 5.2.

Table 5.2. Mean Percentage Accuracy Rates and Mean Memory Estimates in the VSTM Task in Experiment 12.

VSTM load	VSTM Accuracy (%)	Memory estimates (K)
Low	96 (2)	0.93 (0.04)
High	73 (11)	1.81 (0.92)

SDs are listed in parenthesis.

As the table shows, VSTM task accuracy decreased significantly from the low to the high VSTM load condition t(6) = 6.23, p <.001, d = 1.64. The memory estimates were significantly increased from the low to the high VSTM load condition, t(6) = -2.60, p = .04, d = 1.46. These results demonstrate that the VSTM load manipulation in Experiment 12 was effective.

A mixed model ANOVA between experiment comparison with experiment (Experiment 11, Experiment 12) as the between subjects factor and with load (low, high) as the within subjects factor on the VSTM task accuracy rates revealed a main effect of experiment indicating that using a memory set size of four items in this experiment (instead of six items in Experiment 11) resulted in improved VSTM task performance in this experiment (M = 85%, SD = 14%) compared to Experiment 11 (M = 79%, SD = 17%), *F*(1, 13) = 4.61, p = .05, $\eta^2 = 0.26$. A trend for an interaction between experiment and load indicated that the effect of load was greater in Experiment 11 (VSTM accuracy rates reduced by 31%) than in Experiment 12 (VSTM accuracy rates reduced by 23%), *F*(1, 13) = 4.41, p = .056, $\eta^2 = 0.25$.

No significant main effects of experiment or interaction effects between experiment and the level of load were obtained in a similar mixed ANOVA between experiment comparison on the memory estimates (Cowan's K), both *F* < 1.

Contrast gain vs. response gain. Figure 5.4a depicts the group-average psychometric functions for the low and high VSTM load and their Weibull fits. Goodness-of-fit analysis confirmed good fits for all participants (all p-values > .05). As predicted by the contrast gain account and consistent with the findings of Experiment 1, the function of the high VSTM load condition, compared with low load, is shifted to the right. Importantly no differences in the asymptotic performance or the slopes between the two conditions are observed.

The estimated contrast thresholds from the Weibull fits are depicted in Figure 5.4a for each participant. As predicted by contrast gain, high (vs. low) VSTM load led to a significant increase in the contrast-threshold (low load, M = 16%, SD = 7%; high load, M = 30%, SD = 13%, t(6) = 2.52, p <.05, d = 1.14). No evidence for a reliable change in the asymptote (low load, M = 85%, SD = 10%; high load, M = 86%, SD = 12%, t(6) = -0.20, p =.85, d = .07) or the slope (low load, M = 5.38, SD = 7.54; high load, M = 7.73, SD = 11.61), t(6) = 0.60, p =.57, d = .20) of the psychometric function was found.

Importantly, these findings are equivalent to those of perceptual load as indicated by a mixed ANOVA between experiment comparison on the estimated contrast-thresholds, with load as the within-subject factor (low, high) and the type of load as the between subject factor (perceptual, VSTM). This analysis revealed a significant main effect of load (*F*(1, 13) = 21.01, p = .004, η^2 = .48). Critically, the main effect of type of load and the interaction, were not significant, both *F* < 1. No significant effects were found with the same analysis on the estimated slopes and asymptotes (all *F* < 1). These findings indicate that the load-induced increase in contrast-thresholds was of similar magnitude in the two types of load manipulation.

This pattern of results demonstrates a rightward shift in the contrast response function with higher VSTM load. Importantly, the slope and the asymptote of the contrast response function are not affected by VSTM load. This pattern of results is characteristic of effects of contrast gain. Taken together, these findings indicate that VSTM load exerts effects that are interchangeable to those of contrast. Similar to perceptual load, VSTM load does not affect the strength of neural response to contrast but it instead reduces the contrast sensitivity of neurons. This reduction in contrast sensitivity is analogous to a reduction in the physical contrast of a visual stimulus.

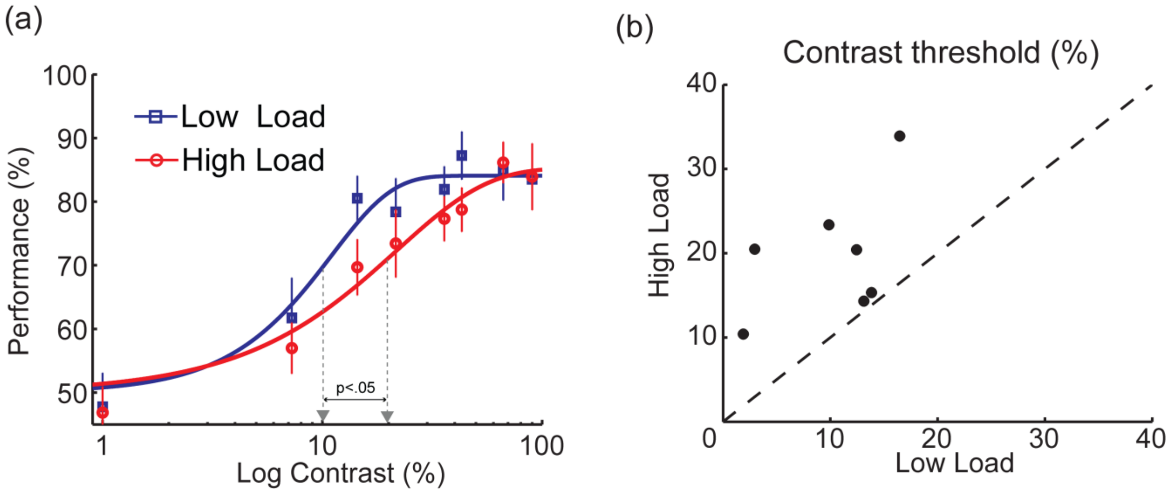

Figure 5.4. Effects of VSTM load on discrimination accuracy performance in Experiment 12. (a) Psychometric functions for low (blue curve) and high (red curve) VSTM load. The estimated contrast threshold parameter for each psychometric function is also shown (contrast threshold yielding half-maximum performance). Each data point represents the mean across participants. Error bars are +/-1 SEM. (b) The estimated contrast threshold of individual participants plotted for high versus low VSTM load.

5.4 Experiment 13

5.4.1 Introduction

Central to the debate about the neural mechanisms that underlie the effects of attention have been monkey electrophysiology studies that recorded neural activity while the animals directed attention on a stimulus presented either inside or outside the recorded neuron’s receptive field. Whereas some reports indicated that attention increases neural responses multiplicative via a fixed gain factor as predicted by response gain (McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999), other studies reported effects consistent with contrast gain, that is, a horizontal shift of the contrast response function (Martinez-Trujillo & Treue, 2002; Reynolds et al., 2000). Still other studies found evidence suggestive of additive effects of attention (Thiele et al., 2009; for neuroimaging evidence for an additive effect in human V1 see Buracas & Boynton, 2007) or of mixed effects of both response gain and contrast gain (Williford & Maunsell, 2006).

Recently, Reynolds and Heeger (2009) proposed the normalization model of attention with the aim of reconciling these conflicting reports for the effects of attention on the neural responses in the macaque visual cortex. This computational model suggests that two critical factors determine how attention affects contrast response functions: the stimulus size and the spread of spatial attention (attention field size). By changing the relation between these two factors, the model can exhibit response gain changes, contrast gain changes, and various combinations of response and contrast gain changes. Specifically, when the stimulus is large and the attention field small, the normalization model predicts that attention will affect contrast sensitivity via response gain. In contrast, when the stimulus is small and the attention field is large, the model predicts contrast gain changes. The predictions of this model have been confirmed recently psychophysically by manipulating conjointly the stimulus size and the size of the attention field (Herrmann, Montaser-Kouhsari, Carrasco & Heeger, 2010).

Here I tested predictions derived from the normalization model of attention with two aims. Firstly, confirming that the effects of load depend on the size of the visual stimulus relative to the attention field size would be a novel extension of the normalization model to effects of VSTM load. So far, previous psychophysical evidence relied only on one study that manipulated attention using the spatial cueing paradigm (Herrmann et al., 2010). Secondly, if the effects of load are confirmed to depend on the size of the visual stimulus relative to the attention field size independent of the VSTM task difficulty, then such findings would confirm the specificity of the effects obtained in Experiment 12 and convincingly rule out an alternative interpretation of the results in terms of task difficulty.

The predictions of the normalization model were tested using the same design as Experiment 12 but now manipulating the attention field size by varying the spatial ambiguity of the target in the orientation discrimination task. In a 2 × 2 design, VSTM load was manipulated by varying the number of items in the memory set (same as Experiment 12) and spatial uncertainty was manipulated through the presence (certain condition) or absence (uncertain condition) of a placeholder (spatial cue) that was present throughout each trial within which the target stimulus appeared during the memory delay. The presence of the placeholder indicated the spatial location of the stimulus and thus reduced the attention field size to be roughly the same size as that of the target. However, in the absence of the placeholder, attention spread throughout a larger spatial field around fixation (see Figure 5.5) while the stimulus size remained the same. If the effects of load depend on the size of the visual stimulus relative to the attention field size as suggested by the normalization model, then load should exert the contrast gain effects observed in Experiment 12 only when the placeholder is absent (and thus the relative size of the attention field is large). Similarly, because the presence of the placeholder would reduce the attention field size relative to the stimulus size, it should exert effects of response gain independent of VSTM load. If, however, the contrast gain effects with higher VSTM load of Experiment 12 are not due to increased demands on perceptual representational resources (as claimed here) but rather on increased demands on some general cognitive capacity resource, then the effects of load should not interact with the spatial ambiguity of the target in the orientation discrimination task.

5.4.2 Method

Participants. A separate group of ten volunteers (6 Females; mean age = 23; age range: 18-30) took part in Experiment 13. The data of one participant who failed to produce a reliable psychometric function (performance did not increase with contrast) for the whole experiment were replaced with a new participant.

Procedure. The stimuli and procedure were identical to those used in Experiment 12 except that in the certain condition the Gabor was presented within a 1.4° × 1.4° placeholder that was present throughout the entire duration of each trial (see Figure 5.5).

Participants completed twelve 64-trial runs. The VSTM load condition and the uncertainty condition were blocked in 8-trial blocks presented in a counterbalanced fashion within each run.

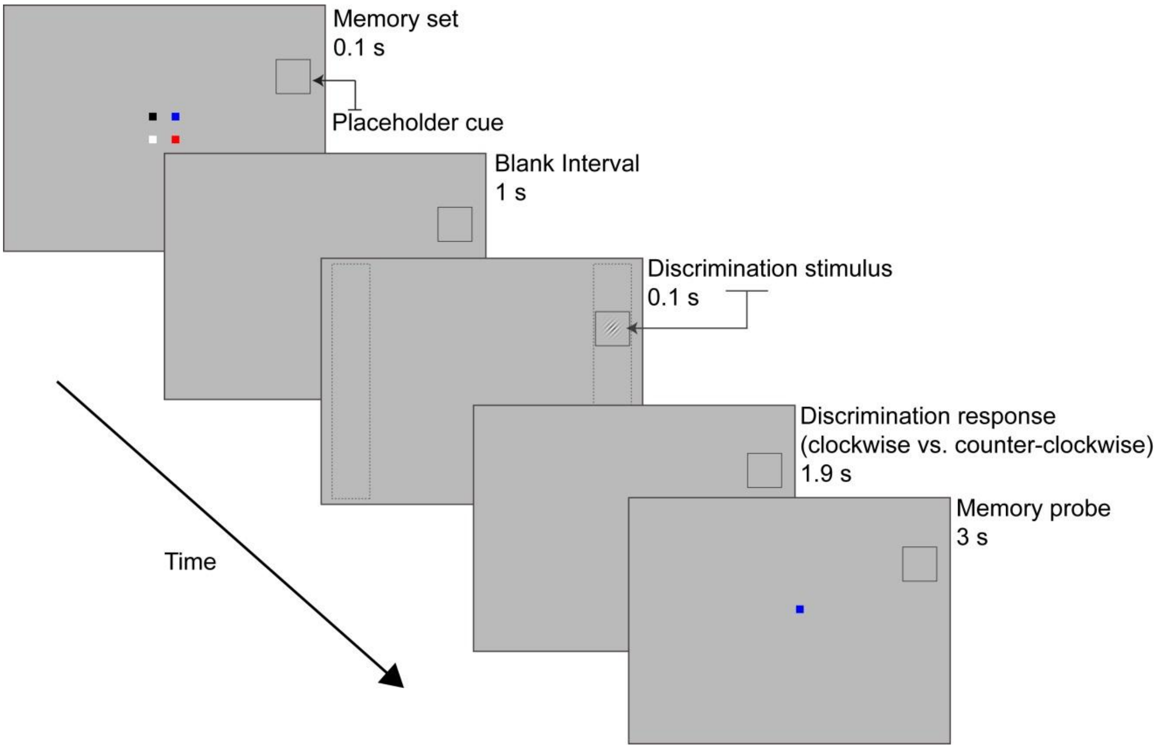

Figure 5.5. An example of a high VSTM load trial in the certain condition in Experiment 13. The procedure was identical to that of Experiment 12 except that here a placeholder that indicated the spatial location of the Gabor patch was present throughout the duration of each trial.

5.4.3 Results & Discussion

VSTM. As expected, the memory task was of higher difficulty in the high compared to the low VSTM load condition as confirmed by a two-way repeated measures ANOVA on the memory task accuracies with factors VSTM load (low, high) and placeholder certainty (certain, uncertain). This analysis revealed a significant main effect of VSTM load (low load, M = 96%, SD = 1%; high load, M = 87%, SD = 7%), $F(1,9) = 29.32$, $p < 0.001$, $\eta^2 = .77$. The same analysis on the memory estimates (Cowan's K) also revealed a main effect of VSTM load (low load, K = .95, SD = .03; high load, K = 3.02, SD = .62) , $F(1,9) = 118.05$, $p < 0.001$, $\eta^2 = .93$, indicating that participants held more information in memory during the high (vs. the low) VSTM load condition. These findings indicate effective manipulation of VSTM load.

Importantly, no main effect of placeholder certainty (both $F < 1$, for accuracy rates and for memory estimates) or interaction effects ($F(1,9) = 1.17$, $p = 0.31$, $\eta^2 = .115$ for accuracy rates; $F < 1$ for memory estimates) were found with the above analysis. This result thus ensures that the spatial uncertainty manipulation did not affect VSTM task difficulty and performance.

Contrast gain vs. response gain. Figure 5.6 shows the low and high VSTM load group-average psychometric functions for the certain and uncertain conditions. Goodness-of-fit analysis indicated good fits for all participants (all $p > .05$)

As predicted by the contrast gain account, when the location of the discrimination stimulus was uncertain, VSTM load led to an increase in the contrast threshold of the psychometric function, consistent with the findings of Experiment 12 (Figure 5.6a, c; reliable differences in contrast threshold, but no evidence for a change in slope or asymptote). Conversely, when the location of the discrimination stimulus was cued by the placeholder thus reducing the attention field size, no evidence for reliable differences in any of the estimated parameters was found (Figure 5.6b, d). Hence, in contrast with the consistent increase of contrast threshold with higher load observed when the stimulus location was uncertain, these findings demonstrate that the contrast gain effects of VSTM load are eliminated when the size of the attention field relative to the size of the visual stimulus is small.

Analyses on the parameter estimates from the individual data confirmed the findings from the group average data. A two-way repeated measures ANOVA on contrast-threshold estimates with factors VSTM load (low, high) and placeholder certainty (certain, uncertain) revealed a significant interaction between VSTM load and placeholder-certainty, *F*(1,9) = 8.42, p = 0.017, η^2 = .48 (see Figure 5.7). As can be seen in Figure 5.7, this interaction reflects the fact that contrast-threshold estimates were increased under high VSTM load in the uncertain condition (low load, M = 11%, SD = 4%; high load, M = 16%, SD = 5%), t(9) = 2.80, p = .02, d = 1.05, but not in the certain condition (low load, M = 13%, SD = 4%; high load, M = 12%, SD = 5%), t(9) = 0.60, p =.56, d = .16 (see also Figure 5.6c and d). The results also revealed a trend for increased contrast-threshold with higher load (low load, M = 12%, SD = 4%; high load, M = 14%, SD = 5%; *F*(1,9) = 3.68, p = 0.087, η^2 = .29), but no effects of placeholder-certainty (p = .30).

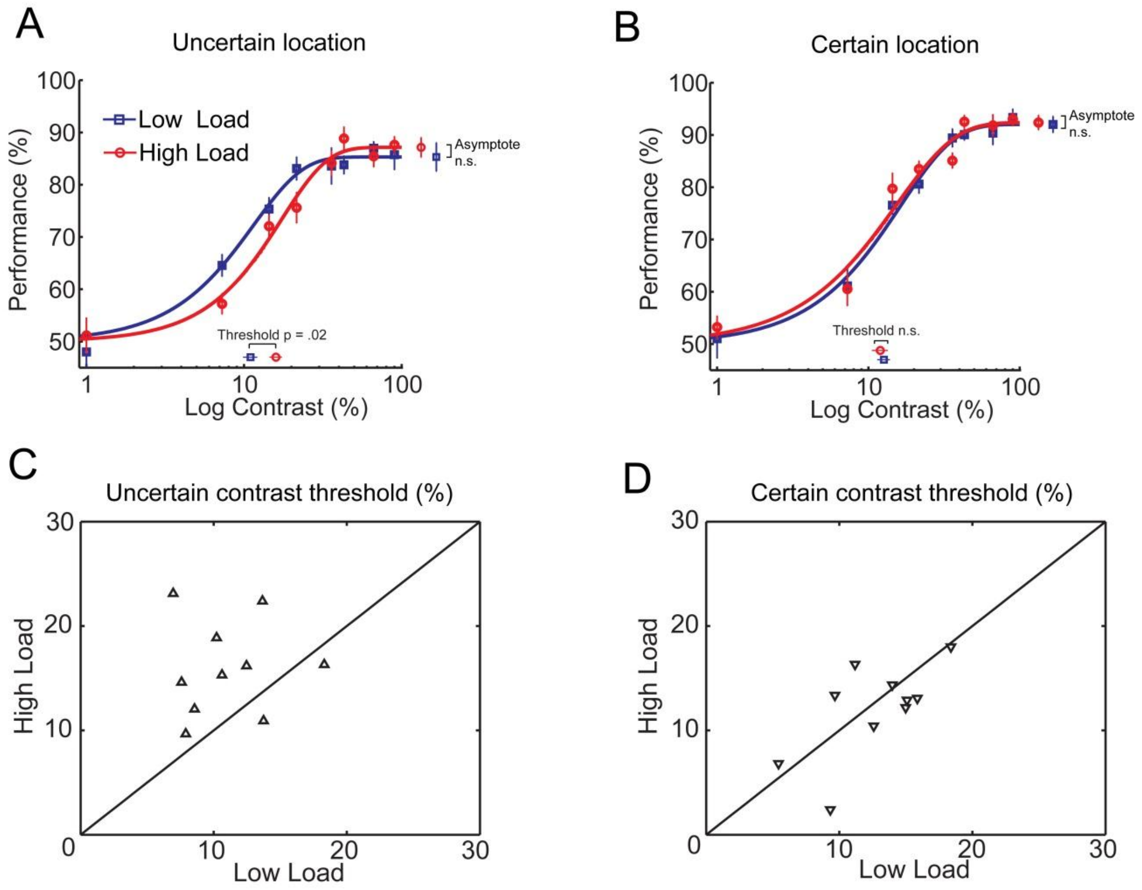

Figure 5.6. Effects of VSTM load on discrimination accuracy in the certain and the uncertain target location conditions in Experiment 13. Shown are psychometric functions of the low (blue curves) and the high (red curves) VSTM load for the uncertain (a) and the certain (b) conditions. The estimated parameters from each psychometric function are also shown (contrast threshold yielding half-maximum performance; asymptotic performance). Each data point represents the mean across participants. Error bars are +/-1 SEM. The bottom panels show the estimated contrast threshold of individual participants in the uncertain (c) and the certain (d) conditions plotted for high versus low VSTM load.

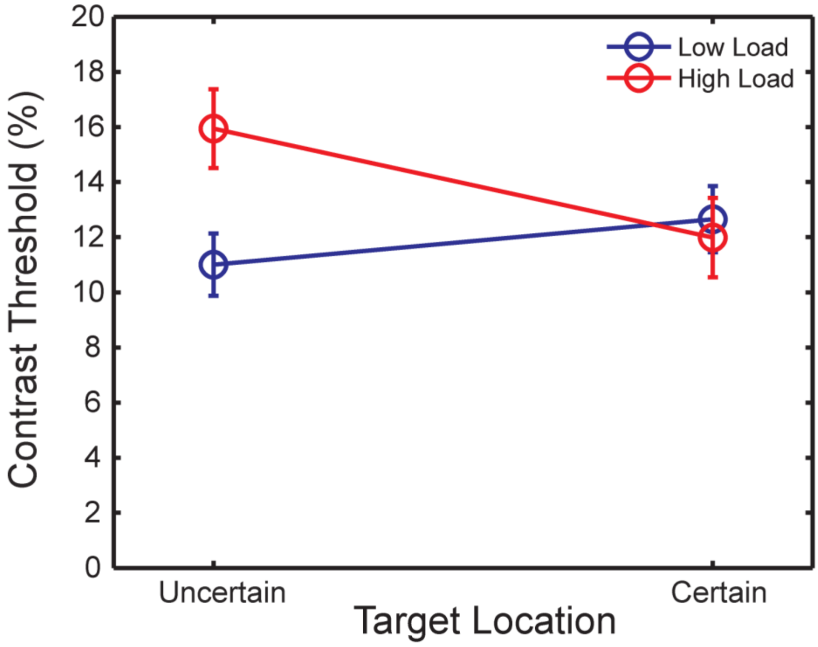

Figure 5.7. Group average estimated contrast thresholds in Experiment 13 illustrating the interaction between VSTM load and target certainty. High VSTM load increased the contrast threshold estimates only in the uncertain, but not in the certain, condition.

Importantly, a similar ANOVA on the estimated asymptote level of the individual psychometric functions revealed a significant main effect of certainty, $F(1,9) = 14.71$, $p = 0.004$, $\eta^2 = .62$. As shown in Figure 5.8, asymptotic performance was higher under the certain condition compared with the uncertain condition. This finding is important as it confirms the normalization model prediction of response gain effects (independent of load) when the relative size of the attention field is small, as was the case in the certain condition, relative to when the attention field is large, as was the case in the uncertain condition. No effects of load and placeholder-certainty conditions were observed on the estimated slope of the functions (all $F<1$).

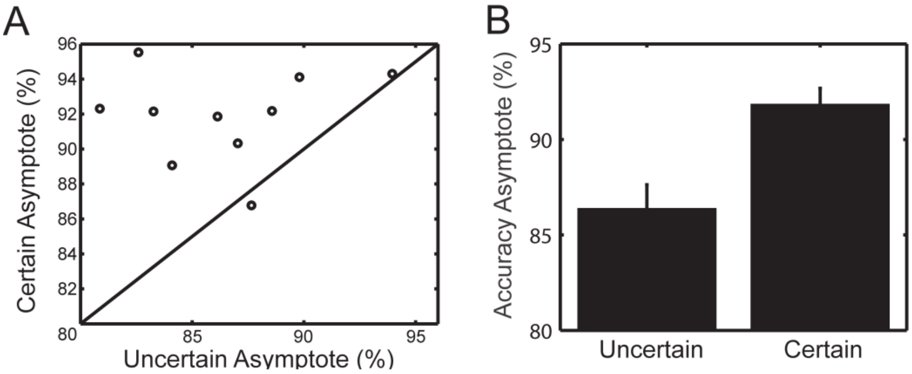

Figure 5.8. Effects of certainty on the orientation discrimination task asymptotic accuracy in Experiment 13. A) The estimated asymptote of individual participants, averaged across load, plotted for certain versus uncertain conditions. B) Mean estimated asymptote across low and high VSTM load conditions for the uncertain and certain conditions. Errorbars represent +1 SEM.

Taken together, these findings demonstrate that high VSTM load exerts effects of contrast (but not response) gain. Importantly, as predicted by the normalization model of attention, these effects are not due to general task difficulty with higher VSTM load but depend on the relative size of the attention field.

5.5 Chapter Conclusions

The experiments in this chapter have demonstrated the effects of perceptual load and VSTM load on the contrast response function. Loading perceptual representational resources with either perceptual load or VSTM load induced effects of contrast gain as indicated by the finding of reduced sensitivity of the contrast response function with higher load. This finding clarifies the mechanism by which load reduces detection sensitivity for an unrelated visual stimulus: when brain resources involved in perception are occupied, either in a high perceptual load or a high VSTM load task, then the neural response to an unrelated stimulus of a given contrast is equivalent to the response to the same stimulus but of higher contrast. It is as if load, by reducing the available perceptual resources, reduces the effective contrast of the rest of the visual stimuli in the environment.

Importantly, these effects of VSTM load on the contrast response function are not due to task difficulty or greater non-specific demands on some general cognitive resource. As demonstrated in Experiment 13, the effects of VSTM load on the contrast response function depended on the size of the attention field relative to the visual stimulus size. Although the certain and uncertain conditions were both difficult, high VSTM load exerted contrast gain effects only when the relative size of the attention field was large. When, however, the attention field was small, compared with the uncertain condition when the attention field was large, effects of response gain were observed, independent of VSTM load.

These findings establish the specificity of the VSTM load effects, since the effects of contrast gain were only observed under the condition of large relative size of the attention field. Moreover, these results extend the normalization model to accommodate new forms of competitive interactions between neural responses to visual stimuli and visual representations held in short-term memory under load.

Chapter 6:

General Discussion

6.1 Overview and Implications of Findings

The research reported in this thesis established the role of VSTM load in visual detection while comparing these effects to those of perceptual load and WM cognitive control load. The results demonstrated that VSTM load reduced detection sensitivity (*d'*) and the associated primary visual cortex (V1) response to an unrelated visual stimulus presented during the delay interval of a high load (vs. low load) VSTM task. They also demonstrated that both, VSTM load and perceptual load, affect visual detection by reducing the effective contrast of an unrelated visual stimulus.

The effects of VSTM load on detection sensitivity were found on foveal, parafoveal and peripheral stimuli, and extended for up to 4 s. These effects were comparable in magnitude to the effects of perceptual load (Chapters 2 and 3). In contrast, WM cognitive control load either had no effect on detection sensitivity (Chapter 3) or in some circumstances has even increased detection sensitivity (Chapter 2). Thus, the VSTM load effects were not due to general task difficulty or due to load on some general cognitive capacity resource.

The effects of reduced detection sensitivity with higher VSTM load were shown not to be accompanied by differences in response criterion. In all the experiments reported in this thesis, beta (β) measures of response bias remained unaffected by load. Instead, the load manipulation only affected the sensitivity (*d'*) for detecting a visual stimulus. These effects persisted when a concurrent attention task (visual letter-search task, Chapter 2) was eliminated and the visual detection task was the only priority during the VSTM delay interval. This finding demonstrates that the VSTM load effects did not depend on some form of interaction between load and attention employed during the concurrent attention task. Neither are these effects due to an interaction of load with the task priorities of the visual detection task and the concurrent attention task (in other words with a particular low level of prioritization for the visual detection task) or with the preceding attention response on the encoding or remembering of the detection target stimulus.

Furthermore, the effects of VSTM load on detection sensitivity were replicated under conditions of articulatory suppression ruling out any significant contributions from verbal strategies either through affecting performance on the VSTM task (Cowan’s K memory estimates as well as VSTM task accuracies) or through directly affecting detection sensitivity. These effects were also shown not to be due to shifting spatial attention between the central locations of the VSTM task displays and the peripheral locations of the detection task stimuli,indeed the effects extended to cases where the stimuli in both task overlapped on the same foveal and parafoveal spatial locations.

6.1.1 Relation to Load Theory

The findings that different types of load have opposite effects on stimulus detection extend load theory to now accommodate the effects of load on different WM processes of maintenance and cognitive control and demonstrate a the distinct roles of these different WM processes in the fundamental perceptual process of visual detection. As reviewed in Chapter 1, load theory proposes that the demand on perceptual representation resources imposed by a task determines whether a visual stimulus will be perceived: in situations of low load, task-unrelated stimuli are easily perceived since spare capacity is available to be devoted to their processing; however, in situations of high load these stimuli are not perceived since now capacity is fully consumed by task demands, leaving none remaining to process any further information.

Previous studies testing predictions of load theory focused almost exclusively on indirect measures of perception, such as the degree to which distractors interfere with target RTs and error rates (e.g. Beck & Lavie, 2005; Jenkins, Lavie, & Driver, 2005; Lavie, 1995;

2000; Lavie & Cox, 1997; Lavie & Fox, 2000; Lavie, Ro & Russell, 2003; Theeuwes, Kramer, & Belopolsky, 2004), or the level of neural activity they elicit in visual cortex (e.g. Bahrami et al., 2007; O'Connor et al., 2002; Pessoa et al., 2002; Pinsk et al., 2003; Rees et al., 1997; Schwartz et al., 2005; Yi et al., 2004).

Two recent studies have tested directly load theory's predictions for visual perception: Cartwright-Finch and Lavie (2007) assessed awareness reports using the inattentional blindness paradigm. However, these results are confined to the case of unexpected stimuli, and may have involved memory failure rather than conscious perception. However, a later study (Macdonald & Lavie, 2008), addressed the limitations of the inattentional blindness paradigm and found support for load theory's prediction that this "load-induced blindness" phenomenon is specifically due to load on perceptual processes rather than differences in response bias, memory failures, goal-neglect, expectation, task difficulty or demand on general cognitive resources. The findings of this thesis complement these previous studies by demonstrating this "load-induced blindness" phenomenon for the first time with load on perceptual resources imposed by a visual short-term memory task. This effect is similar in magnitude to that of perceptual load imposed by a visual perception task.

Importantly, the findings of VSTM load were contrasted to those of another type of WM load, namely cognitive control load; these different types of WM load (VSTM vs. cognitive control) were found to have different effects on stimulus detection sensitivity (that in some cases were even opposite) and thus cannot be explained in terms of a general effect of increased task-difficulty under higher load. All high load conditions were more difficult but the effect on detection sensitivity critically depended on the type of process loaded. This is important because general effects of task difficulty can explain some of the previous reports that inattentional blindness rates are increased with higher load, irrespective of whether cognitive control WM load or VSTM load was manipulated (e.g. Fougnie, & Marois, 2007; Todd, Fougnie & Marois, 2005). One likely general effect of increased task difficulty is the adaptation of a more conservative response criterion for reports about unexpected and task-irrelevant stimuli. Indeed the awareness measures used in the previous studies were based on a single subjective response (noticed or not) per participant. Therefore increased rates of "did not notice" reports under higher load may have reflected elevation of the response criterion. In contrast, the effects presented in this thesis were established for an expected stimulus (instead on an unexpected stimulus in IB studies; Todd, Fougnie & Marois, 2005) with a criterion-free measure of detection sensitivity (*d'*), and the results showed no effects of load on response bias. These conclusions are thus immune to the alternative interpretations of the results in terms of response bias and task difficulty.

Loading cognitive control processes did not always lead to enhanced detection sensitivity: the effect critically depended on the existence of a potential conflict in task priorities between the visual detection task and another concurrent visual search task. Specifically, when participants performed the low priority visual detection task concurrently with a visual search task of higher priority, depriving cognitive control resources with high WM load led to enhanced detection sensitivity due to the visual detection task gaining priority over the visual search task. Importantly, when the visual search component of the task was eliminated, and thus the visual detection task was the only priority during the WM task delay period, high cognitive control load (vs. low load) did not affect detection sensitivity. This finding was as predicted by load theory (c.f. Lavie et al., 2004) and it importantly clarifies empirically load theory's suggestion that cognitive control resources are only employed in situations that impose a high demand on task processing priorities.

These findings also have implications for recent suggestions that perceptual load effects on distractor processing may be attributed to a low level visual interference effect whereby distractor processing is "diluted" by the mere presence of additional items (Tsal &

Benoni, 2010). This alternative “dilution” account is particularly relevant in situations where perceptual load is manipulated by increasing the set size of a visual search array, similar to the perceptual load manipulations (Chapters 2 and 3) in this thesis. Relating the “dilution account” to the present findings, the reduced detection sensitivity in the high perceptual load condition could be due to the mere presence of the non-target items in the search array under the high load condition exerting low level visual interference whereby the non-target letter features compete with those of the detection target, degrade its visual representation, and therefore reduce its perception. However, the convergence of results on showing the same effects of load across manipulations of either VSTM load or perceptual load suggests that the same mechanism underlies both types of load effects. These convergence of findings, taken together with the finding that VSTM load reduces detection sensitivity for a visual stimulus appearing up to 4 seconds following the memory set (Chapter 3) strongly suggests that the effects of both VSTM load and perceptual load are due to increased demands on perceptual representation capacity rather than mere visual clutter or “dilution” (see also Lavie & Torralbo, 2010).

6.1.2 Relation to Working Memory Research

Previous studies that investigated the effects of WM load on visual perception have focused on the effects of WM load on distractor processing, but their findings were inconclusive. Some of these studies have found evidence for increased distractor processing with higher WM load. For example, as reviewed in Chapter 1, under conditions of high (vs. low) working memory load the effects of response competing distractors (Lavie et al., 2004) as well as attentional capture by singletons (Lavie & De Fockert, 2005) were increased. These findings were obtained with well-established WM tasks that load cognitive control, for example, in a verbal WM recognition task of one (low WM load) versus six (high WM load) digits (Kelley & Lavie, 2011; Lavie et al., 2004; Lavie & De Fockert, 2005; Macdonald & Lavie, 2008; for a very similar task and results see also Rissman, Gazzaley & D'Esposito, 2009), in single (low WM load) versus dual task (high WM load) manipulations (Lavie & De Fockert, 2005), as well as a successor naming WM task similar to that used in Experiment 3 (Chapter 2) and Experiment 6 (Chapter 3; De Fockert et al., 2001; Lavie & De Fockert, 2005).

However, other studies reported that high (vs. low) WM load has led to reduced distractor processing (Bollinger, Masangkay, Zanto & Gazzaley, 2009; Rose, Schmid, Winzen, Sommer & Buchel, 2005; Sreenivasan & Jha, 2007). These different effects of WM load on distractor processing appear discrepant on a unitary view of WM. But the framework I propose here can accommodate all these findings because although the authors discussed the effects in general terms as effects of working memory, the findings of reduced distractor processing were in fact obtained in tasks that loaded maintenance VSTM processes instead of WM cognitive control processes. For example, Rose et al. (2005) found that two-back, compared to one-back memory tasks (for digits presented at fixation) led to both reduced lateral occipital cortex (LOC) BOLD activity and the LOC associated N1 event related potential (ERP) component related to background (distractor) images of natural scenes. Rose et al. (2005) did not separate the effects of memory load on encoding from those on memory maintenance. In other words, their participants may have been more engaged in encoding of each digit in the two-back compared to the one-back task. Thus, it is not clear whether these effects are due to VSTM load or perceptual demands during encoding. Their findings however are compatible with the effects of VSTM load (as well as those of perceptual load) reported in this thesis.

In another study, Sreenivasan and Jha (2007) asked participants to perform a delayed-recognition memory task for either shoes or faces. This was discussed as WM task but is in fact a classic VSTM task. During the delay interval of this VSTM task, participants were instructed to ignore distractor stimuli. The distractors either belonged to the same category as the relevant stimulus category in the VSTM task (e.g. face distractor presented during memory for faces) or belonged to the irrelevant stimulus category in the VSTM task (e.g. face distractor during memory for shoes). When a face distractor was presented during the delay interval of the VSTM task for faces (relevant category), it resulted in slower RTs and reduced face-sensitive N170 ERP component related to these distracting faces compared to when the face distractor was presented during memory for shoes (irrelevant category). These results demonstrate specific interference by VSTM maintenance on category-selective markers of visual perception as expected from my hypothesis.

A more recent study (Bollinger et al., 2009) collected electroencephalographic recordings while participants performed a VSTM task for relevant, while ignoring irrelevant, images of faces and scenes. Once again the authors discussed the task in general as a WM task however this was clearly a visual maintenance task. Specifically, participants viewed four sequential cue stimuli (two faces and two scenes), followed by a delay period and a probe stimulus. Instructions informed participants of the category (i.e. face or scene), temporal position (1st, 2nd, 3rd, 4th), and number of stimuli to be maintained (0, 1, or 2) in VSTM. Results indicated a significant VSTM load dependent modulation of N170 amplitude, such that increased VSTM load resulted in decreased evoked N170 amplitudes for both relevant and irrelevant stimuli as expected from my hypothesis.

In sum, Bollinger et al., (2009), Rose et al. (2005) and Sreenivasan and Jha (2007) have all compared visual distractor processing (e.g. FFA and N170 evoked potentials related to distractor faces) while participants performed a VSTM task of either low load (maintaining one visual image, e.g. of a place or a coloured square) or high load (maintaining two or more such images). While they discussed it as effects of WM load and thus their results appear discrepant on a unitary model of WM (as previous manipulations of WM cognitive control load led to an opposite effects, e.g. De Fockert et al., 2001) their manipulations clearly affected VSTM maintenance processes. These findings are therefore consistent with the VSTM load effects I report in this thesis.

The effects of VSTM load reported in this thesis are also consistent with another line of research that has demonstrated interactions between the contents held in VSTM and the efficiency of selective attention: selection of relevant information (e.g. in a visual search task) has been shown to be facilitated when the representations held in VSTM match the search target (Duncan & Humphreys, 1989; Olivers, Meijer, & Theeuwes, 2006; Soto, Heinke, Humphreys, & Blanco, 2005; Soto, Humphreys, & Rotshtein, 2007; for a recent review see Soto, Hodsoll, Rotshtein, & Humphreys, 2008). However, these facilitation effects are eliminated in situations of high VSTM load. For example, Downing and Dodds (2004) failed to find any VSTM effects on a visual search task when participants held in memory 2 items. Similarly, Soto, Greene, Chaudhary and Rotshtein (2011) demonstrated that holding 3 items (vs. holding a single item) in VSTM results in weaker bias in a visual search task performed during the memory delay. The elimination of these facilitation effects by high VSTM load is consistent with the present thesis suggestion that VSTM and perception share representation resources.

The finding of different results between the effects of different types of working memory load on visual detection is consistent with previous suggestions that short-term storage and cognitive control processes are independent components of working memory (Smith & Jonides, 1999). A monolithic, unitary view of working memory cannot account for the different effects of working memory load on distractor processing. In contrast, such effects can easily be accommodated within the framework I propose in this thesis, because as discussed above, the findings of reduced distractor processing with higher load were obtained with manipulations of VSTM load similar to that used here.

Notice, these previous effects of load on WM maintenance processes (i.e. VSTM load) were demonstrated on category-selective visual association brain areas (e.g. fusiform face area responses to distractor faces, Bollinger et al. 2009; Rose et al. 2005; Sreenivasan & Jha, 2007). The findings presented in thesis extend these previous reports to now demonstrate an effect on primary visual cortex (V1) response to contrast, an early fundamental visual process.

6.1.3 Relation to Sensory Recruitment Hypothesis of Visual Working Memory

The demonstration of the effects of VSTM load on visual processing in V1 during the maintenance delay provides a new line of evidence for the sensory recruitment models of VSTM (e.g. Pasternak & Greenlee, 2005; Postle, 2006 for reviews). As discussed in Chapter 1, while previous studies demonstrated that VSTM maintenance recruits sensory representations in visual cortex, the consequences for sensory response to incoming information during high load on visual maintenance resources have not previously been addressed. For instance, previous studies revealed that VSTM maintenance is associated with activity in the same sensory visual cortices that were active during perceptual encoding (e.g., Bisley, Zaksas, Droll & Pasternak, 2004; Lee, Simpson, Logothetis & Rainer, 2005; Malecki et al., 2009; Munneke et al., 2010; Supèr, Spekreijse & Lamme, 200l). Moreover, the pattern of sensory activity during maintenance has also been shown not only to maintain information about the stimulus (e.g. allowing classification of the stimulus orientation, Harrison & Tong, 2009) but also to be closely similar to the same pattern associated with stimulus encoding (Serences et al., 2009). Furthermore, the activity related to the maintained information in visual short term memory has been shown to result in increased V1 BOLD responses that are indeed retinotopically specific (Munneke et al., 2010).

The neuroimaging findings of reduced retinotopic BOLD response in primary visual cortex to a contrast-increment target with higher VSTM load presented in this thesis complement these previous reports in highlighting a novel consequence of sensory recruitment during VSTM maintenance for sensory retinotopic processing involved in the fundamental visual processes of contrast detection. Moreover, the evidence for a strong negative correlation between the amount of information maintained in visual short term memory (Cowan's K memory estimates) and the level of detection sensitivity (*d'*) is an indication of shared resources and indeed allows prediction of detection sensitivity from the extent to which VSTM capacity is loaded.

Chapter 5 provided further evidence for the suggestion that sensory visual cortex is involved in VSTM maintenance by demonstrating that load on perceptual representation processes with the requirement to maintain a higher VSTM load (as well as with higher perceptual load) exerts effects of contrast gain. Because the contrast of a visual stimulus is computed at early visual cortex, these contrast gain effects indicate that VSTM load and perceptual load interact directly with the response of sensory visual cortex to the contrast of visual stimuli. Specifically, these contrast gain findings indicate that VSTM load and perceptual load reduce the neural response to a visual stimulus of a given contrast to the equivalent response to a visual stimulus of higher contrast. That is, the effective contrast of a visual stimulus is reduced when perceptual resources are consumed in the short term maintenance of visual information. These findings thus converge with previous findings for the involvement of early visual cortex in visual short term maintenance (e.g. Munneke et al., 2010) as well as with the evidence reported in this thesis that VSTM load reduces detection sensitivity (Chapters 2 and 3) and modulates early sensory level as evidenced by the reduced primary visual cortex response to a contrast-increment detection target (Chapter 4).

However, as demonstrated in Chapter 5, VSTM load does not always exert effects of contrast gain. As shown in Experiment 13, these contrast gain effects depend on the spatial extent of visual processing during the visual stimulus presentation: when attention is distributed among a relatively large spatial area, consuming perceptual resources in a high load VSTM task, reduces the effective contrast of a visual stimulus, compared with low VSTM load; however, when attention is directed to the upcoming spatial location of the visual stimulus via a spatial cue, these contrast gain effects are eliminated. Indeed, as predicted by the normalization model of attention (Reynolds & Heeger, 2009), cueing the spatial location of the upcoming visual stimulus and thus reducing the spatial extent of visual processing, resulted in effects of response gain, compared to conditions of a relatively large spatial extent of visual processing. Importantly, these results establish the specificity of the effects of VSTM load on the contrast response function, since although all the conditions of higher VSTM load were equally difficult, VSTM load exerted contrast gain effects only when the relative size of the attention field during the VSTM delay period was large. These findings thus provide further support to the suggestion that these contrast gain effects are specifically due to higher VSTM load rather than increased demands on general cognitive capacity resources.

6.2 Future Research

In this section I describe several directions for future research that stem directly from the findings presented in this thesis.

6.2.1 Different VSTM Load Manipulations

Visual short term memory load was always manipulated in the same way in this thesis. The method involved increasing the number of items that participants were asked to maintain in a VSTM task (Luck & Vogel, 1997; Todd & Marois, 2004). Future research could seek to generalize the effects of VSTM load on detection sensitivity established in this thesis over a variety of other visual short term memory tasks. For example, the task employed in this thesis required the maintenance of only a feature (colour) in the low VSTM load condition and maintenance of a conjunction of feature and spatial location in the high VSTM load condition. Future research could attempt to separate the effects VSTM load manipulations on features from those of spatial locations by increasing either only the number of features that need to be maintained or only the number of spatial locations.

For instance, a recent neuroimaging study (Harrison, Jolicoeur & Marois, 2010) manipulated selectively the amount of different features ("what" information) and the amount of different spatial locations ("where" information) that participants were asked to maintain. Specifically, Harrison et al. (2010) employed a similar VSTM task and in the memory set they presented a rapid sequence of 3 coloured disks with a short interval between each disk. The disks were presented either at the same location or at three different out of six possible locations arranged in a circle around fixation. After a short retention interval, participants viewed a single probe disk and were asked to report whether it matched in colour or location one of the disks in the memory set. In half of the trials the probe disk matched one of the disks in the memory set. In the other unmatched half, 50% of the trials changed only location and the other 50% change only colour. This design resulted in 4 conditions. In the What1-Where1 condition, the 3 disks in the memory set were in the same colour and were presented at the same location. In the What3-Where1 condition, the memory set disks were in different colours each but were presented at the same location. In the What1-Where3 condition, the three memory set disks were in the same colour and were presented at three different locations. In the What3-Where3 condition, the memory set contained three different coloured targets that were presented in three different locations. A similar task to that of Harrison et al. (2010) could therefore be used to dissociate the effects of feature-based VSTM load from that of a purely spatial based VSTM load on detection sensitivity.

Alternatively, given evidence that VSTM capacity limitations arise from both, the number of items stored in memory and the amount of information load contained in each maintained object (Alvarez & Cavanagh, 2004; Xu & Chun, 2005), it would be interesting for future research to investigate how the effects of reduced detection sensitivity with higher VSTM load are affected by the complexity as well as the number of objects stored in VSTM. To examine this, future research could utilize a set of five stimulus classes used by Alvarez & Cavanagh (2004) demonstrating that VSTM capacity is not fixed by the number of objects but varies across the different classes of visual stimuli depending on the information load of each type of object. Given that in this study Alvarez & Cavanagh (2004) found that more VSTM resources need to be allocated to more complex stimuli (e.g. random polygons), it would be important for future research to investigate whether a set of a fewer number but more complex stimuli (e.g. two random polygons) exert the same magnitude of reduction in detection sensitivity as a set of more items with less complexity (e.g. four coloured squares).

6.2.2 Generalizing Within and Across Modalities

Recently, Macdonald and Lavie (2011) demonstrated cross-modal effects of visual perceptual load by establishing a phenomenon of inattentional deafness with visual load. This new finding addresses an ongoing debate in the attention literature concerning whether perceptual capacity is modality specific (Allport, Antonis, & Reynolds, 1972; Duncan, Martens, & Ward, 1997; McLeod, 1977; Treisman & Davies, 1973) or shared between different modalities (Broadbent, 1958; see, e.g., Santangelo, Belardinelli, & Spence, 2007;

Sinnett, Costa, & Soto-Faraco, 2006, for more recent claims). However, given the fact that the effects of VSTM load on visual detection sensitivity were demonstrated in this thesis to be akin to those of perceptual load, future research could attempt to extend the findings by Macdonald and Lavie (2011) to address the cross-modal effects of WM load on maintenance versus cognitive control processes.

This could be achieved by measuring detection of a task-unrelated stimulus presented to one modality while increasing short term maintenance load or WM cognitive control load in a different modality. For example, detection sensitivity could be assessed while increasing memory load in the auditory domain. Conversely, it may be possible to modulate sensitivity to an auditory stimulus depending on whether WM load draws on maintenance or cognitive control process. Indeed, such experiments could involve any pairing of the five modalities.

Future research may also extend the findings of this thesis to dissociating cognitive control from other forms of sensory maintenance (e.g. for verbal material or in other sensory modalities) while taking into consideration whether the target and distractor stimuli share the same sensory representations with the content maintained in WM or may involve distinct neural correlates (e.g. Park, Kim & Chun, 2007; Kim, Kim & Chun, (2005).

6.2.3 Other Types of Detection Stimuli

It is possible that the VSTM load effects depend, at least to some extent, on the type of the visual stimulus presented. The image of a face, for example, may always be perceived irrespective of the level of VSTM load. Indeed, this is consistent with recent suggestions that faces are prioritised for processing over other objects and may even be perceived automatically (Austen & Enns, 2000; Downing, Bray, Rogers & Childs, 2004; Jenkins, Lavie & Driver, 2003; Ro, Russell & Lavie, 2001; Willis & Todorov, 2006). Other types of meaningful stimuli may also automatically be perceived: emotional pictures, words, or the participant's name, for example. Future research could investigate such claims. The experiments reported here examined detection sensitivity for task-unrelated stimuli in static displays. A further test of the effect of VSTM load on detection sensitivity could be with dynamic displays. A failure to perceive moving stimuli in dynamic displays that involved high perceptual load has already been demonstrated with the sustained inattentional blindness paradigm (e.g. Most et al., 2000, 2001, 2005; Simons & Chabris, 1999). Such experiments are, however, susceptible to confounds in terms of expectation and memory. A demonstration of reduced detection sensitivity with higher VSTM load (and perceptual load) with dynamic displays would therefore be more conclusive.

6.2.4 Effects of VSTM Load on Distraction

So far, the studies presented in this thesis establish the effects of VSTM load on the sensitivity for visual detection. However, one important contribution of Load Theory has been to the understanding of the factors that determine distraction. The theory proposes that whereas high perceptual load reduces distractor processing, high WM cognitive control load increases distractor processing. A further test of the effects of VSTM load could therefore be to investigate whether these effects generalize to effects on distractor interference.

A series of studies could address this question using various measures of distraction previously shown to be modulated by perceptual load as well as cognitive control WM load. For instance, Lavie et al. (2004) used the response competition paradigm in which a task-irrelevant, but either response-congruent or response-incongruent peripheral distractor is presented concurrently with a visual letter-search display. Despite instruction to ignore these distractors, participants' reaction times (RTs) were slower during the presence of incongruent distractors compared with congruent distractors, demonstrating that the identity of the distractor had been processed and its association with the target response acknowledged

(Eriksen & Eriksen, 1974; Flowers & Wilcox, 1982; Gathercole & Broadbent, 1987; Miller, 1987; Murphy & Eriksen, 1987). However, whereas perceptual load reduced distractor processing, Lavie et al. (2004) demonstrated that high WM cognitive control load increased distractor processing. Specifically, when participants were asked to remember a set of six digits (high working memory load condition) compared with a condition of requiring maintenance of a single digit (low working memory load condition) incongruent distractors produced a larger RT reduction and a larger decrease in accuracy rates compared to congruent distractors

In addition to examining the effects of VSTM load on response competing distractors, future research could also use the attentional capture by singletons paradigm used by Lavie and De Fockert (2005). This study demonstrated that high (vs. low) WM cognitive control load during shape-based search tasks increases attentional capture by a salient but task-irrelevant odd colour "singleton" distractor. If VSTM load indeed utilizes perceptual resources as indicated by the findings presented in this thesis, then VSTM load should reduce distractor processing similar to the effects of perceptual load but opposite to the effects of WM cognitive control load.

Alternatively, the effects of VSTM load could be compared to those of WM cognitive control load in Stroop-like effects (De Fockert et al., 2001). For example, De Fockert et al. (2001) demonstrated the effects of WM cognitive control load on response competition distractor effects of pictures of faces in a neuroimaging study. In this study, a successor naming task similar to that used in Experiments 3 and 6 in this thesis was interleaved with a name categorisation task, in which famous politicians' and pop stars' names had to be identified as such while congruent or incongruent pictures of the faces of the same celebrities were presented. In this study face distractor interference effects were greater in high (compared with low) cognitive control WM load, for both RTs and error rates, and neural activity in the fusiform gyrus and other areas of extrastriate cortex known to be associated with the processing of faces (e.g. Kanwisher, McDermott & Chun, 1997) occurring when the distractor faces were presented, was also greater under conditions of high cognitive control WM load compared with low load. Future research could thus contrast these cognitive control WM load effects on behavioural as well and neural response competition effects to those of load on maintenance processes of working memory (i.e. VSTM load).

Recently, the effects of perceptual load on distractor processing have been extended by Forster and Lavie (2008) to effects of attentional capture by entirely irrelevant stimuli. Specifically, Forster and Lavie (2008) introduced a novel laboratory measure of attentional capture by stimuli (e.g. cartoon figures) that capture attention even when they are entirely irrelevant and bear no relation to a central concurrent task (e.g. letter-search task). In situations of low perceptual load in the search task, these task-unrelated distractors capture attention and disrupt task performance. However, increasing perceptual load in the central visual letter-search task eliminated completely any task-irrelevant attentional capture. However, so far only the effects of perceptual load on these irrelevant attentional capture measures have been investigated. It would be important for future research to test predictions derived from Load Theory and contrast the effects of VSTM load with the effects of cognitive control WM load using the measures of attentional capture by irrelevant stimuli introduced by Forster and Lavie (2008).

6.2.5 VSTM Load Effects on Unconscious Processing

The research presented in this thesis establishes that conscious detection of a visual stimulus is modulated by VSTM load. Though this indicates that resources employed in VSTM are a necessary condition for conscious perception, it still remains uninformative as to whether VSTM load also reduces unconscious perception. It would therefore be interesting for future research to establish whether these VSTM load effects are restricted to conscious representations. For example, according to load theory the effects of perceptual load do not depend on conscious perception of irrelevant stimuli. Indeed, Bahrami et al. (2007) have shown that primary visual cortex activity related to an unconscious irrelevant stimulus is modulated by perceptual load. In this study participants performed a central RSVP task of either low or high perceptual load. Concurrently with the central RSVP task participants were shown irrelevant monocular peripheral stimuli that were suppressed from awareness using continuous flash suppression in the other eye. Retinotopic activity in primary visual cortex elicited by the invisible monocular stimuli was found to be modulated by the amount of perceptual load in the central RSVP task. These findings raise the interesting question regarding the effects of VSTM load on primary visual cortex response to unconscious stimuli. Such effects would in fact provide very strong evidence that sensory visual resources needed for early stages of processing that remain unconscious are indeed required for the short term maintenance of visual information.

6.3 Conclusions

This thesis established the role of VSTM load in visual detection. The research reported demonstrates the importance of considering the level and type of WM load in determining visual detection. Working memory is not unitary and a major distinction has been drawn between maintenance processes that draw on perceptual representation resources and cognitive control processes that maintain processing priorities and draw on frontal cortices. A high VSTM load task that engages perceptual representation resources impairs visual detection by directly interacting with the retinotopic V1 response to incoming visual stimuli and reducing the effective contrast of a visual stimulus. The VSTM load effects were shown to be akin to those of perceptual load but different to those WM cognitive control load, clarifying the role WM cognitive control resources in visual detection, suggesting that WM cognitive control is needed for maintaining stimulus processing priorities. These findings extend load theory to now account for competitive interactions between incoming visual information and visual representations held in VSTM. Future research should aim to generalize these findings to other VSTM load manipulations while comparing these effects within and across modalities on various other types of detection stimuli. Other promising avenues for future research include load theory's predictions that these VSTM load effects can be extended to distractor processing and to processing that remains unconscious.

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