

Visual Short-term Memory Load Reduces Retinotopic Cortex Response to Contrast

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Abstract

■ Load Theory of attention suggests that high perceptual load in a task leads to reduced sensory visual cortex response to task-unrelated stimuli resulting in “load-induced blindness” [e.g., Lavie, N. Attention, distraction and cognitive control under load. *Current Directions in Psychological Science*, 19, 143–148, 2010; Lavie, N. Distracted and confused?: Selective attention under load. *Trends in Cognitive Sciences*, 9, 75–82, 2005]. Consideration of the findings that visual STM (VSTM) involves sensory recruitment [e.g., Pasternak, T., & Greenlee, M. Working memory in primate sensory systems. *Nature Reviews Neuroscience*, 6, 97–107, 2005] within Load Theory led us to a new hypothesis regarding the effects of VSTM load on visual processing. If VSTM load draws on sensory visual capacity, then similar to perceptual load, high VSTM load should also reduce visual cortex response to incoming stimuli leading to a failure to detect them. We tested this hypothe-

sis with fMRI and behavioral measures of visual detection sensitivity. Participants detected the presence of a contrast increment during the maintenance delay in a VSTM task requiring maintenance of color and position. Increased VSTM load (manipulated by increased set size) led to reduced retinotopic visual cortex (V1–V3) responses to contrast as well as reduced detection sensitivity, as we predicted. Additional visual detection experiments established a clear tradeoff between the amount of information maintained in VSTM and detection sensitivity, while ruling out alternative accounts for the effects of VSTM load in terms of differential spatial allocation strategies or task difficulty. These findings extend Load Theory to demonstrate a new form of competitive interactions between early visual cortex processing and visual representations held in memory under load and provide a novel line of support for the sensory recruitment hypothesis of VSTM. ■

INTRODUCTION

Sensory visual processing has been shown to depend on the level and type of information load involved. Much previous work concerned specifically the effects of loading perceptual processing and the effects of loading working memory cognitive control processes. However, the effects of visual STM (VSTM) load on sensory visual processing have not yet been addressed. This was the purpose of this study.

The effects on sensory processing of the different types of load have been extensively studied within the framework of Load Theory (e.g., Lavie, Hirst, De Fockert, & Viding, 2004; Lavie, 1995). Load Theory suggests that competition for capacity-limited resources results in either reduced or increased sensory cortex responses to unattended stimuli depending on the type of load involved in the attended task. Tasks that involve high perceptual load (e.g., those involving search for a target stimulus among many stimuli that are highly similar to that target; Lavie, 2005, 2010, for reviews) result in reduced sensory response to unattended items, because sensory processing capacity is consumed in the perception of the attended stimuli. These effects are

found throughout visual cortex, as early as primary visual cortex (e.g., Schwartz et al., 2005; O’Connor, Fukui, Pinsk, & Kastner, 2002) and are associated with failures to detect the very presence of competing stimuli during tasks of high perceptual load: the phenomenon of “load induced blindness” (e.g., Macdonald & Lavie, 2008). In contrast, tasks that load working memory cognitive control processes (e.g., those requiring to maintain a random digit sequence) result in increased processing of unattended stimuli because of the reduced capacity to control task processing in line with the current attentional priorities (Lavie et al., 2004; De Fockert, Rees, Frith, & Lavie, 2001).

Working memory, however, is a complex system, and much recent research on VSTM emphasizes the demands on sensory representation resources involved in visual maintenance. Indeed, according to the sensory recruitment hypothesis of VSTM (e.g., Ester, Serences, & Awh, 2009; Serences, Ester, Vogel, & Awh, 2009; Postle, 2006), maintenance of visual information in memory involves the same sensory brain areas as those involved in perceptual encoding (e.g., Postle, 2006; Pasternak & Greenlee, 2005, for reviews). Here we relate Load Theory to the sensory recruitment hypothesis of VSTM to address the consequences of VSTM load for sensory perception.

Consideration of the sensory recruitment hypothesis within the framework of Load Theory leads to a novel

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hypothesis concerning the effects of VSTM load on the sensory processing of incoming visual stimuli: Loading VSTM would impose a larger demand on the sensory visual cortices involved in memory maintenance; because these same visual cortices are also involved in perception, their higher engagement in memory maintenance should reduce their capacity for sensory processing that is required for visual perception. This hypothesis thus leads to the prediction that the impact of VSTM load on perception should be similar to that of perceptual load: Increased VSTM load should reduce sensory visual cortical responses to visual stimuli presented during the maintenance delay, resulting in failure to detect them.

To test this prediction, we presented a contrast detection task during the delay of a VSTM task. Participants were required to memorize the color and location of a memory sample of either one (low load) or six colored squares (high load) and indicate whether a memory probe presented at the end of the trial was a match on these features. Four gratings were presented during the memory delay, and on half of the trials, one of them was presented with a higher contrast. Participants were asked to detect this contrast increment and make present/absent responses. We report a series of experiments that assessed the effects of VSTM load on contrast detection using this method.

To determine whether the effect of VSTM load could be found as early as in the visual cortex responses related to contrast detection we used fMRI in the first experiment and assessed BOLD responses in the areas of the occipital cortex retinotopically specific to the peripheral location of the gratings (Figure 1A). In this experiment and in closely related psychophysical experiments, we also used signal

detection analysis to assess visual detection sensitivity for the contrast increment during the delay. Our measures of detection sensitivity allowed us to further establish our load hypothesis. In the signal detection experiments (Experiments 2–4), we have directly related the effects on detection to the extent to which VSTM capacity is loaded, compared the effects of loading VSTM and loading working memory cognitive control processes, and ruled out alternative accounts in terms of task difficulty and spatial allocation strategies.

EXPERIMENT 1

Method

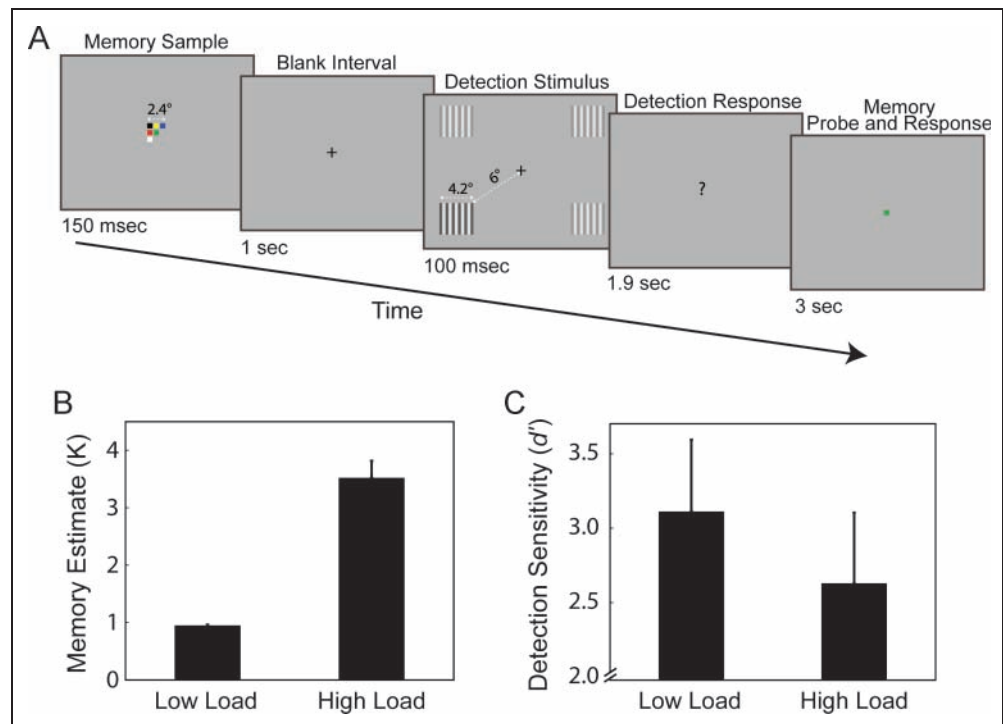
Participants

Eight healthy volunteers took part in Experiment 1 (age range = 20–30 years; $M = 23.88$ years, $SEM = 1.22$ years; four women). All participants in this experiment as well as in the following experiments were recruited from the University College London subject pool, were naive to the purpose of the experiment, provided informed consent, were compensated for their participation, and had normal color vision and normal visual acuity. The experiment was approved by the local ethics committee.

Stimuli and Procedure

The experiment was controlled using Cogent toolbox (www.vislab.ucl.ac.uk/cogent.php) for MATLAB (Mathworks, Inc., Natick, MA). Stimuli were projected onto a screen mounted at the back of the scanner bore through an

Figure 1. Experiment 1: Stimulus sequence and behavioral results. (A) Participants viewed one (low load) or six (high load; shown here) colored squares. Following a blank period, a contrast increment (the detection target) appeared in one of the four gratings. Participants were asked to detect it and make present/absent responses. A memory probe then appeared, and participants were asked to respond whether its color was the same as that of a square that was in the same location in the memory sample. Behavioral performance averaged across subjects on the memory task (B) and detection task (C) as a function of VSTM load. Error bars represent $\pm 1 SEM$.



LCD projector (display resolution: 800×600). Participants viewed the stimuli through a mirror mounted on the head coil. Figure 1A depicts the stimuli and the sequence of events. A uniform light gray background ($\sim 70 \text{ Cd/m}^2$) was used throughout the experiment. Each trial began with a fixation cross display presented for 1000 msec and following a 500-msec blank interval, the VSTM sample was presented for 150 msec. The memory sample contained one or six different colored squares subtending 0.6° , randomly chosen on each trial from a sample of nine clearly distinguishable colors (red, green, blue, yellow, cyan, magenta, black, white, and dark gray) and randomly placed among nine possible locations in a 3×3 matrix ($2.4^\circ \times 2.4^\circ$).

Following a 1000-msec blank interval, four achromatic vertical square wave gratings ($4.2^\circ \times 4.2^\circ$; spatial frequency of 2.5 cycles per degree, contrast: 10%) were presented for 100 msec 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 within and across each run. The target contrast increment was individually assessed for each participant using a staircase procedure before the experiment ($M = 10\%$, $SEM = 1\%$), with an accelerated stochastic approximation method (Kesten, 1958) for obtaining target-contrast estimate of approximately 75% hit rate. Following the 100-msec presentation of the detection stimuli, a “?” appeared at fixation for 1900 msec, thus providing the participants with a 2000-msec response window from the onset of the detection stimuli. Participants made a right hand “present” (index finger) or “absent” (middle finger) button press response. After the response window for the detection task, the memory probe (one colored square) appeared for up to 3000 msec at one of the positions occupied in the memory sample. Participants indicated whether the color of the memory probe matched the color of the memory sample 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 sample. 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 sample or the remaining color sample. None of the responses were speeded, and no feedback was given in any of the tasks. Trials were separated by a variable intertrial interval of 10.8–11.3 sec.

Each run consisted of 8-trial blocks within each 64-trial run in the order of an ABBABAAB design that was counterbalanced across participants. Each participant completed four or five runs (325 volumes per run) and each load condition appeared four times within each 64-trial run. Before the experiment, each participant completed a short (32 trials) practice of the behavioral task outside the scanner. While in the scanner, participants performed the staircase threshold procedure for determining the target contrast as described above.

In a second session, we acquired two runs of retinotopic mapping and two runs of functional stimulus localizer (160 volumes each; 353 sec) 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 (e.g., Wandell, Chial, & Backus, 2000; Sereno et al., 1995). Each run consisted of five repetitions of each meridian (duration = 10 volumes, 22 sec) separated by six volumes (13 sec) of rest. During the functional localizer scans, participants viewed flashing black and white disks (same diameter as the pedestal gratings) at a frequency of 10 Hz presented at the same area as the pedestal gratings, while maintaining fixation. Each stimulus localizer run consisted of five repetitions of the disks presented alternately along the 45° or the 135° diagonal (Figure 2B; duration = 10 volumes, 22 sec) followed by six volumes (13 sec) of rest.

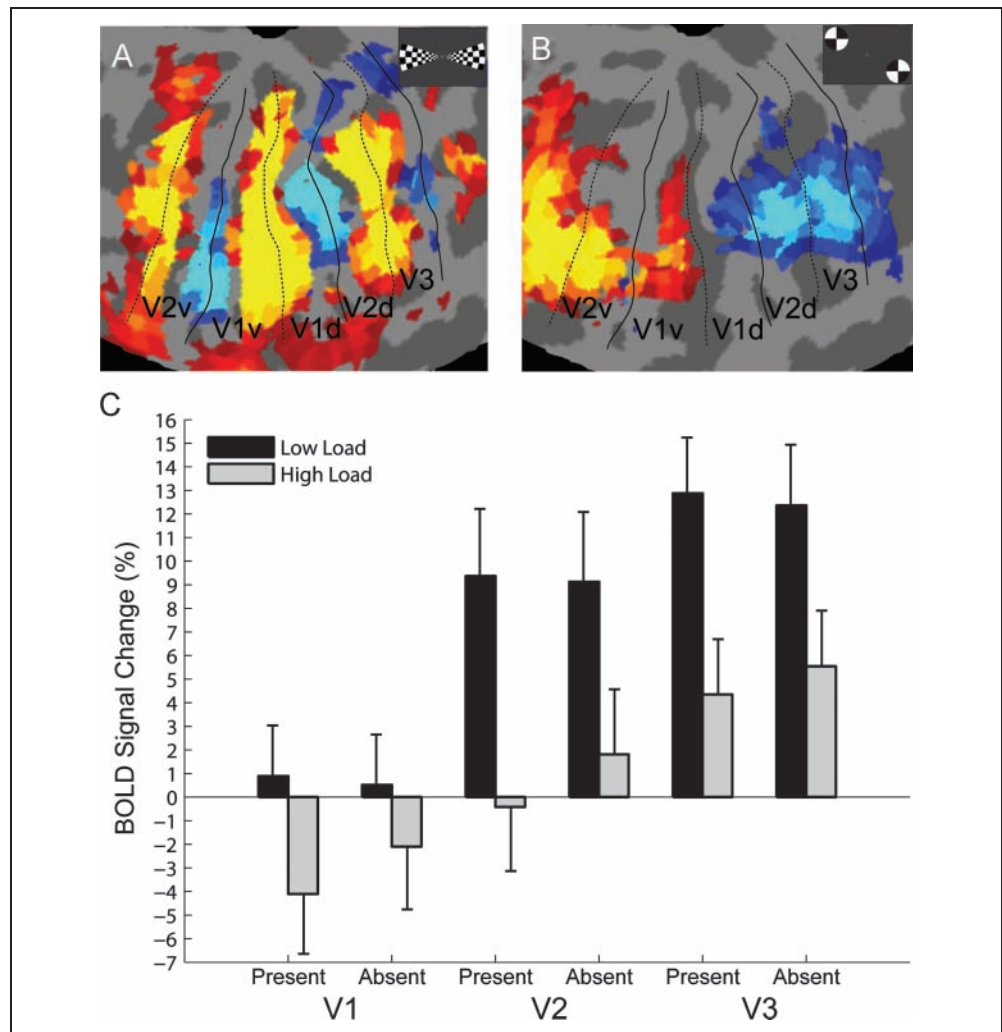
fMRI Data Acquisition and Analysis

Imaging data were collected at the Wellcome Trust Centre for Neuroimaging (London, UK) using a 3T Allegra Siemens MRI scanner. We used gradient-echo echoplanar T2*-weighted imaging (echo time = 65 msec; repetition time = 2210 msec; 34 axial slices; voxel size = 3 mm isotropic) to acquire BOLD contrast functional images covering the cortex. A T1-weighted MPRAGE structural image volume was also acquired for each participant (176 sagittal slices of 1 mm thickness, no gap; matrix size = 256×240 ; field of view = 256×240 mm; in-plane resolution = 1×1 mm; echo time = 2.4 msec; acquisition time per slice = 7.92 msec).

Data were analyzed using SPM8 (www.fil.ion.ucl.ac.uk/spm). We discarded the first five volumes of each run 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 8 mm FWHM, and spatially normalized (only for the whole-brain analysis). A high-pass filter (cutoff, 128 sec) was applied to the data for removing low-frequency signal drifts.

Each participant’s early visual cortex (V1, V2, V3) was defined using data from the retinotopic mapping scans (Figure 2A) using conventional retinotopic mapping methods (Wandell et al., 2000; Sereno et al., 1995). Data from the localizer scans were used to define ROIs within the retinotopic regions defined for each participant’s V1, V2, and V3 that responded most strongly to the gratings (Figure 2B). 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 (surfer.nmr.mgh.harvard.edu/). These surface-based

Figure 2. Retinotopic mapping and imaging data for V1, V2, and V3 ROIs. Retinotopic meridian mapping stimulus example (top right) and data (A) and functional localizer stimulus example (top right) and data (B) from a representative participant overlaid on an inflated surface of the right occipital pole. (C) Mean BOLD responses in V1, V2, and V3 ROIs as a function of target-stimulus presence (present, absent) and VSTM load (low, high). Error bars represent ± 1 SEM.



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. In the statistical analyses, the mean BOLD signal for the target present conditions was calculated across the ROIs that contained a contrast increment target (from the target present trials, 50% of all trials), whereas for the target absent conditions the mean BOLD signal was calculated across the four ROIs with no target (from the target absent trials: the other 50% of trials).

The design matrix also included separate regressors in each load condition for the following parts of each trial: memory sample, memory probe, memory probe response, and detection response. Motion parameters were also included in the model to capture any motion-related artifacts. Each of these events was modeled using a finite impulse response approach and was convolved with a canonical hemodynamic response function.

For the whole-brain analysis, the general linear model employed a separate regressor for each of the two load conditions (low/high VSTM load) with duration of 6.15 sec capturing the whole trial period as well as the motion parameters. 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 voxel-wise threshold of $p < .001$ (uncorrected), and whole-brain false discovery rate correction using cluster extent, $p < .05$ (FWHM = 11.7 mm \times 11.9 mm \times 12.4 mm, resels = 794.13).

Results and Discussion

Behavioral Results

In all experiments, analyses of the detection task performance were made on trials with a correct response on the memory task.

Mean VSTM task accuracy rate was significantly reduced from the low ($M = 97\%$, $SEM = 1\%$) to the high VSTM load condition ($M = 73\%$, $SEM = 3\%$), $t(7) = 7.41$, $p < .001$, $d = 1.76$ (two tailed, as in all the rest of the results except when otherwise reported). VSTM estimates (Cowan's $K = N \times [\text{Hit rate} - \text{False alarm rate}]$, where K is the memory estimate and N is the number of items presented in the memory sample; Cowan et al., 2005) increased significantly with higher VSTM load (low load: $K = .95$, $SEM = .01$; high load: $K = 3.52$, $SEM = 0.30$), $t(7) = 8.52$, $p < .001$, $d = 1.78$ (Figure 1B), confirming that our behavioral manipulation was effective and the high load condition occupied more VSTM capacity than the low load condition.

Importantly, contrast increment detection sensitivity (d') was significantly reduced under the high ($d' = 2.63$, $SEM = 0.48$) compared with the low ($d' = 3.11$, $SEM = 0.48$) VSTM load condition, $t(7) = 4.13$, $p = .004$, $d = .36$ (Figure 1C). There was no effect of VSTM load on response bias ($\beta = \exp \{[\text{norminv}(\text{False alarm rate})^2 - \text{norminv}(\text{Hit rate})^2]/2\}$, where norminv is the inverse of the normal cumulative distribution function; Macmillan & Creelman, 2005; low load: $M = 1.49$, $SEM = 4.27$; high load: $M = -.46$, $SEM = 6.04$, $t < 1$). These findings demonstrate that "load induced blindness" results from depletion of perceptual representation resources not just in tasks of high perceptual load (Macdonald & Lavie, 2008) but also in tasks of high VSTM load.

Imaging Results

Trials with an incorrect response on the VSTM task were excluded from the imaging analyses. A whole-brain contrast of activity in the high versus low VSTM load conditions revealed that similar parietal areas (e.g., intraparietal sulcus, MNI coordinates (x, y, z): right/left, $+24/-21, -61/-67, +52/+58$; see Table 1) as those previously implicated in VSTM maintenance (e.g., Mitchell & Cusack, 2008; Todd & Marois, 2004; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002) also showed significantly greater activity in the high compared with the low VSTM load condition in our task. This finding confirms the validity of our VSTM load manipulation within our modified VSTM and detection task.

Repeated-measures ANOVAs were conducted on the V1–V3 BOLD signal in the retinotopic stimulus locations during the memory delay as a function of Load (low, high) and Target Presence (present, absent). These analyses revealed a main effect of Load (V1, $F(1, 7) = 8.65$, $p = .02$, $\eta^2 = .55$; V2, $F(1, 7) = 8.93$, $p = .02$, $\eta^2 = .56$; V3, $F(1, 7) = 6.36$, $p = .04$, $\eta^2 = .48$), indicating that high (vs. low) VSTM load suppressed the retinotopic V1, V2, and V3 responses during the memory delay (Figure 2C). These suppressions were found both in the target present (V1, $t(7) = 3.49$, $p = .010$, $d = .38$; V2, $t(7) = 2.85$, $p = .025$, $d = .61$; V3, $t(7) = 2.60$, $p = .035$, $d = .63$) and target absent trials (V1, $t(7) = 1.97$, $p = .045$, $d = .20$ (one tailed); V2, $t(7) = 3.05$, $p = .018$, $d = .46$; V3, $t(7) = 2.37$, $p = .049$, $d = .49$). There was no main effect of Target Presence (V1, $F(1, 7) =$

Table 1. 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.

1.91 , $p = .21$, $\eta^2 = .21$; V2, $F(1, 7) = 3.62$, $p = .10$, $\eta^2 = .34$; V3, $F < 1$). In addition, the V1 ANOVA revealed a significant interaction (Load \times Target Presence, $F(1, 7) = 6.21$, $p = .04$, $\eta^2 = .47$) reflecting a larger effect of suppression by high (vs. low) load when the target was present than when the target was absent. Areas V2 and V3 showed similar trends for an interaction, but these were not statistically significant (V2, $F(1, 7) = 2.59$, $p = .15$, $\eta^2 = .27$; V3, $F(1, 7) = 2.85$, $p = .13$, $\eta^2 = .29$). This interaction suggests that the effect of load was larger for the target present than the target absent condition as expected from our hypothesis that VSTM load will reduce the ability to perceive an incoming sensory stimulus.

The same 2×2 (Load \times Target Presence) ANOVAs were also run on the V1–V3 data after exclusion of trials with incorrect detection responses (as well as the incorrect VSTM responses as before). The results of these analyses replicated the main effect of Load (V1, $F(1, 7) = 15.44$, $p = .006$, $\eta^2 = .69$; V2, $F(1, 7) = 16.73$, $p = .005$, $\eta^2 = .71$; V3, $F(1, 7) = 5.50$, $p = .03$ (one-tailed), $\eta^2 = .52$). There was now also a main effect of Target Presence in V1, $F(1, 7) = 6.91$, $p = .03$, $\eta^2 = .50$, and in V2, $F(1, 7) = 9.21$, $p = .02$, $\eta^2 = .57$, as well as a nonsignificant trend for this effect in V3, $F(1, 7) = 3.30$, $p = .13$, $\eta^2 = .40$. The effect of Target Presence is likely to have surfaced in these analyses because it was no longer diluted by trials in which the target presence was not detected. There was no interaction between Load and Target Presence in this analysis (all areas' F s < 1). This suggests that the interaction in the form of larger load effect for target present (vs. absent) trials that was previously

found for the data including the undetected targets is likely to be because of a greater suppression by load leading to missed detections of the target presence.

These effects of Load were only found during the maintenance period. During the presentation of the VSTM sample, there was no effect of VSTM load on activity in the peripheral target locations in either V1 (low load: percent signal change $M = -4.62$, $SEM = 2.87$; high load: $M = -3.77$, $SEM = 2.76$; $t(7) = .37$, $p = .72$, $d = .11$), V2 (low load: $M = -5.36$, $SEM = 2.98$; high load: $M = -4.11$, $SEM = 2.62$; $t(7) = .65$, $p = .54$, $d = .17$), or V3 (low load: $M = -7.12$, $SEM = 2.78$; high load: $M = -0.60$, $SEM = 2.08$; $t(7) = 1.96$, $p = .09$, $d = .87$). The specificity of the VSTM load effects to the maintenance period only suggests that they reflect competition for shared representational resources between the visual detection stimuli and visual representations held in VSTM under load, in line with our hypothesis.

Overall, the results confirmed our prediction that high VSTM load would reduce perception and the correlated visual sensory cortex response to incoming stimuli during memory maintenance. The finding that VSTM load affected retinotopic responses to contrast, resulting in true reduction in detection sensitivity, is strongly supportive of our hypothesis that VSTM load affects visual processing in a similar manner to perceptual load.

EXPERIMENT 2

In Experiment 2, we considered an alternative account for the results in terms of a purely spatial suppression effect. Previous studies showed that shifting focused attention to some parts of the visual field (e.g., the periphery or the fovea) leads to suppression in the unattended parts of the visual field (Smith, Singh, & Greenlee, 2000; Tootell et al., 1998).

Is it possible to attribute the suppression effects we observed to the high (vs. low) VSTM load in Experiment 1 involving more spatial attention shifts or greater spatial attention attraction to the location of the memory sample items at the fovea, thus leading to suppression of the periphery? The lack of suppression effect during the memory sample presentation period (where attention had to be allocated to the memory sample items during encoding) argues against this account. In addition, the suppression of activity at retinotopic representations of the peripheral detection locations during the maintenance period is unlikely to be because of spatial attention shifts, because any such spatial shifts are likely to be in the form of shifts from the location of the memory sample stimuli in the fovea to the locations of the detection stimuli in the periphery. Such stimulus-induced shifts should thus result in suppression of the foveal retinotopic representations, not the peripheral retinotopic representations that we observed.

Nevertheless, we attempted to replicate the effects in a design that ruled out any alternative account in terms of

spatial suppression. In Experiment 2, we presented both the visual detection and VSTM stimuli in the same locations. If the effects of VSTM load were in any way due to spatial shifts of attention to the locations of the memory stimuli under higher load, then this design should either eliminate any suppression effects or indeed even reverse the effect (i.e., greater visual detection sensitivity within the memory stimulus locations with higher VSTM load). If, however, the effects were due to load on shared representation resources, then the findings of Experiment 1 should be replicated even when there was no longer any spatial separation between the memory and detection stimuli.

Method

Participants

Thirteen new healthy volunteers gave informed consent to participate in Experiment 2. The age range was 19–35 years ($M = 24.31$ years, $SEM = 1.26$ years), 11 were women, and the experiment was approved by the local ethics committee. The experiment (and all the remaining experiments reported in this article) was performed in a dimly lit room on a PC attached to a 19-in. CRT monitor (resolution = 800×600 ; refresh rate = 60 Hz; mean background luminance = ~ 70 Cd/m²). A viewing distance of 60 cm was maintained with a chin rest.

Stimuli and Procedure

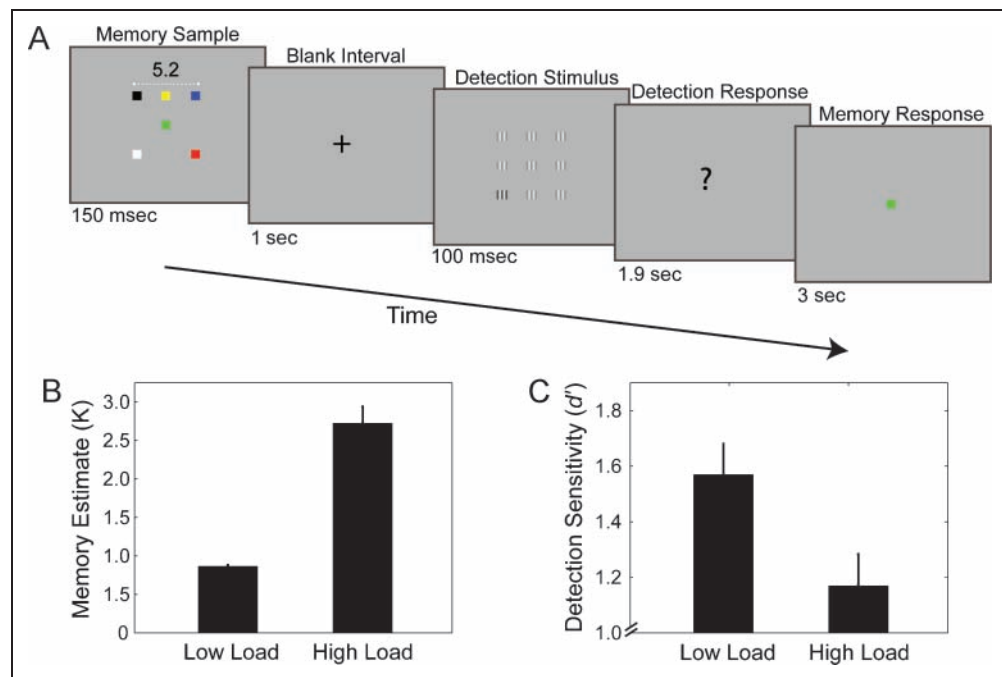
The stimuli and procedure were identical to Experiment 1 except for the following changes: (a) The four peripheral gratings (one in each quadrant of the screen) of Experiment 1 were now replaced by nine achromatic vertical square wave gratings (10 cycles per degree; contrast: 10%) of the same size as the VSTM sample stimuli (0.6°) and presented after a 1-sec blank interval in each of the nine possible locations of the memory sample (Figure 3A). 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 sample and the detection gratings were presented in a 3×3 matrix that now subtended 5.2° (instead of 2.4° in Experiment 1) with nearest contours 1.7° .

Participants completed a total of 256 trials in eight blocks of 32 trials each, with VSTM load counterbalanced in the order of ABBABAAB. Before 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 1 ($M = 9\%$, $SEM = 1\%$).

Results and Discussion

Mean accuracy rates in the VSTM task were significantly reduced from the low ($M = 93\%$, $SEM = 1\%$) to the high VSTM load condition ($M = 73\%$, $SEM = 4\%$; $t(12) = 6.27$, $p < .001$, $d = 1.44$). VSTM estimates (K) increased

Figure 3. Experiment 2: Stimulus sequence and behavioral results. (A) An example (high VSTM load) trial sequence and timing. The detection task consisted of nine gratings presented in the same spatial locations as the memory sample items. The contrast-increment target was presented on 50% of the trials in one of the nine gratings (here present at bottom left corner of the “detection stimulus” display). Behavioral performance averaged across participants on the memory task (B) and detection task (C) as a function of VSTM load. Error bars represent ± 1 SEM.



significantly from the low ($K = 0.87$, $SEM = 0.03$) to the high VSTM load condition ($K = 2.72$, $SEM = 0.43$; $t(12) = 4.39$, $p < .001$, $d = 1.29$; Figure 3B). These findings confirm the effectiveness of the VSTM load manipulation.

Importantly, although the detection stimuli were now presented in the same locations as the memory sample items, detection sensitivity was significantly reduced from the low ($d' = 1.57$, $SEM = 0.22$) to the high ($d' = 1.17$, $SEM = 0.23$) VSTM load condition, $t(12) = 2.64$, $p = .021$, $d = .49$ (Figure 3C). No effects of VSTM Load on response bias (β) were found (low load: $M = 1.86$, $SEM = .57$; high load: $M = 1.57$, $SEM = .52$, $t < 1$). These findings strengthen our claim that the effects of VSTM load were specifically due to increased demands on representational capacity, rather than to differences in the spatial allocation of attention.

EXPERIMENT 3

In Experiment 3, we considered an alternative account for our results that attributes the detection suppression effects to a general increase in the task difficulty with higher VSTM load rather than to a specific increase in the demands on visual representation capacity.

To address this account, we sought another manipulation of load that would increase task difficulty without increasing the demands on visual representation capacity. Load Theory suggests that loading working memory cognitive control processes, using a verbal memory task, will not draw on visual representation resources and thus should not lead to any visual suppression effect (e.g., Macdonald & Lavie, 2008, Experiment 6). In fact, with increased demand on cognitive control resources, distractor perception increases under high cognitive load because of

reduced capacity to control distractor processing (see, e.g., Lavie, 2005; Lavie et al., 2004; De Fockert et al., 2001).

We, therefore, reasoned that increased WM cognitive control load in our visual detection task would increase task difficulty but will not load visual representation capacity and hence will not affect visual perception. To test this hypothesis, in Experiment 3 we contrasted the effects of VSTM load and WM cognitive control load on visual detection sensitivity. In the WM cognitive control load condition, we used the same paradigm as that used in Experiment 1 but replaced the VSTM task with a WM “successor naming” task requiring order-recall for digits (e.g., De Fockert et al., 2001). The successor naming task engages WM cognitive control (e.g., Marshuetz, 2005; D’Esposito, Postle, Ballard, & Lease, 1999) while relying on verbal rather than on visual maintenance (Conrad, 1964).

Method

Participants

Thirty-one healthy volunteers gave informed consent to take part in Experiment 3 (age range = 19–37 years; $M = 25.29$ years, $SEM = 0.93$ years; 16 women), which was approved by the local ethics committee. Fifteen of those volunteers participated in the VSTM load condition (age range = 19–36 years; $M = 24.13$ years, $SEM = 1.18$ years; 10 women), and the remaining 16 participated in the WM cognitive control load condition (age range = 20–37 years; $M = 26.44$ years, $SEM = 1.45$ years; 6 women).

Stimuli and Procedure

The stimuli and procedure of the VSTM load condition were identical to those of Experiment 1. The WM cognitive

control load condition was identical to the VSTM load condition, except that the VSTM task was now replaced by a WM successor-naming task that required participants to indicate which digit followed the memory probe digit in the memory sample. The memory sample consisted of nine black digits (1–9, each subtending 0.7° by 0.5°) presented in a row, in fixed numerical order for 500 msec (low load condition) or in random order for 2000 msec (high load condition), with the constraint that no more than two digits were presented in sequential order. 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 sample) was presented at fixation until a response was made (or 4 sec elapsed).

Participants completed 256 trials in eight blocks of 32 trials each. The condition of load was blocked in counter-balanced order (ABBABAAB). Before the experiment participants completed 32 practice trials and the staircase threshold procedure for determining the target contrast as described in Experiment 1 ($M = 9\%$, $SEM = 0.4\%$).

Results and Discussion

VSTM task accuracy decreased significantly from the low ($M = 94\%$, $SEM = 1\%$) to the high VSTM load condition ($M = 61\%$, $SEM = 2\%$), $t(14) = 16.06$, $p < .001$, $d = 1.87$. The memory estimates (K) were significantly increased from the low ($K = 0.88$, $SEM = 0.02$) to the high VSTM load condition ($K = 1.36$, $SEM = 0.20$), $t(14) = 2.41$, $p = .03$, $d = 0.82$, indicating that VSTM load was manipulated effectively. WM task accuracy also decreased significantly from the low ($M = 97\%$, $SEM = 1\%$) to the high ($M = 56\%$, $SEM = 4\%$) WM load condition, $t(15) = 10.92$, $p < .001$, $d = 1.77$, indicating that WM cognitive control load was also manipulated effectively. A mixed ANOVA comparison with Type of Load (VSTM, WM cognitive control) as the between-subject factor and Level of Load (low, high) as the within-subject factor on the accuracy rates of the two memory tasks has confirmed that the two tasks were of equivalent difficulty, $F(1, 29) = 3.62$, $p = .067$, $\eta^2 = .11$. Notice that the nonsignificant numerical trend was in the direction of a stronger load effect on accuracy in the successor-naming WM task (mean load effect = 41%) compared with the VSTM task (mean load effect = 33%).

A mixed ANOVA on detection sensitivity scores with the between-subject factor of Load Type (VSTM load, WM cognitive control load) and the within-subject factor of Level of Load (low, high) revealed a significant interaction, $F(1, 29) = 4.69$, $p = .039$, $\eta^2 = .14$. As shown in Figure 4, this interaction reflects the different effects of each load type on detection: whereas VSTM load reduced detection sensitivity, $t(14) = 4.74$, $p = .003$, $d = 0.65$, high WM cognitive control load had no effect on visual detection, $t(15) = 0.64$, $p = .53$, $d = 0.17$. A similar ANOVA on response bias (β) did not reveal significant effects of Load Type, Load Level, or an interaction (VSTM: low load = 1.07, $SEM = .20$; high load = 1.11, $SEM = .27$; WM cognitive

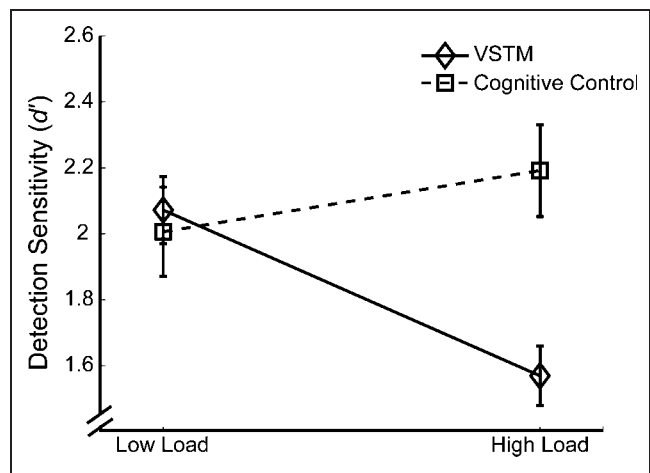


Figure 4. Detection sensitivity scores in Experiment 3 depicting the interaction between the level of load (low load, high load) and the type of load (VSTM load, cognitive control load). Error bars represent $\pm 1 SEM$.

control: low load = 1.12, $SEM = .14$; high load = 1.60, $SEM = .29$; all $F < 1$).

Thus, visual detection sensitivity was only reduced by increased VSTM load. In contrast, manipulation of WM load that led to an equivalent increase in task difficulty but draws on frontal cortices involved in cognitive control (e.g., De Fockert et al., 2001) had no effect on visual detection sensitivity. This confirms the specificity of the VSTM load effect to the demand on visual cortex representation resources during maintenance.

EXPERIMENT 4

In Experiment 4, we tested our shared resources hypothesis further by examining whether there is a tradeoff between visual detection sensitivity and VSTM capacity. Our hypothesis that both VSTM and visual perception rely on common sensory resources with limited capacity suggests that visual perception can only utilize resources that are not currently occupied in the short-term maintenance of visual information. Thus, our hypothesis leads to the prediction of a trade-off between visual detection sensitivity and the amount of information maintained in VSTM. To test this prediction, we used our combined VSTM and detection task but now varied VSTM load parametrically, gradually increasing the memory set size from one through to six. We predicted that detection sensitivity would be negatively correlated with the amount of information maintained in VSTM (estimated by Cowan's K).

Method

Participants

Twenty-two new healthy paid volunteers (14 women, $M = 23.45$ years, $SEM = 1.67$ years, age range = 19–34 years) gave informed consent to participate in Experiment 4, which was approved by the local ethics committee.

Stimuli and Procedure

The task stimuli and trial procedure were identical to Experiment 1 except that VSTM set sizes of one, two, three, four, five, or six items were now used. Following one practice block of 32 trials, each participant completed 128 trials for each set size, for a total of 768 trials.

Before the experiment, participants completed the staircase threshold procedure for determining the target contrast as described in Experiment 1 ($M = 9\%$, $SEM = 1\%$). Twelve participants completed the experiment in four experimental blocks of 192 trials each, where set size was randomly intermixed between one and six items (three of those participants completed the experiment in two separate sessions). Initial inspection of the data indicated lower memory task performance in this group compared with that of the previous experiments. For example, K in the set size 1 condition ($M = 0.71$, $SEM = 0.09$) and set size 6 condition ($K = 0.77$, $SEM = 0.27$) was lower in this group

compared with those in Experiment 3 (set size 1 $K = 0.88$, $SEM = 0.02$, $t(25) = 2.01$, $p = .05$, $d = 0.74$, for the between-group difference; set size 6 $K = 1.36$, $SEM = 0.20$, $t(25) = 1.82$, $p = .04$, $d = 0.68$ [one-tailed] for the between-group difference).

To address the lower performance in this group, we added 10 participants who performed the experiment under more equivalent conditions to those of the previous experiments. The set size levels were blocked (rather than intermixed within a block) for these participants, and they were run in two sessions of six 64-trial blocks each. The mean target contrast threshold was 10% ($SEM = 1\%$) in this group. Memory performance in the new group was no longer different to that in the previous experiments. For example their K in set size 1 ($M = 0.82$, $SEM = 0.08$) and in set size 6 ($M = 1.42$, $SEM = 0.20$) was no different to that for set size 1 ($t(23) = 0.86$, $p = .40$, $d = 0.35$) and set size 6 ($t(23) = 0.20$, $p = .84$, $d = 0.08$) in Experiment 3. As the function relating d' to K remained the same between the two groups, we report the function pooled across both groups.

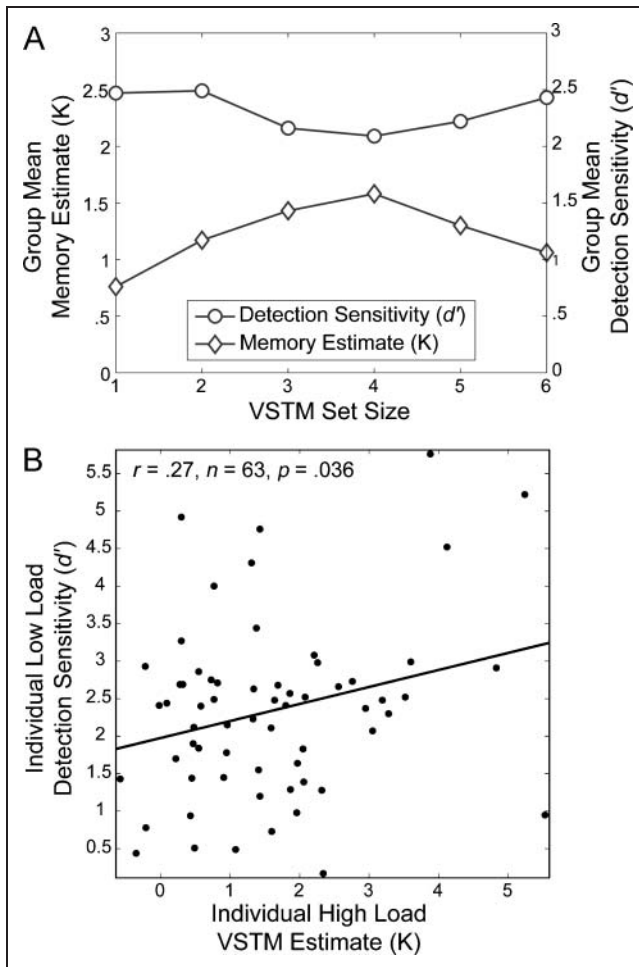


Figure 5. Relating VSTM capacity estimates with detection sensitivity. (A) Mean memory estimates (K) and mean detection sensitivity scores (d') as a function of memory set size in Experiment 4. (B) Scatter plot depicting the correlation between individual estimates of VSTM capacity (K ; x axis) and individual estimates of detection sensitivity (d' ; y axis) from the individual differences analysis. The line represents the least square linear fit.

Results

Mean VSTM task accuracy was reduced as VSTM load was increased (set size: one, $M = 82\%$, $SEM = 4\%$; two, $M = 70\%$, $SEM = 3\%$; three, $M = 65\%$, $SEM = 3\%$; four, $M = 61\%$, $SEM = 3\%$; five, $M = 58\%$, $SEM = 2\%$; six, $M = 54\%$, $SEM = 2\%$), $F(5, 105) = 50.71$, $p < .001$, $\eta^2 = 0.71$, and memory estimates (Cowan's K) were significantly increased with load, $F(1, 21) = 4.81$, $p = .04$, $\eta^2 = 0.19$ (see Figure 5A).

Importantly, a strong negative correlation between the effect of set size on VSTM capacity estimate (K) and on detection sensitivity was found (d' ; $r = -.87$, $n = 6$, $p = .02$). As can be seen in Figure 5A, detection sensitivity set size function reversely mirrored the capacity set size function. As in all the previous experiments, no effects of VSTM load on response bias (β) were found (set size: one, $M = .93$, $SEM = .22$; two, $M = 1.23$, $SEM = .49$; three, $M = 1.01$, $SEM = .23$; four, $M = 1.00$, $SEM = .21$; five, $M = .91$, $SEM = .20$; six, $M = .92$, $SEM = .23$; $F < 1$).

Individual Differences Analysis: Correlating Individual VSTM Capacity and Detection Sensitivity

Our shared resources hypothesis suggests that an individual's VSTM capacity should be positively correlated with their visual detection sensitivity because they both depend on common visual representation resources. To test this, we analyzed data from 63 participants pooled together from four experiments with comparable methods: Experiments 1, 3, and 4 of this study and Konstantinou (2011, Experiment 7 that replicated the same effect of VSTM load on detection using Experiment 1's method with an added articulatory suppression demand, where participants repeated two digits throughout task performance, and a longer retention interval of 4 sec). Individual d' scores at the memory set size 1 condition were used as a load-free estimate of

detection ability and individual K scores at the memory set size 6 condition were used to assess VSTM capacity (because this condition loaded capacity). Pearson product-moment correlation analysis of these scores revealed a significant positive correlation between VSTM capacity estimates and detection sensitivity (see Figure 5B) in support of our shared visual presentation resources hypothesis.

DISCUSSION

The present results demonstrate that visual detection and the mediating retinotopic signals in early visual cortical areas V1–V3 critically depend on the extent to which VSTM is loaded. High VSTM load led to both reduced retinotopic V1–V3 response to visual contrast increment and reduced detection sensitivity during the maintenance delay. The effects of VSTM load on visual detection were generalized across tasks with (Experiment 2) or without a spatial overlap (Experiments 1, 3, and 4) between the VSTM and detection task stimuli and thus could not be accounted for in terms of different spatial attention allocation strategies. Loading VSTM was shown to specifically reduce detection sensitivity with no effects on response bias. Moreover, the effect of load was shown to be specific to a memory load manipulation that drew on visual maintenance rather than on cognitive control (Experiment 3). Thus, the effect of VSTM load could not be accounted for in terms of a general increase in the task difficulty. Instead, the findings suggest that it is the specific demand placed on visual representation capacity under conditions of high VSTM load that leads to reduced sensory visual processing. Further support for this conclusion also comes from our findings that there was a clear tradeoff between detection sensitivity and the extent to which VSTM capacity was filled with more information (Experiment 4) and that individual estimates of VSTM capacity positively correlated with visual detection ability. Both of these findings suggest shared resources between VSTM and visual perception as we hypothesized.

Overall, the present findings provide strong support for our hypothesis that sensory recruitment during VSTM maintenance results in an effect of VSTM load on elemental visual processing akin to the effect of perceptual load (e.g., Lavie, 2005; Schwartz et al., 2005; O'Connor et al., 2002, for reviews). Like perceptual load, VSTM load led to reduced sensory cortical responses to incoming stimuli resulting in “load induced blindness” (Macdonald & Lavie, 2008) but now during memory maintenance under high load. Clearly, competitive interactions in sensory visual processing under load include not just stimulus competition (cf. Torralbo & Beck, 2008) but also competition with visual representations held in memory.

Evidence for the Sensory Recruitment Hypothesis of VSTM

The adaptation of Load Theory to account for the effects of VSTM load on perception, and related signals in visual

cortex allows us to provide a new line of evidence for the sensory recruitment hypothesis of VSTM (e.g., Postle, 2006; Pasternak & Greenlee, 2005, for reviews). Previous VSTM studies demonstrated that visual maintenance recruits sensory representations in visual cortex but have not as yet addressed the consequences of this recruitment for sensory responses to incoming information. 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., Munneke, Heslenfeld, & Theeuwes, 2010; Malecki, Stallforth, Heipertz, Lavie, & Duzel, 2009; Lee, Simpson, Logothetis, & Rainer, 2005; Bisley, Zaksas, Droll, & Pasternak, 2004; Supér, Spekreijse, & Lamme, 2001). Moreover, the pattern of sensory activity during maintenance is very similar to the pattern associated with stimulus encoding (Serences et al., 2009) and allows classification of stimulus orientation (Harrison & Tong, 2009). Our findings complement these previous reports in now highlighting a novel consequence of the sensory recruitment during VSTM maintenance for the retinotopic processing involved in the fundamental case of visual contrast detection.

Implications for Working Memory Theory

The present findings also enhance the understanding of working memory systems. The dissociation we establish between the effects of VSTM load and the effects of loading verbal WM, in a task that draws on cognitive control rather than visual sensory capacity, is consistent with previous suggestions that short-term storage and cognitive control processes are independent components of working memory (Smith & Jonides, 1999). Importantly, our findings can resolve apparent discrepancies in previous reports showing either increased distractor processing (e.g., Rissman, Gazzaley, & D'Esposito, 2009; Lavie & De Fockert, 2005; Lavie et al., 2004; De Fockert et al., 2001) or reduced distractor processing (Bollinger, Masangkay, Zanto, & Gazzaley, 2009; Sreenivasan & Jha, 2007; Rose, Schmid, Winzen, Sommer, & Buchel, 2005) under high working memory load. 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 our proposed dissociation: whereas the findings of reduced distractor processing with higher load were obtained with manipulations of VSTM load similar to that used here, effects of increased distractor processing with higher load were found with manipulations of WM cognitive control (e.g., De Fockert et al., 2001).

It is important to note that, in this study, detection was assessed for a task-relevant stimulus, presented alone during the delay, rather than for an irrelevant distractor. Whether a stimulus is task-relevant or not does not bear on the effects of VSTM load: High VSTM load reduces the available sensory representation capacity, and thus, there will be less capacity to perceive any stimulus be it task

relevant or irrelevant. In contrast, the effects of high WM cognitive control load are confined to cases where the stimulus in question competes with the task stimuli for processing. A task-relevant stimulus that appears alone during the memory delay and thus does not compete with other stimuli for selection does not involve any draw on cognitive control; its processing should therefore be unaffected by cognitive control loading (see also Macdonald & Lavie, 2008).

Conclusion

The present research extends Load Theory to account for the role of VSTM load in detection and thus reports a new form of competition between early visual cortex processing and visual representations held in memory under load. This demonstration offers a new line of evidence in support of the sensory recruitment hypothesis and clarifies previous discrepancies in the research of WM.

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