Author/s:
Liu, P;Forte, J;Sewell, D;Carter, O

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Cognitive load effects on early visual perceptual processing

Ping Liu[1], Jason Forte[1], David Sewell[2], Olivia Carter[1]

1. Melbourne school of psychological sciences, The University of Melbourne

2. School of psychology, The University of Queensland.

Abstract

Contrast-based early visual processing has largely been considered to involve autonomous processes that do not need the support of cognitive resources. However, as spatial attention is known to modulate early visual perceptual processing we explored whether cognitive load could similarly impact contrast-based perception. We used a dual-task paradigm to assess the impact of a concurrent working memory task on the performance of three different early visual tasks. The results from Experiment 1 suggest that cognitive load can modulate early visual processing. No effects of cognitive load were seen in Experiment 2 or 3. Together, the findings provide evidence that under some circumstances cognitive load effects can penetrate the early stages of visual processing and that higher cognitive function and early perceptual processing may not be as independent as was once thought.

Keywords: cognitive load, early vision, dual-task, spatial attention, working memory

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Introduction

At any given moment, our brain is overwhelmed by incoming information from our sensory environment. At the same time, our behavioral goals and the execution of actions need to be maintained. The ability of the brain to coordinate concurrent perceptual processing and higher cognitive functions is crucial for us to behave in a coherent and efficient manner in daily life.

The influence of cognitive processes on concurrent visual perceptual processing has been mainly explored in two seemingly related but independent literature streams. One stream focuses on how working memory content can bias concurrent visual processing when there is a content overlap between the two [66, 108, 111]. This line of research has provided evidence for strong links between cognitive processes and low-level visual perceptual mechanisms. The second stream focuses on understanding to what extent cognitive load may affect early visual processing when there is no content overlap between the two [38, 68, 69]. The current study falls into the second category.

Top-down attettion mechanisms supporting perceptual information processing have been the subject of countless studies [19, 23, 27, 43, 72, 73]. Visual attention can be selectively directed to different visual properties such as location, color, etc. The majority of such studies have looked at how visual spatial attention facilitates the processing of attended information and suppresses unattended information [19, 31]

Whether spatial attention modulates early visual processing was difficult to prove for more than two decades due to the variety of visual tasks and methodologies employed in spatial attention studies [19, 138]. The flow of visual perceptual processing is believed to follow an approximately hierarchic feedforward path, i.e., from early to high level vision. Each stage is associated with its specific category of tasks that have been developed to rigorously assess the relevant level of visual processing [83, 138]. Contrast sensitivity tasks are generally considered to assess early processing stages. Demonstrating spatial attention effects on early visual processing with only behavioral measures has required rigorous control of stimulus configuration and experimental methodology [33, 52, 78, 96]. For example, the target has to be presented alone free from any distractors and external noise [33, 78, 96] and the stimulus size of the target needs to be carefully controlled in relation to the spatial attention distribution [52].

The majority of cognitive load studies, however, have not made a clear distinction between the visual tasks used to assess cognitive load on early versus high level visual processing and this has led to some discrepancies in the interpretations of results obtained. For example, findings from a class of studies employing flanker tasks have been interpreted as suggesting that cognitive load doesn't modulate early visual processing [38, 69]. Flanker tasks represent an experimental paradigm known to be more closely associated with a higher-level visual mechanism, i.e., visual crowding [29, 70, 71, 122]. While these studies are interesting and informative they cannot be used to rule out an impact of cognitive load on early visual processing.

Recently a few studies using early visual tasks have provided some initial indication that such tasks may be sensitive to cognitive load. Cocchi et al. [26] reported an unexpected finding that visual spatial working memory loads facilitated the performance of a concurrent but independent visual grouping-by-proximity task. Similarly, Fockert and Leiser [39] showed that high cognitive load enhanced collinear facilitation, which is an established early visual perceptual mechanism. The "facilitative" effects reported in Cocchi et al. [26] and Fockert and Leiser [39] are at odds with the existing research (i.e., cognitive load and other dual-task studies) that suggests cognitive load has no impact on concurrent early visual processing [38, 69, 92]. However, the grouping-by-proximity task in Cocchi et al. [26] and the collinear facilitation task in Fockert and Leiser [39] differ considerably from the flanker tasks employed in cognitive load studies. Firstly, both the grouping and the collinear facilitation tasks are generally considered early visual tasks whereas flanker tasks are considered a high-level vision task. Secondly, there is literature suggesting that the grouping and the collinear facilitation tasks are facilitated by a more distributed visual spatial attention field [7, 20, 40, 41, 46, 47, 59, 81]. In contrast, a focused spatial attention field has been shown to improve performance on flanker tasks [22, 37, 49, 50, 79, 87, 99, 109, 122]. The finding and design differences in the research raise the crucial question as to whether cognitive load can indeed modulate early visual processing.

The center-surround antagonistic organization of the receptive field of early visual neurons is thought to be fundamental to optimal contrast-based visual information processing. The center excitatory drive to the classical receptive field (CRF) establishes a neuron's basic stimulus selectivity, which can be strongly modulated by the surround inhibition from the extra-classical receptive field (eCRF) in many neurons along the visual pathway [1, 42, 54, 55]. This center-surround interaction has been proposed to be one of the most fundamental underlying mechanisms supporting the efficient encoding of raw visual inputs [51, 82, 138].

Neurophysiological findings of top-down modulation effects on center excitation and surround inhibition suggest that variations in top-down modulation strength lead to differential effects on the final output of neural responses in early visual cortical neurons [57, 58, 89, 106, 133]. Specifically, inactivation of feedback to V1 neurons has been found to reduce responses in some neurons to low-contrast stimuli confined to the CRF, suggesting that cortico-cortical feedback provides a weak, predominantly excitatory influence on the CRF [57, 58, 106, 133]. In contrast, when assessed using stimuli that engage both the CRF and eCRF, eliminating feedback results in strong and consistent response facilitation, effectively reducing the strength of surround inhibition on center excitation in V1 neurons [3, 4, 89]. Thus, theoretically in the presence of both center excitation and surround inhibition, the final outputs reflect the balance between these two forces in the absence of spatial attention.

Spatial attention has been argued to shift the balance between center excitation and surround inhibition, which in turn alters the neural response to visual stimulation. The modulation effects have been characterized by many computational models [28, 96, 104]. For example, according to the normalization model of spatial attention [104], the size of the attentional field determines how much surround inhibition enters into the normalization process and, consequently, the final response intensity of a given neuron [104].

The aim of the current study is to explore cognitive load effects on early visual processing. Given center excitation and surround inhibition are the fundamental contrast-based early visual processing mechanisms, the current study explored cognitive load effects on center excitation and surround inhibition separately with established early vision tasks in three experiments. Spatial attention effects were taken into account in the design of the experiments and interpretation of results because of its possible modulation effects on the interaction between the two forces.

Experiment 1 Cognitive load effects on center excitation

Converging evidence from psychophysical, neurophysiological and imaging studies suggests that top-down modulation enhances neural response to visual stimulation when the dominant driver of the neural response reflects the center excitation mechanism. Findings from psychophysical studies of spatial attention suggest that the effects of spatial attention are equivalent to increasing the contrast of weak stimuli when the target stimulus is small relative to the spatial attention field [52, 75, 95]. Neurophysiological and imaging studies of spatial attention have also found spatial attention effects are equivalent to increasing stimulus contrast for small stimuli [74, 102, 103]. Together with the neurophysiological findings that cortico-cortical feedback provides a weak excitatory influence on the CRF for low-contrast stimuli [57, 58, 106, 133], these results suggest top-down modulation can enhance center excitation.

In Experiment 1, cognitive load effects on center excitation were assessed. As cognitive load is assumed to tax limited cognitive resources, it was hypothesized that it may reduce the brain's ability to provide top-down modulation for concurrent early perceptual processing. In other words, the capacity for top-down enhancement of center excitation should be diminished causing contrast sensitivity to be lower under high load conditions.

An orthogonal orientation discrimination task was employed as a proxy for a typical peripheral contrast detection task. This task was adapted from previous spatial attention studies and was carefully chosen based on three major considerations. Firstly, the performance on this task is generally believed to reflect the contrast responses of orientation selective early cortical visual neurons [114]. Secondly, the orthogonal discrimination and yes-no detection tasks produce equivalent contrast thresholds [130]. Thirdly, by asking participants to judge the orientation contingent dimension of interest (contrast) rather than contrast itself, the task minimizes response bias usually associated with yes-no contrast detection tasks [118]. Similar methodology has been adopted in multiple spatial attention studies [18, 77, 114, 119]. While it is acknowledged that orientation discrimination is generally regarded as requiring high-level visual processing [138], the processing demand on orientation discrimination in this task is, however, minimal. A peripheral contrast detection was employed because it is thought to recruit a distributed spatial attention. Cognitive load has been shown to defocus spatial attention when focused spatial attention is required [16, 76]. By using an early visual task that requires a distributed spatial attention, the design minimized the chance that cognitive load effects on center excitation could be confounded by its effects on altering spatial attention distribution.

The cognitive load was manipulated with a general alphanumeric working memory task similar to that used previously [38], in which observers held zero, one or five alphanumeric characters in working memory. If cognitive load reduces top-down modulation on early visual processing, our high working memory load condition should result in a relative elevation of contrast detection thresholds.

Methods

Participants. Four graduate students (3 females and 1 male aged 21 to 35 years) from the University of Melbourne participated in the experiment. Three were experienced psychophysical participants and one had no previous experience observing psychophysics experiments. All had normal or corrected-to-normal vision. Participants were screened and consented in accordance with approval from the human research ethics board of the University of Melbourne.

Apparatus. Stimuli were created on a MacPro computer using MATLAB (version 7.8) and the Psychophysics Toolbox 3.0 [11, 94] and displayed on a gamma-corrected 17-inch CRT monitor, 1024-by-768-pixel at 85Hz in a dimly lit room. The background was a uniform gray with the luminance set to the middle of the monitor's range, about 55 cd/m^2. The stimuli were viewed binocularly at 80 cm with participant's head position stabilized with a chin rest.

Stimuli.

The contrast detection task. The target stimuli for the contrast detection task were Gabor patches (sinusoidal gratings embedded in a Gaussian window) subtending 1° of visual angle presented at 4° eccentricity from the fixation. The Gabor stimuli had a center spatial frequency of 3.6 cycles per degree (cpd). On each trial, a Gabor patch was presented with equal probability at one of the four corners of an imaginary square, centered on a fixation square (0.2° × 0.2° of visual angle), which was present at the center of the screen throughout the perceptual task. Half of the trials contained a vertical Gabor and the other a horizontal Gabor.

The luminance profile L (x, y) of a static vertical Gabor patch as a function of spatial coordinates along the horizontal (x) and vertical (y) axes was

$$L\left(x,y\right) = L_0 + L_0 \cdot m \cdot exp\left[-\frac{(x-x_0)^2}{2\sigma^2}\right] \cdot exp\left[-\frac{(y-y_0)^2}{2\sigma^2}\right] \cdot cos(2\pi f(x-x_0)+\theta) \quad (1)$$

where L_0 is the mean luminance of the display, m is the amplitude (contrast) of the Gabor function, x_0 and y_0 are its horizontal and vertical center positions respectively, σ is the standard deviation of the Gaussian envelope, f is the frequency of the sinusoid, and θ is the phase of the sinusoid with respect to the center of the Gaussian window. All Gabors were in cosine phase with θ set at 0.

To signal the target location and terminate visual perceptual processing, a square mask consisting of a high contrast checkerboard pattern (subtending 1.1° of visual angle) was presented for 200 ms at the same location of the target immediately after the offset of the Gabor patch.

The method of constant stimuli was used. All participants performed the contrast detection task prior to formal testing to establish the contrast levels required to measure the full extent of the psychometric function (five or six levels of contrast linearly spaced on a log scale from chance to asymptote performance level).

The working memory task. The working memory set was displayed in a 3×3 grid at the center of the monitor in font Arial size 18. The grid was made of English consonants randomly selected from the available 20 without replacement. The remainder of the grid was filled with tilde symbols (~). The entire grid measured approximately 2.5° squared, with each letter within the grid subtending approximately 0.6°. The combination of the letter and tilde symbols within the grid varied as a function of load (no load, low load & high load). In the no load condition, the grid consisted purely of tilde symbols. In the low load condition 1 letter was presented in the central location of the grid. In the high load condition 5 letters were presented with 1 at each corner and 1 at the center. The memory grid was presented in dark red to indicate the encoding phase of the working memory task.

In the low and high load conditions, the memory of the letter set was later probed by a single letter presented in one of the locations previously occupied by a letter, with all remaining locations filled by the tilde. In half of the trials the probe letter was identical to the one previously presented at the exact location and different in the other half. In no load conditions, a grid of tilde symbols was presented to occupy the time. The probe array was presented in dark green to indicate that this was the probe phase of the working memory task. The luminance of the red letters of the memory array and the green letters within the probe array were matched.

Procedure. As depicted in Figure 1, each trial started with a light grey fixation square, appearing for 1000 ms, indicating the start of a new trial. The fixation square was then replaced by the memory grid presented for 1500 ms (individually adjusted for one of the participants to be 2000 ms). This was then followed by the presentation of a fixation square for 1000 ms before the Gabor patch was presented. The Gabor patch was presented for 50 ms. A square mask consisting of a high contrast checkerboard pattern (subtending 1.1° of visual angle) was presented for 200 ms at the same location of the target immediately after the offset of Gabor patches. Each trial ended with a probe grid that was presented for 800 ms. The working memory load, location of the Gabor stimulus and contrast level were all randomized within sessions.

Participants were instructed to fixate on the central square throughout the trial except for reading the memory grid and the probe grid. With respect to the memory and detection tasks, participants were told to remember and maintain the memory set online for the full length of each trial and to report the target orientation as accurately as possible immediately following the presentation of the Gabor. Their response of orientation (vertical vs. horizontal) of the Gabor was indicated by pressing the arrow (left vs. right) key on the computer keyboard using a finger (index vs. middle) of their right hand respectively. Feedback for an incorrect response was given by a high-frequency tone to encourage stability of decision criteria [121]. A response window of 1500 ms was provided for the contrast detection task. Participants then responded to the memory task indicating whether the probe letter was the same vs. different to the one in the memory set (in the exact location) by pressing the arrow (left vs. right) key on the computer keyboard using a finger (index vs. middle) of their right hand. A response window of 2000 ms was provided for the working memory task. No feedback was provided for the working memory task. Responses made outside the response time window for each task were not recorded.

Each session of the dual-task paradigm was about 1 hour long with multiple breaks. The inexperienced participant was trained on the contrast detection task for 10 sessions with a total of 100 trials per contrast level. The three experienced participants were given 1 practice session each with a total of 10 trials per contrast level. All participants performed a total of 20 1-hour testing sessions. The trial randomization process ensured that at least 180 valid trials were completed per contrast level per working memory load. Trials with missing responses and responses with reaction time less than 200 ms for either the visual perceptual task or working memory task (high and low load conditions) were excluded. Depending on the number of excluded trials, participants typically completed between 180 - 200 trials per condition. See the results section below for specific details regarding the percentage of trials excluded for respective participants.

Analysis and Results

All data were analyzed in R (R Development Core Team, 2011). The psychometric function fitting and associated model comparisons were analyzed using the psychy 0.1-7 package [63]. All figures were plotted using ggplot2 package [136]. Analyses of performance for both tasks were only made on trials with legitimate responses. The percentages of trials that were excluded from the final analyses of individual participants were 3.18%, 3.29%, 5.87% and 0.54% respectively.

The working memory task. Accuracy and reaction time of the working memory task for the four participants are reported in Table 1. The working memory task performance in the current experiment was comparable with the 92% and 98% performance and mean reaction times of 953 and 1394 ms for the low and high load conditions respectively reported in previous cognitive load studies [38], suggesting that our cognitive load manipulation was successful.

The contrast detection task. To assess whether cognitive load modulates the contrast detection task, a modified cumulative Gaussian function was fitted to the data from each participant, where x is the stimulus contrast, α, β, λ, and γ are the fitted model parameters which determine the shape of the psychometric function,

$$F(x, \alpha, \beta, \gamma, \lambda) = \gamma + (1 - \gamma - \lambda) F(x, \alpha, \beta) \tag{2}$$

and F is the cumulative Gaussian function:

$$F(x; \alpha, \beta) = \frac{\beta}{\sqrt{2\pi}} \int_{-\infty}^{x} exp\left(-\frac{\beta^2 (x-\alpha)^2}{2}\right) \tag{3}$$

with $\alpha \in (-\infty, +\infty)$, $\beta \in (-\infty, +\infty)$. The contrast threshold (α) and the slope (β) of the psychometric functions were left to vary freely and estimated separately for the no-, low- and high-load conditions. The range of the asymptote (λ) was constrained to be within 1~5%, and additionally, was forced to be equal across all levels of working memory load due to the limits of computational capacity of the psychy 0.1-7 package [63]. Gamma (γ) represented the chance performance and was set at 0.5 [134, 135].

Fits were performed using maximum-likelihood estimation. To determine whether there was a change in threshold (α) and a change in slope (β) of the psychometric functions under different working memory load, three models were compared using a nested hypothesis test [85]. In the one-function model, a single psychometric function was fit to all the data; the threshold (α) and slope (β) of the psychometric functions for the three working memory loads were constrained to be the same. In the threshold model, three psychometric functions were fit to the three working memory load conditions with the threshold (α) being varied freely but the slope (β) being constrained to be the same. Finally, in the threshold-slope model, both the threshold (α) and slope (β) were estimated for each working memory condition. Goodness-of-fit was assessed with deviance scores, which were calculated as the log-likelihood ratio between nested models [134, 135]. The deviance scores of the one-function model and the threshold model were compared to assess whether thresholds were different across working memory load conditions, and the deviance scores of the threshold model and threshold-slope model were compared to evaluate whether slope differed across working memory load conditions. The results of these fits are summarized in Table 2.

Figure 2 shows the psychometric functions for the three working memory load conditions for each of the four participants with the fits of the threshold model. As expected, performance increased as a function of target contrast under all working memory loads. The psychometric function for the high load condition shifted to the right compared to the no- and low-load conditions. Although two participants showed slope (β) changes, the slope effects were not consistent across participants, and potentially reflected individual differences.

Reaction time was evaluated as a secondary measure of the contrast detection task performance. The mean RT for each participant was fitted with the two parameter Piéron's law function [100, 117]:

$$F(c) = \alpha c^{-\beta} \tag{4}$$

Piéron's law is a power function that describes the decrease in mean RT with increasing stimulus contrast, c [117]. It describes an empirical rather than a theoretical relationship, which is known to characterize the dependency of RT on stimuli intensity in a variety of tasks [128, 129]. As with accuracy data, the cognitive load effects were quantified by comparing the fits of a one-function model in which the scale (α) and exponent (β) were constrained to be the same and a multi-function model in which the scale (α) and exponent (β) varied with working memory load condition. Goodness-of-fit was assessed with deviance scores, which were calculated as the log-likelihood ratio between nested models [85]. The deviance scores of the single-function and multi-function models were compared to assess whether RT changes differed across working memory load conditions. The model fits are given in Table 3. The mean RT data were better described for all participants by the multi-function model. Plots of mean RT for each participant are shown in Figure 3. These results show that participants almost always responded faster as contrast increased and mean RTs were generally longer under the high-load condition (vs. the no- and low-load conditions).

Discussion

The aim of Experiment 1 was to evaluate whether cognitive load modulates the strength of the center excitation mechanism. We assessed the effects of an unrelated but concurrent working memory task on the contrast detection thresholds of small Gabors. Under the high working memory load, the contrast detection thresholds were found to be higher in three participants. The same pattern was seen in the 4th participant although the model comparison did not reach significance for this participant. Reaction time data suggest that participants were generally slower on the contrast detection task under the high working memory (vs. no- and low-loads), suggesting there was no speed accuracy tradeoff on the contrast detection task. The model comparisons showed no significant difference between the low and no load conditions in either contrast thresholds or reaction time.

To the best of the authors' knowledge, this experiment represents one of the first demonstrations of cognitive load effects on early visual processing with an established early visual perceptual task. We believe that the behavioral effects found in Experiment 1 are consistent with a slight reduction in top-down enhancement to center excitation under high cognitive load based on several factors. Firstly, the performance on the orientation discrimination task is generally accepted to be dependent on orientation selective neurons in early visual cortical areas (e.g. V1) [53, 54, 114]. Secondly, because the single target Gabor was presented against a blank background and in the absence of flankers, the current experiment maximally reduced the processing demand at later cognitive levels [33, 93, 96]. Thirdly, placing a backward mask at only the target location helped minimize spatial uncertainty [116] and associated performance decrements due to increased decisional noise believed to be related to target selection from multiple spatial channels [33, 93]. Any performance difference seen therefore can be more confidently attributed to reductions in the quality of perceptual representation due to diminished strength of top-down modulation associated with increased working memory load. While our use of backward masking had some clear advantages, one interesting question that arises is whether cognitive load effects on early visual processing are only evident when stimulus presentation time is limited. The spatial attention literature suggests that behavioral measures of top-down modulation effects on early visual processing may be dependent on the use of backward masking [14, 18, 116]. However, neurophysiological measures demonstrate top-down modulation effects in early visual area when stimulus presentation time is less strictly controlled [13, 59, 90, 105, 113, 131]. This issue is discussed further in the general discussion.

Experiment 2 Cognitive load effects on surround inhibition

Under natural viewing conditions, the center excitation and surround inhibition mechanisms are believed to function in a coordinated fashion to best process contrast variations in visual scenes [8, 80, 97, 127]. While the visual task in Experiment 1 was designed to optimally measure cognitive load effects on center excitation, the aim of Experiment 2 was to determine whether cognitive load could also be shown to impact surround inhibition in early vision.

It is, however, not straight forward to psychophysically separate out top-down modulation effects on surround inhibition from its effects on center excitation. Surround inhibition by definition is modulatory in nature - behaviorally assessing surround inhibition effects usually involves measuring the contrast sensitivity to a central target with versus without the presence of a high contrast surround mask. At the behavioral level, measuring contrast sensitivity of the target recruits spatial attention as participants are usually explicitly instructed to focus on the central target and ignore the high contrast mask. This creates a confound as spatial attention has been shown to alter the interaction between center excitation and surround inhibition [52, 104]

To measure cognitive load effects on surround inhibition strength relatively independent of spatial attention effects, here we used a motion discrimination task that is thought to represent a perceptual correlate of surround inhibition [127]. One key aspect of this motion task is that only one large size stimulus is used as the target for the perceptual task so that there is no distinction between a target and its surrounding. This has the benefit that the task does not require spatial attention to play the typical dual role of focusing on a target while ignoring its surroundings.

Tadin et al. [127] showed that when a high contrast drifting stimulus was presented very briefly, motion direction discrimination deteriorated with increasing stimulus size. The results were interpreted as suggesting that the high contrast large motion stimulus induces strong surround inhibition. This, in turn, reduces the motion direction signal rendering the motion direction more difficult to perceive [127]. The counterintuitive psychophysical observation for the motion task is believed to result from the neuronal surround inhibition in the middle temporal area (MT or V5) [126]. MT neurons are known to be highly selective for motion direction, and roughly half of them exhibit inhibitory center-surround interactions at high contrasts but show weak or nonexistent surround inhibition at low contrasts [9, 10, 56, 60, 132]. This surround inhibition is direction-specific and strongest for large, slow-drifting stimuli [91]. It has also been shown that MT neurons with surround inhibition integrate motion signals relatively quickly compared to MT neurons without surround inhibition [24, 25]. This finding suggests that brief motion stimuli preferentially probe MT neurons that have strong center-surround configurations [24, 25].

Consistent with neurological findings that top-down modulation through feedback connections enhances surround inhibition, a recent study provided novel evidence that higher cognitive capacity might provide more efficient top-down modulation, which in turn, might result in stronger surround inhibition. Melnick et al. [84] found that individual variability in surround inhibition reflected in the motion task negatively correlated with IQ (r = -0.71), a measure thought to reflect mainly higher cognitive functions. Thus high-IQ individuals exhibited disproportionately large impairments in the performance of this motion task when the stimulus was large and of high contrast. The finding suggests that higher cognitive capacity may be associated with stronger surround inhibition.

Taken together, the current literature suggests that strong top-down modulation may increase surround inhibition in early visual processing. Since the results of Experiment 1 were consistent with cognitive load reducing top-down enhancement of center excitation, Experiment 2 aimed to identify evidence consistent with effects of high cognitive load on surround inhibition. With respect to the motion discrimination task used here, any reduction in surround inhibition should result in better performance on the task (i.e., shorter exposure duration thresholds) under high cognitive load (vs. no and low loads).

Methods

Participants. Four students (1 male and 3 females aged 21 to 35 years) from the University of Melbourne participated in the experiment. One participant, the first author, PL, had previous experience observing the motion task. Two were experienced psychophysical observers but had no previous experience observing the motion task. One participant had no prior experience observing psychophysical experiments. One of the experienced participants also participated in Experiment 1. All had normal or corrected-to-normal vision. Participants were screened and consented under approval of the human research ethics board of the University of Melbourne.

Apparatus. The apparatus was the same as in Experiment 1.

Stimuli and design. The target stimuli for the motion discrimination task were vertical sine gratings of a spatial frequency 1 cpd windowed by a stationary two-dimensional Gaussian envelope (Gabor patches) subtending 5° of visual angle drifting left or right at 1°/s. The contrast of Gabor patches was fixed at 92% and was ramped on and off with a temporal Gaussian envelope, allowing the presentation of brief motion stimulus. Contrast was defined as the peak contrast within the spatial envelope. Exposure duration of the stimulus was defined as 2 standard deviations of the temporal Gaussian envelope. The spatial and temporal phase terms were set to zero for simplicity (same as described in Equation 1).

The parameters of the target stimulus were chosen primarily based on the findings from Tadin et al. [127]. All participants practiced on the motion task prior to formal testing to establish the exposure durations required to measure the full extent of the psychometric function (five durations producing performance ranging from chance to asymptote). Three experienced participants were given two practice sessions of the single motion task each lasting approximately 40 minutes. The one inexperienced participant required 4 practice sessions (approximately 40 minutes) to achieve stable performance. All participants in this experiment showed large performance improvement on the motion discrimination task during practice sessions. This performance improvement, termed "perceptual learning" has been found in many psychophysical tasks [34]. During practice, stimulus exposure duration was progressively shortened over successive practice blocks as the participants became better at the task. As a result, the drifting speed was reduced from 2°/s to 1°/s due to the marked performance improvement during training sessions.

The working memory stimuli were the same as described in Experiment 1.

Procedure. The procedure of Experiment 2 was similar to that of Experiment 1 with the motion discrimination task replacing the contrast detection task. For the motion task, participants were asked to report the motion direction as accurately as possible but in a timely manner immediately following the presentation of the drifting Gabor. Participants indicated the perceived direction (left vs. right) by pressing the arrow (left vs. right) key on the computer keyboard using the finger (index vs. middle) of their right hand respectively. Feedback for an incorrect response was given by a high-frequency tone.

Participants were given 1 practice block on the dual task paradigm and completed 12 separate 1-hour testing sessions. The method of constant stimuli was used. The working memory loads and exposure durations of the drifting Gabor were randomized within sessions. As in Experiment 1, each participant completed at least 180 valid trials per exposure duration per working memory load, resulting in approximately 180 - 200 trials per condition. Trial exclusion criteria were the same as in Experiment 1. The percentage of trials excluded for respective participants are reported in the following results section.

Analysis and results

The data analyses methods and model fitting procedure for the motion discrimination task accuracy data were as described in Experiment 1.The percentages of trials that were excluded from the final analyses for the four participants were 2.39%, 0.2%, 0.73%, 0.58% respectively.

The working memory task. Accuracy and reaction time of the working memory task for the four participants are reported in Table 4. The patterns of results were comparable with Experiment 1 and previous cognitive load studies [38]. Both accuracy and reaction time data showed the general trend that the working memory task performance was better in the low compared to the high load condition.

The motion discrimination task. The model fitting procedure for the motion discrimination task accuracy data was as described in Experiment 1. The results of the model fits under the three load conditions are summarized in Table 5. As expected, performance increased as a function of exposure duration of the drifting Gabor under all three load conditions. However, there were no significant differences between psychometric functions of the motion discrimination task under the three load conditions (Figure 4).

Discussion

The effects of cognitive load on surround inhibition in a visual motion task were assessed in Experiment 2. Because the psychometric functions under the three working memory load conditions did not differ significantly, we were unable to demonstrate cognitive load effects on the surround inhibition mechanism in early visual processing.

Taken in isolation this finding could imply that the impact of cognitive load on surround inhibition is either absent or not as great as the effects on center excitation. There are, however, potential factors associated with practice effects and individual differences that may have contributed to the non-significant results found in Experiment 2 and are considered in detail in the final discussion.

Experiment 3 Cognitive load effects on surround inhibition in a classical surround inhibition task

Experiment 2 found no effects of cognitive load on surround inhibition using the motion discrimination task from Tadin et al. [127]. This motion task differs from classical surround inhibition tasks in many aspects. Consequently, the surround inhibition mechanisms measured by such different tasks may be different. The aim of Experiment 3 was to assess cognitive load effects on surround inhibition using a classical surround inhibition task, adopted from Petrov and McKee [98]. In this task, participants detected a peripheral contrast target surrounded by a high contrast mask (Figure 5). The target was a small Gabor presented randomly in one of two possible peripheral locations at 8° eccentricity to the fixation. Strong surround inhibition was elicited by the presentation of a high contrast sine wave mask in half of the trials.

Given this surround inhibition task naturally involves focusing spatial attention to the target while ignoring the surround mask, spatial attention effects were considered during the experimental design. According to the normalization model of spatial attention [104], the relative size of the stimulus and the spatial attention field shifts the balance between excitation and inhibition and determines the amount of surround inhibition that is included in the normalization process. Previous studies have shown that high cognitive load leads to a more distributed spatial attention when optimal task performance requires focused spatial attention [16, 76]. To reduce the confounding effects of spatial attention, we directly combined the working memory manipulation with the surround inhibition task requiring detection of a peripheral target. This resulted in a multifocal spatial attention paradigm, as detection of the peripheral target required simultaneously monitoring two locations. The current evidence relating to spatial attention allocation suggests that when multiple spatial locations are to be simultaneously attended to, attention can concurrently select multiple locations excluding interposed locations [5, 17]. But spatial attention in such situation would not be as focused as in tasks requiring focused spatial attention to a single location. Nevertheless, the possibility that cognitive load also leads to more a distributed spatial attention in tasks requiring multifocal spatial attention cannot be entirely ruled out. Therefore, in the final experiment, high cognitive load was expected to influence the performance on the surround inhibition task in two main possible ways. If high cognitive load diminishes top-down modulation to both center excitation and surround inhibition and if its effects on altering spatial attention distribution are negligible, it should result in improved contrast detection reflecting diminished surround inhibition. In contrast, if high cognitive load only diminishes center excitation but not surround inhibition as suggested by results of Experiment 2 and if cognitive load effects on spatial attention distribution are negligible, contrast detection thresholds for the central target under the surround condition should be elevated. Additionally, if high cognitive load leads to a more distributed spatial attention, this would only further elevate contrast detection thresholds under the surround condition. In all these scenarios, cognitive load was expected to result in elevated contrast detection thresholds under the no-surround condition based on findings from Experiment 1.

Methods

Participants. Three students (2 males and 1 female aged 21 to 30 years) from the University of Melbourne participated in Experiment 3. None of these three observers participated in Experiments 1 or 2 but two participants had previous experience with psychophysical experiments. All had normal or corrected-to-normal vision. Participants were screened and consented under approval of the human research ethics board of the University of Melbourne.

Apparatus. As described for Experiments 1 and 2 with one exception: the monitor was fitted with a Bits++ box (Cambridge Research Systems) operating in Mono++ mode to give true 14-bit luminance accuracy.

Stimuli and design.

The classical surround inhibition task. For the surround inhibition task, the target stimulus was a standard horizontally oriented Gabor patch (diameter 2.6°) with a center spatial frequency of 1.5 cpd. A two-alternative spatial forced-choice procedure was employed, in which the Gabor was randomly presented in one of two possible peripheral locations, 8° eccentricity left and right to the fixation point. In half of the trials, the target Gabor was presented with a surround mask extending the whole screen. The surround mask was a sinusoidal grating of the same orientation and spatial frequency as the target. The contrast of the surround mask was fixed at 50%. Faint thin circles of 0.1° wide and 2.8° in diameter were presented surrounding the two possible target regions as this has been shown to be particularly important for equalizing the spatial uncertainty of targets presented with and without the surround mask [97]. The contrast of the faint circles was 10%. The faint circles and the fixation square were continuously visible throughout the task. In the other half of the trails, the Gabor was present without the surround mask.

The target contrast was determined using a modified weighted up/down adaptive staircase method, where step size ratio was 3 to 1 for up and down steps to target 75% correct performance [62]. More specifically, 36 contrast levels were chosen linearly spaced in the contrast range between -2 to -0.65 on the log scale, with a step size of ~0.04 log unit. The initial contrast level in each staircase was chosen randomly in the upper middle range within the 36 levels (around 15% contrast). On each of the following trials, the contrast of the stimulus was reduced by 2 step sizes after each correct response and increased by 6 step sizes after each incorrect response until 3 response reversals were reached. After the third response reversal, the contrast of the stimulus was reduced by 1 step size after each correct response and increased by 3 step sizes after each incorrect response.

The working memory stimuli were as described in Experiment 1 and 2.

Procedure. The procedure and testing of the working memory task was the same as in previous experiments. For the surround inhibition task, 1400 ms after the presentation of the memory grid for the working memory task, the Gabor stimulus was presented for 50 ms. Participants pressed the arrow button (left vs. right) to indicate which location (left vs. right) contained the target using a finger (index vs. middle) of their dominant hand respectively. There was a 1500 ms response window for the surround inhibition task.

In each testing session, two randomly interleaved staircases (each of 60 trials) were run for each combination of load (no, low and high load) and surround condition (no surround and surround), resulting in 12 staircases for each testing session. Participants were given two training sessions (four staircases per surround condition per session) on the surround inhibition task prior to the formal testing. Each session of the dual-task paradigm took about 1 hour with multiple breaks during which participants remained in the dimly lit room. Each participant completed 12 sessions.

Analyses and results

All data were analyzed in R (R Development Core Team, 2011) with lme4.0 package [6]. Trial exclusion criteria were the same as in previous experimentsThe percentages of trials that were excluded from the final analyses for the three participants were 1.92%, 0.14%, 0.66%, respectively. Where the results of a staircase did not converge, the data from the corresponding session was discarded. Data from 11, 10 and 8 sessions for participant one, two and three respectively were included in the final analyses.

The working memory task. Accuracy and reaction time of the working memory task for the three participants are reported in Table 6. The patterns of results were comparable with Experiment 1 and those reported in cognitive load studies [38].

The contrast detection task. The staircase results of individual participants were fitted with a general linear mixed model (GLMM) with a probit link function [64, 86]. Ordinary GLMs assume that the responses are independent and conditionally identically distributed. One way to satisfy these assumptions is to provide extensive training prior to formal testing in order to stabilize participants' performance and reduce the variability between sessions. When training is intentionally provided at a limited level to minimize practice effects, responses collected from multiple sessions may violate these assumptions. In GLMMs the overall variability is separated into a fixed and a random component. The fixed component estimates the variance of the effects of interest (i.e., working memory load), whereas the random component estimates the heterogeneity between staircases as an approximation for sessions. In this way, a single model was fitted with all data across all staircases for each participant, but each staircase was allowed to have a different level of variability. In particular, the following model was adopted:

$$Y_{ij}^{*} = \alpha + \beta x_{ij} + v_{ij} \tag{5}$$

where Y_{ij}^{*} is a latent response variable, assumed to have a cumulative Gaussian function. The response variable Y_{ij}^{*} for trial j in staircase i is linked to the linear predictors through the probit link function, such that the expected value of the latent variable E (Y_{ij}^{*}) is the inverse of the cumulative Gaussian function (Φ) of the response probability:

$$\Phi^{-1}\left[p\left(Y_{ij}=1\right)\right] = \alpha + \beta x_{ij} \tag{6}$$

α and β are the intercept and slope of the fixed effects parameters of the GLMM. The detection threshold can be calculated as

$$threshold = -\frac{\beta}{\alpha} \tag{7}$$

The error term υ_{ij} is the sum of two components μ_i and ε_{ij}, such that:

$\upsilon_{ij} = \mu_i + \varepsilon_{ij}$

$\mu_i \sim N(0, \sigma_\mu^2)$

$\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2)$

The error-term ϵ_{ij} represents the variability within staircase and the error-term μ_i the variability between staircases; μ_i is also known as random effects parameter. In GLMMs, the errors ε_{ij} are independent only conditional on the random parameter u_i. The estimation of the parameters is based on the maximum likelihood (ML). The guess rate (i.e., asymptotic chance probability) of the probit link function was set at 0.5.

To determine whether the contrast detection thresholds differ under no-surround versus surround conditions and under the three working memory load conditions, three models were compared using likelihood ratio tests. In the one-function model, the response was modeled as a sum of the fixed effect covariate, target contrast, and a random intercept per staircase. In the surround model, a fixed effects term (surround condition) was added to the one-function model. In the surround-working-memory model, there were two fixed effects terms (surround condition and working memory load). The results of the fits are summarized in Table 7. The random and fixed effects fitting parameters of the model are reported in Table 8 and Table 9 respectively. The surround model appears to be superior to both the one-function model and the surround-working-memory model. Thus, model comparison results suggest adding the fixed effect factor surround explains the variance of the data better than the one-function model with only the contrast covariate whereas no benefits can be obtained by adding the working memory load factor. The thresholds under no-surround and surround conditions for all participants calculated according to Equation

7 are summarized in Figure 6.

Data of a single staircase with the fit of the surround-working-memory model for each participant are shown in Figure 7. There was significant effect of surround with the psychometric function shifting to the right under the surround condition, corresponding to higher contrast thresholds under the surround (vs. no-surround) condition. In contrast the psychometric function did not vary according to working memory load conditions.

Discussion

The goal of Experiment 3 was to assess if cognitive load modulates surround inhibition in a classical surround inhibition task in the periphery. The elevated contrast thresholds under the surround condition (vs. no-surround condition) are consistent with the findings in Petrov and McKee [98], demonstrating that the surround inhibition manipulation in the current study was successful. The model comparison indicated there was no significant difference between our two models comparing surround only versus surround with working memory load as an additional parameter. Thus, for the stimulus configurations used in the current experiment, there were no significant effects of cognitive load on surround inhibition in this classical surround inhibition task. The results also suggest that cognitive load did not affect contrast detection thresholds under the no-surround mask condition.

One alternative is that the null findings reflect a failure of our stimulus to selectively capture surround inhibition effects by inadvertently stimulating both the excitatory center and the inhibitory surround. In the current experiment, however, we feel confident that this was not the case. In line with the study by Petrov and McKee [98] we selected surround mask parameters believed to cause minimal activation of the excitatory center of target responsive neurons with relatively selective activation of the surround based on existing physiological and psychophysical data [2, 3, 4, 21, 30, 107]. The significance of stimulus parameters in interpreting the results of Experiment 3 is considered in the general discussion.

General Discussion

The aim of the current study was to explore whether cognitive load modulates early visual processing. In Experiment 1 cognitive load was found to significantly diminish contrast sensitivity, whereas no effect of cognitive load was seen in Experiment 2 or 3. Since the three established early vision tasks are known to reflect center excitation and surround inhibition effects, it is important to consider how these results relate to the existing literature and the potential impact of the stimulus configurations and experiment designs used in the 3 experiments.

In Experiment 1, the finding of diminished contrast sensitivity provides arguably the first behavioral evidence of cognitive load effects on early visual processing. Although two recent studies claimed to have found cognitive load effects on early visual processing [26, 39], their conclusions may be premature given their design and technical methodologies. Cocchi et al. [26] found that concurrent spatial working memory load improved performance on a grouping by proximity task and concluded that concurrent cognitive load facilitated early visual processing. However, these results are difficult to interpret because the spatial working memory task and the grouping task may interact in some modality specific ways as both are believed to recruit visual cortex [48, 65, 66, 111]. In the case of Fockert and Leiser [39], they showed that high cognitive load enhanced collinear facilitation - an established early visual mechanism. However, it is unclear how the very low contrast stimuli would have been achieved using the methodologies described, i.e., 0.3% (low contrast), 0.5% (medium contrast), and 0.9% (high contrast) without any special method to increase luminance resolution such as the Bits++ box.

The diminished contrast sensitivity observed in Experiment 1 is consistent with reduced top-down modulation on early visual processing associated with high cognitive load. One important feature of the design of Experiment 1 is the employment of backward masking, which is a tool regularly used by vision researchers to control the difficulty of contrast detection tasks by limiting the period of time observers have visual access to the target [12]. It served two major functions in Experiment 1. Firstly, it helped ensure that performance accuracy fell into a measurable range [35]. In our case, it was instrumental in controlling the task difficulty such that performance accuracy covered the whole psychometric function using luminance resolutions that are technically possible with modern computers and monitors. Secondly, because the backward mask was presented only at the target location this helped to reduce the impact of decisional noise associated with spatial uncertainty [116]. This was important because the peripheral contrast detection task invovled monitoring multiple locations and was associated with high overal background noise against which the judgment has to be made Dosher and Lu [33]. Consequently, one might argue that cognitive load might have interacted with this high decisional noise associated with spatial uncertainty at post-perceptual processing stages in Experiment 1. However, backward masks have been shown to reduce spatial uncertainty by serving as peripheral cues that attract exogenous attention to the cued location [61, 88, 101, 115, 137]. Exogenous attention involves reflexive orienting and cognitive load is known to have no impact on it [61]. Consequently, high cognitive load could not have affected the ability of higher cognitive functions to use backward masks as peripheral cues to reduce spatial uncertainty at post-perceptual processing stages. Since the mask occurred after target presentations, it could only have reduced spatial uncertainty at post-perceptual processing stages but should not have affected early visual processing of the target prior to the mask onsets. Thus, in Experiment 1, the found diminished contrast sensitivity under high cognitive load is best explained by a reduced top-down modulation on early visual processing.

It is crucial to recognize that although backward masking may be required to control task difficulty in order to demonstrate cognitive load effects on early visual processing with only behavioral measures as in Experiment 1, this does not suggest cognitive load only modulates early visual processing when stimulus presentation time is limited. In the visual spatial attention literature, it is now accepted that with only behavioral measures, the demonstration of spatial attention effects on early visual processing is dependent on backward masking in simple contrast detection tasks [14, 18, 19, 116, 117, 118, 119]. But with neuroimaging and neurophysiological methods, spatial attention has been shown to modulate neural activity in visual areas as early as V1 and the thalamus without backward masking [13, 22, 37, 57, 59, 87, 90, 96, 105, 112, 113, 120, 123, 124, 131]. Similarly, although backward masking is necessary for the demonstration of behavioral effects of cognitive load on early visual processing, we believe cognitive load modulates early visual processing regardless the employment of backward masking.

We feel that our findings in Experiment 1 are consistent with changes in centre excitation associated with a reduction in top-down enhancement because of the consideration given to ensure the correspondence between our stimuli and the underlying CRF that they were designed to stimulate. The parameters of our stimuli were carefully chosen based on existing understanding of neurons in early visual cortex. Recent neurophysiological and neuroimaging studies have provided converging evidence that the average size (diameter) of CRFs, measured with small high contrast stimuli, varies from 0.8° for low eccentricities to 2.1° for large eccentricities (mean=1.0°) [2, 3, 4, 21, 30, 107]. It is impossible to selectively activate only the center because the surround is spatially continuous across the receptive field [3, 4, 21, 30, 107]. However, we can be confident that the contribution of the surround is negligible for our small low-contrast stimuli, as the surround is thought to have a much higher threshold than the center [3, 4, 21]. The target Gabor size (1°) in Experiment 1 ensured minimal concurrent surround inhibition was evoked. Consequently, the reduction in contrast sensitivity observed with increased cognitive load, provides evidence consistent with a load-induced reduction in center excitation.

In Experiment 2, we were unable to demonstrate an impact of cognitive load on surround inhibition in the motion task. However, the potential impact of practice effects [34, 36, 44, 45, 110] and individual differences [15, 125] is worth considering in the interpretation of the null results. Firstly, because our participants' baseline performance on the motion discrimination task was not comparable to that reported in Tadin et al. [127], we believe our results need to be considered with caution and are likely to have been impacted by the extensive practice required in Experiment 2. In the initial study by Tadin et al. [127], a staircase method was used such that the stimulus exposure duration was adjusted based on the participant's performance on previous trials to quickly and successively home in on the threshold (40 trials per staircase). In contrast, the method of constant stimuli in Experiment 2 required approximately 200 trials per stimulus condition in order to obtain sufficient number of trials to cover the whole psychometric function. In their study, Tadin et al. [127] used a drifting rate of 2°/s and the duration thresholds when taken at 82% were in the range of 100 ~ 140 ms. In Experiment 2, the drifting rate was reduced to 1°/s to make the motion discrimination task more challenging as performance improved during the training sessions. Yet, the duration thresholds when taken at 82% were still much shorter (60 ~ 80 ms) than those reported by Tadin et al. [127]. Consistent with a possible role of practice effects, performance on simple perceptual tasks has been shown to improve with repeated task exposure, typically over multiple sessions spreading over several days due to perceptual learning [34, 36, 44, 45, 110]. Compared to the center excitation mechanism, surround inhibition mechanisms seem to be particularly sensitive to practice effects and it has been reported that practice effects may even cancel out surround inhibition effects [32]. If surround inhibition had been reduced by repetitive practice on the motion task in Experiment 2, it would be impossible for top-down modulation effects to alter surround inhibition. As a result, it may have rendered cognitive load effects difficult to detect behaviorally.

In addition to any impact of practice effects, individual differences may have also contributed to the shorter exposure durations seen in Experiment 2 compared to those reported in Tadin et al. [127]. Our exposure durations were similar to those reported in another motion perception study using the same motion task [67] and may reflect individual differences in the magnitude of surround inhibition that have previously been reported [15, 125]. If our participants had relatively limited surround inhibition, top-down modulation effects may have been difficult to detect.

In Experiment 3, although the surround inhibition manipulation was successful, we were unable to demonstrate an impact of cognitive load on surround inhibition in the classical surround inhibition task in the periphery. The results also indicate that cognitive load did not affect contrast detection thresholds under the no-surround condition, which suggests that cognitive load didn't affect center excitation either. Before accepting this interpretation, two alternatives need to be carefully considered.

One alternative is that the null findings reflect a failure of our stimulus to selectively capture surround inhibition effects by inadvertently stimulating both the excitatory center and the inhibitory surround. If so, it is impossible to demonstrate cognitive load effects on surround inhibition. However, given the carefully chosen stimulus parameters, this interpretation is highly unlikely. Neurophysiological findings suggest that the eCRF consists of two fields: a low-contrast summation field immediately outside CRFs and an outer surround field [2, 3, 4, 21, 30, 107]. The low-contrast summation field, measured with low-contrast stimuli, is about twice the diameter of the CRF, i.e., 1.6° for low eccentricities and 4.2° for large eccentricities (mean = 2.0°) [2, 3, 4, 21, 30, 107]. It can be suppressive at high contrast and excitatory at low contrast [2, 3, 4, 21, 30, 107]. Outside this low-contrast summation field, there is an outer surround field with its diameter varying from 2.5° for small eccentricities and to 13° for the large eccentricities (mean = 5.1°). The target Gabor with a size of 2.6° at 8° eccentricity would therefore be expected to cover the CRF and extend into the low-contrast summation field but not activate surround inhibition in the summation field because the targets were primarily presented around threshold level. The gap (outer diameter 2.8°) between the target and the surround mask (mainly falling in the outer surround field) ensured that the surround mask was not presented so close to the target that the surround mask would stimulate the CRF of the neuron responding to the target. The stimulus configuration also avoided the surround mask being coextensive with the target, which may confound the effects of surround and overlay suppression [98]. Thus, surround inhibition was properly manipulated in Experiment 3 and the lack of cognitive load effects on surround inhibition is unlikely to have arisen from inappropriate stimulus configurations.

Another alternative is that the absence of backward masking in Experiment 3 may have contributed to the null findings observed. Despite the apparent similarities between the contrast detection tasks in Experiment 3 (the no surround condition) and Experiment 1, one of the most crucial differences is that backward masking was used in Experiment 1 but not in Experiment 3. As discussed in Experiment 1, backward masking is probably necessary to demonstrate top-down modulation effects on early visual processing with only behavioral measures. To test this possibility, the seemingly simple solution might be to repeat Experiment 3 with the addition of a pattern backward mask. The issue is, however, more complicated. Adding the backward masking to the no-surround condition is straightforward. In contrast, the addition of a backward mask to the surround condition could cause the surround mask and the backward mask to be presented in close temporal order. This, in turn, could lead to interactions between the two, which would make the results difficult to interpret [12]. It is unclear how these potential confounds can be avoided using current behavioral methods. Further exploration of this issue might therefore require combined imaging or electrophysiological measures.

Conclusion

To summarize, contrast-based early visual processing has largely been considered to involve autonomous processes that do not need the support of cognitive resources. However, the reduced contrast sensitivity associated with high cognitive load found in

Experiment 1 suggests that cognitive load effects can penetrate the early stages of visual perceptual processing. Because the current understanding of top-down modulation effects on the performance of the surround inhibition tasks adopted in Experiment 2 and 3 is limited, it is premature to consider this to be definitive evidence of an absence of load effects on surround inhibition. From the point of view of understanding early visual perceptual mechanisms, it is fully acknowledged that null effects of cognitive load in Experiment 2 and 3 suggest that if cognitive load has any impact on surround inhibition, such effects are likely to be subtle with minimal impact on daily perceptual experience. However, from a systems neuroscience perspective, these findings give reason to question the previously assumed independence of cognitive functions and early perceptual processing. Given that real-world visual processing rarely (if ever) happens in the absence of concurrent cognitive demands, future research is required to better understanding cognitive load effects on center excitation and surround inhibition mechanisms fundamental to early visual processing.

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Table 1
Working memory task performance for each participant in Experiment 1.

Participant	Accuracy (%) Low	Accuracy (%) High	Mean reaction time (ms) Low	Mean reaction time (ms) High
ID 1	92	91	1026 (414)	1082 (419)
ID 2	99	99	1023 (131)	1054 (140)
ID 3	97	94	728 (167)	803 (132)
ID 4	97	93	769 (205)	1180 (318)

Note. Reaction time standard deviations shown in parentheses

Table 2
GLM model fits and model comparisons for each participant in Experiment 1

Participant	One-function model	Threshold model	Threshold-slope model	Difference			
	$\chi^2(13)$	$\chi^2(11)$	$\chi^2(9)$	$\Delta\chi^2_{o\&th}$ (2)	p	$\Delta\chi^2_{th\&ths}$ (2)	p
ID 1	61.43	47.14	32.78	14.29	.001	14.36	.001
ID 2	14.01	9.94	7.77	4.07	.13	2.17	.34
ID 3	41.07	28.59	25.85	12.48	.01	2.74	.25
ID 4	53.09	40.22	17.32	12.88	.001	22.91	.001

$\Delta\chi^2_{th\&th}$:chi-square improvement from the one-function model to the threshold model;
$\Delta\chi^2_{th\&ths}$:chi-square improvement from the threshold model to the threshold-slope model.

Table 3
Piéron's law model fits for reaction time data for each participant in Experiment 1.

Participant	One-function model	Multi-function model	Difference	
	$\chi^2(13)$	$\chi^2(11)$	$\Delta\chi^2(2)$	p
ID 1	854.42	714.26	139.17	<.001
ID 2	71.74	35.05	36.69	<.001
ID 3	703.55	496	207.54	<.001
ID 4	1285.99	113.20	1172.78	<.001

$\Delta\chi^2$:chi-square improvement from the one-function model to the multi-function model.

Table 4
Working memory task performance for each participant in Experiment 2.

Participant	Accuracy (%)		Mean reaction time (ms)	
	Low	High	Low	High
ID 1	93	92	855 (308)	888 (268)
ID 2	99	98	1025 (133)	1051 (114)
ID 3	98	95	679 (169)	789 (138)
ID 4	98	96	615 (89)	775 (132)

Note. Reaction time standard deviations shown in parentheses

Table 5

GLM model fits and model comparisons for each participant in Experiment 2.

Participant	One-function model	Threshold model	Threshold-slope model	Difference			
	$\chi^2(13)$	$\chi^2(11)$	$\chi^2(9)$	$\triangle\chi^2_{o\&th}(2)$	p	$\triangle\chi^2_{o\&ths}(2)$	p
ID 1	4.74	4.61	3.77	.12	.94	.84	.66
ID 2	24.74	21.71	19.95	3.03	.22	1.76	.42
ID 3	14.26	10.02	9.43	4.23	.12	.59	.74
ID 4	40.56	39.49	38.99	1.07	.58	.50	.77

$\Delta\chi^2_{o\&th}$:chi-square improvement from the one-function model to the threshold model; $\Delta\chi^2_{o\&ths}$:chi-square improvement from the threshold model) to the threshold-slope model.

Table 6

Working memory task performance for each participant in Experiment 3.

Participant	Accuracy (%)		Mean reaction time (ms)	
	Low	High	Low	High
ID 1	96	95	791 (233)	881 (233)
ID 2	99	98	649 (155)	731 (135)
ID 3	98	95	928 (284)	940 (238)

Note. Reaction time standard deviations shown in parentheses

Table 7
GLMM model fits and model comparisons for each participant in Experiment 3.

Participant	One-function model			Surround model			Surround-WM model		
	AIC	BIC	χ^2	AIC	BIC	χ^2	AIC	BIC	χ^2
ID 1	1181	1196	1175	1127	1147	1119	1131	1161	1119
ID 2	931	945	925	811	830	803	812	841	799
ID 3	754	768	748	660	678	652	663	690	651

GLMM model evaluation. Notes: The Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) both favor the surround model (the smaller the value is, the better the model fit is).

Table 8

Random effects intercept parameter of the GLMM (the surround model) for each participant in Experiment 3.

Participant	Variance	S.D.	No. observations	No. staircase
ID 1	$<.0001$	$<.0001$	1160	11
ID 2	$<.0001$	$<.0001$	911	10
ID 3	$<.0001$	$<.0001$	703	8

Note: Given the random effects were small, the data could be fit with a model without random effects (i.e., a GLM model). But as suggested by Knoblauch and Maloney [63], since the data resulted from an experiment in which the staircase was be expected to be a random term, it could be included even though it is small.

Table 9

Fixed effects parameter of the GLMM (the surround model) for each participant in Experiment 3.

Participant	Estimate	Std. Error	z value	*p*
	Intercept			
ID 1	.04	.06	.72	.47
ID 2	-.52	.08	-6.78	<.0001
ID 3	-.59	.09	-6.84	<.0001
	Contrast			
ID 1	17.12	1.18	14.82	<.0001
ID 2	18.82	1.19	14.48	<.0001
ID 3	33.74	2.04	16.56	<.0001
	Surround mask			
ID 1	-.39	.05	-7.50	<.0001
ID 2	-.65	.06	-10.82	<.0001
ID 3	-.63	.07	-9.64	<.0001

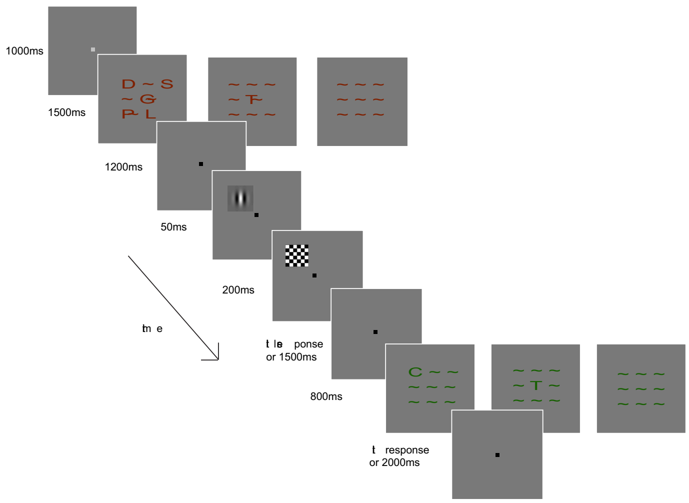

Figure 1. A schematic representation of a trial sequence in Experiment 1. Participants performed a 2AFC orientation discrimination task as a proxy for a contrast detection task on a target Gabor patch (horizontal or vertical) at one of the four corners of an imaginary square centered on the fixation. The target was preceded by a working memory array consisting of either 5, 1 or 0 English constant letters and tilde symbols presented in dark red font. After a response interval of 1500 ms for the contrast detection task, a single letter was presented in dark green font to probe the working memory. A maximum 2000 ms response window was allowed for the working memory task.

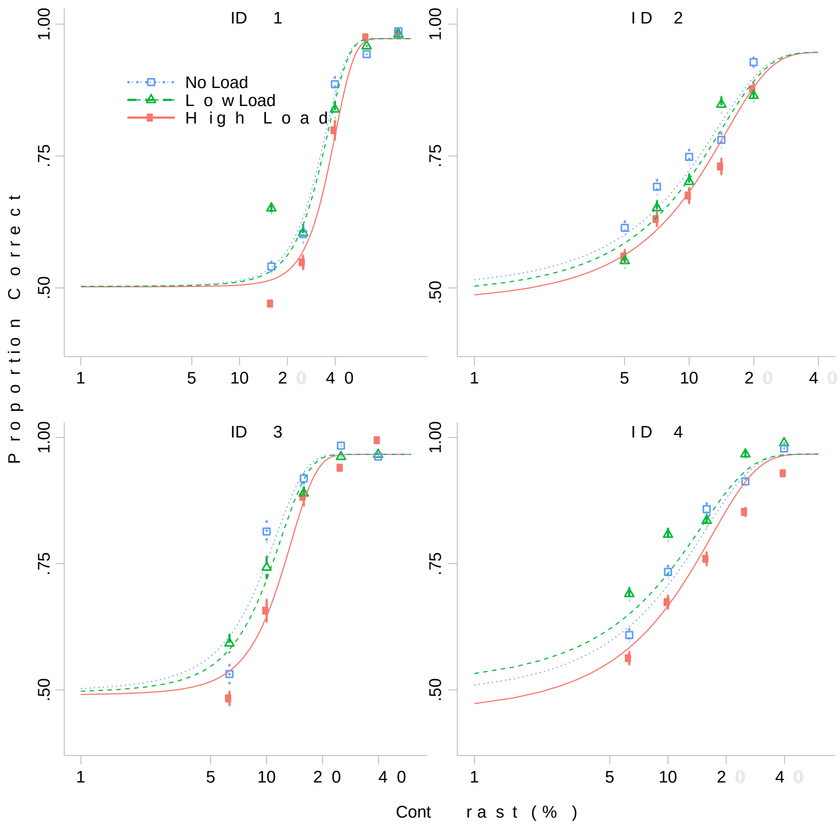

Figure 2. Psychometric functions for the no- (blue dotted lines and squares), low- (green dashed lines and triangles) and high- (red solid lines and circles) working memory load (proportion correct as a function of stimulus contrast) for individual participants with fits of the threshold model in Experiment 1. The fitted functions are cumulative Gaussian functions. The error bars represent one binomial standard error.

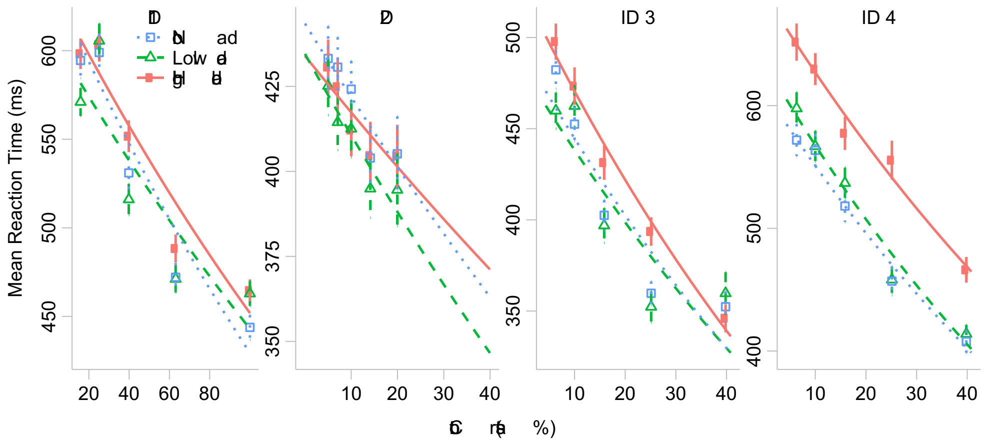

Figure 3. Mean reaction time as a function of stimulus contrast and working memory condition for individual participants in Experiment 1. Blue dotted lines and squares, green dashed lines and triangles and red solid lines and circles represent no-, low- and high-working memory load respectively. The fitted functions are Pieron's Law functions. The error bars represent one standard error of the mean.

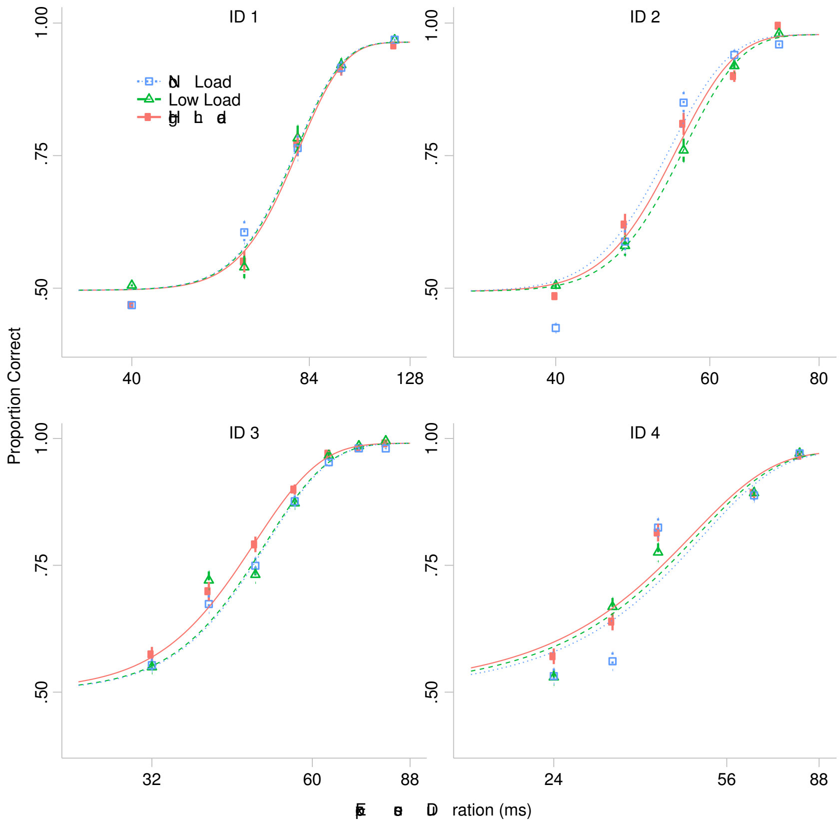

Figure 4. Psychometric functions for no- (blue dotted lines and squares), low- (green dashed lines and triangles) and high- (red solid lines and circles) working memory (proportion correct as a function of stimulus exposure duration) for individual participants with fits of the threshold model in Experiment 2. Performance increased as a function of exposure duration under all three working memory loads. There is no significant difference between psychometric functions of the motion discrimination task under the three load conditions. The fitted functions are cumulative Gaussian function functions. The error bars represent one binomial standard error.

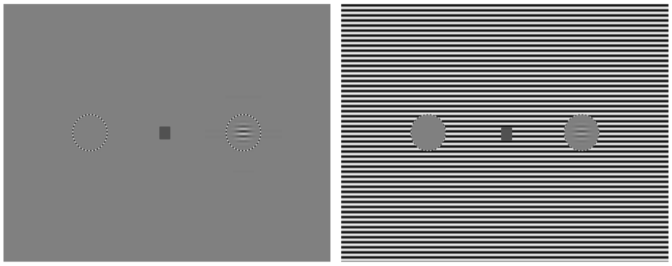

Figure 5. The contrast detection task with and without the high contrast mask in Experiment 3

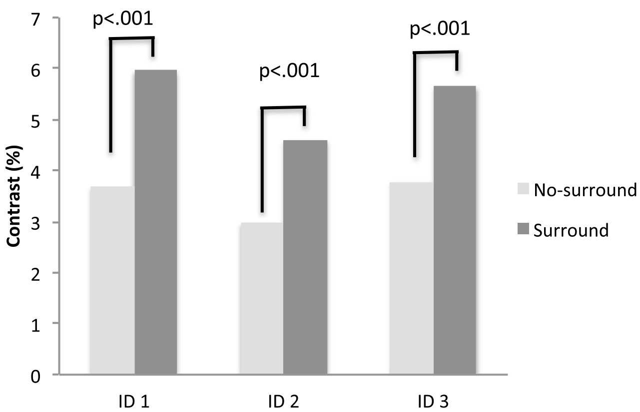

Figure 6. Contrast thresholds (%) for the no-surround and surround conditions and significance levels for each participant in Experiment 3.

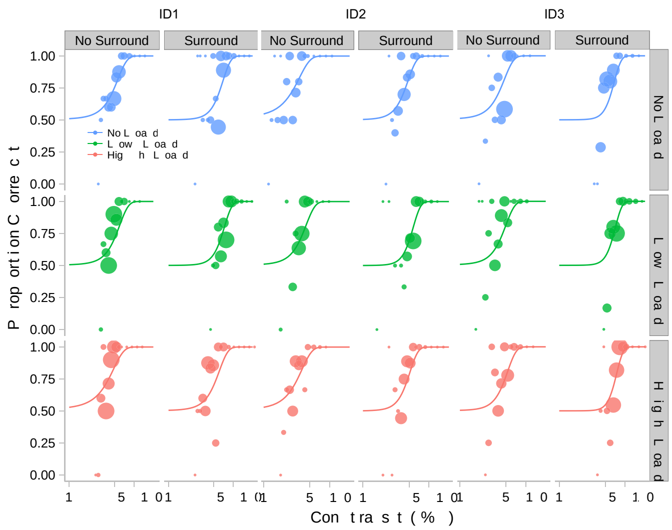

Figure 7. An example staircase of the GLMM fit for the surround-working-memory model. The psychometric functions indicating the proportion correct for detecting the target as a function of its contrast are displayed for no-surround and surround conditions for no- (blue), low- (green) and high- (red) working memory loads for each participant in Experiment 3. The dot sizes are proportional to the number of trials at a particular target contrast (the largest size indicates 15 trials). The functions shift to the right under the surround condition (vs. no surround condition) in all participants.