High perceptual load leads to both reduced gain and broader orientation tuning

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Due to its limited capacity, visual perception depends on the allocation of attention. The resultant phenomena of *inattentional blindness*, accompanied by reduced sensory visual cortex response to unattended stimuli in conditions of high perceptual load in the attended task, are now well established (Lavie, 2005; Lavie, 2010, for reviews). However, the underlying mechanisms for these effects remain to be elucidated. Specifically, is reduced perceptual processing under high perceptual load a result of reduced sensory signal gain, broader tuning, or both? We examined this question with psychophysical measures of orientation tuning under different levels of perceptual load in the task performed. Our results show that increased perceptual load leads to both reduced sensory signal and broadening of tuning. These results clarify the effects of attention on elementary visual perception and suggest that high perceptual load is critical for attentional effects on sensory tuning.

Introduction

The effects of attention on visual perception depend on the level of perceptual load in the task (Lavie, 2005). Due to the capacity limits of visual perception, tasks involving higher perceptual load (e.g., search tasks involving many similar items or tasks requiring complex perceptual discriminations; e.g., Lavie, 1995; Lavie & Cox, 1997) result in reduced visual cortex responses to unattended stimuli (e.g., Rees, Frith, & Lavie, 1997; Schwartz et al., 2005; Yi, Woodman, Widders, Marois, & Chun, 2004; see Lavie, 2005, 2010, for reviews) and lead to the experience of *inattentional blindness* (Carmel, Thorne, Rees, & Lavie, 2011; Cartwright-Finch & Lavie, 2007; Macdonald & Lavie, 2008; Simons & Chabris, 1999). The effects of perceptual load on neural responses are established across different load manipulations and in a variety of tasks. These effects are found to extend throughout the visual cortical hierarchy, from occipital cortex including primary visual cortex area V1, the superior colliculus, and lateral geniculate nucleus (LGN) (e.g., Bahrami, Lavie, & Rees, 2007; O'Connor, Fukui, Pinsk, & Kastner, 2002; Rees, Frith, & Lavie, 1997; Schwartz et al., 2005), through to cortical areas involved in the perception and recognition of complex images, meaningful objects, and scenes (e.g., Pinsk, Doniger, & Kastner, 2003; Yi et al., 2004). Together, the previous behavioral and neuroimaging studies form a large body of research in support of the resolution offered by perceptual load theory for the enduring controversy on the extent to which perception depends on attention (e.g., Lavie, 1995; Lavie & Tsal, 1994). According to perceptual load theory, when the task involves a high enough level of perceptual load to exhaust all available capacity (e.g., a large number of search stimuli that are all highly similar to the target or complex discriminations of conjunctions of features) there is simply none left to process any task-irrelevant stimuli. Visual cortex responses to task-irrelevant unattended stimuli are therefore reduced, resulting in their reduced perception. On the other hand, when the

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task involves only a low level of perceptual load (e.g., a few search stimuli or pop-out feature detection) any spare capacity that the attended task does not use "spills over" to the processing of irrelevant stimuli so that perception of distractors and accompanying neural responses remain unaffected by inattention (see Lavie, 2005, 2010, for reviews).

While providing a clear resolution to the long-going early versus late selection debate on the role of attention in perception, the mechanisms underlying reduced perception under high load (versus low load) need to be elucidated. Specifically, although a simple reduction in neural response signal may account for the well-established finding that high perceptual load in the task reduces perceptual processing, this may only be one part of the explanation. According to signal detection theory, successful visual detection and discrimination do not only depend on the strength of the signal (in other words, the signal gain) but also on the extent to which the signal is precisely tuned (Green & Swets, 1966). Thus, reduced perception, as well as reduced neural response under high load, may be the result of either reduction in the signal gain or broadening of the tuning profile of the population representations for a given stimulus, or both.

In the present study, we therefore examined whether reduced perception under load is due to a reduction in gain or broadened tuning or a combination of the two. We focused on perception of orientation, an elementary operation of visual perception, and assessed the effects of perceptual load on psychophysical measures of orientation tuning curves using a noise-masking paradigm (Baldassi & Verghese, 2005; Blake & Holopigian, 1985; Legge & Foley, 1980; Ling & Blake, 2009). Orientation perception is ideally suited to assess the effects of perceptual load on early visual responses as the obtained psychophysical tuning curves provide a link to the responses of the underlying population. Indeed, in many cases the characteristics of tuning curves recorded from single cells are strikingly similar to those obtained from human observers in behavioral tasks (for review see Neri & Levi, 2006) indicating that such psychophysical measures are particularly useful in revealing the underlying neurophysiological substrates.

Experiment 1

Observers performed a visual search task under either low or high perceptual load, while also detecting an oriented stimulus embedded in a noise mask (Figure 1). The orientation content of the mask was varied, while the orientation of the target remained constant. This allowed us to obtain contrast detection thresholds for each noise orientation in order to plot orientation tuning curves.

Method

Observers

Twelve observers, six of whom were female (aged 20–28), participated in the first experiment. All were recruited from the University College London subject pool, had normal or corrected-to-normal visual acuity, and were naïve as to the purpose of the study.

Apparatus and stimuli

Stimuli were created using MatLab (2007a, The MathWorks, Nattick, MA) and Psychophysics Toolbox (Brainard, 1997) and presented on a 21-in. monitor (1024 × 768 pixel resolution, 75-Hz refresh rate) in a darkened room. Viewing distance was maintained at 57 cm with a chin rest.

In all experiments reported, observers indicated the location of a vertically oriented Gabor patch (1.5° of visual angle in diameter, 6 c/°) which appeared with equal likelihood in one of two locations centered at 1° above or below fixation. The target patch was embedded within a round noise mask (15% root-mean square, RMS, contrast, 5° in diameter) presented at the center of the screen. The noise was low-pass spatial frequency filtered (10 c/° cutoff) and band-pass filtered in the orientation domain with a 20° bandwidth. The center frequency of the noise had one of seven possible orientations in each block: 0°, 8°, 16°, 24°, 32°, 40°, or 90° from vertical (Figure 1c). Noise band-pass orientations were angled symmetrically clockwise and counterclockwise from vertical in order to prevent off-channel looking (e.g., Blake & Holopigian, 1985).

A letter-search task was used to vary the level of perceptual load (Figure 1a). Eight dark gray letters (subtending 0.6° × 0.9° of visual angle) were presented together with the central noise mask, equidistant from fixation centered at 4.5° eccentricity. Participants searched for a target letter (Z or N) among either heterogeneous nontarget letters (X, E, K, L, H, M, F, or T; high-load condition) or homogenous nontarget letters (all Vs; low-load condition). Varying the similarity between distractors and target in this way is a well-established perceptual load manipulation that has been shown to effectively reduce or eliminate distractor interference (e.g., Lavie & Cox, 1997) and reduce sensitivity (e.g., as measured with d') to additional stimuli, presented in the periphery in dual-task settings (e.g., Carmel, Thorne, Rees, & Lavie, 2011; Macdonald & Lavie, 2008). Importantly, the effects of perceptual load in visual search have been dissociated from general effects of task difficulty,

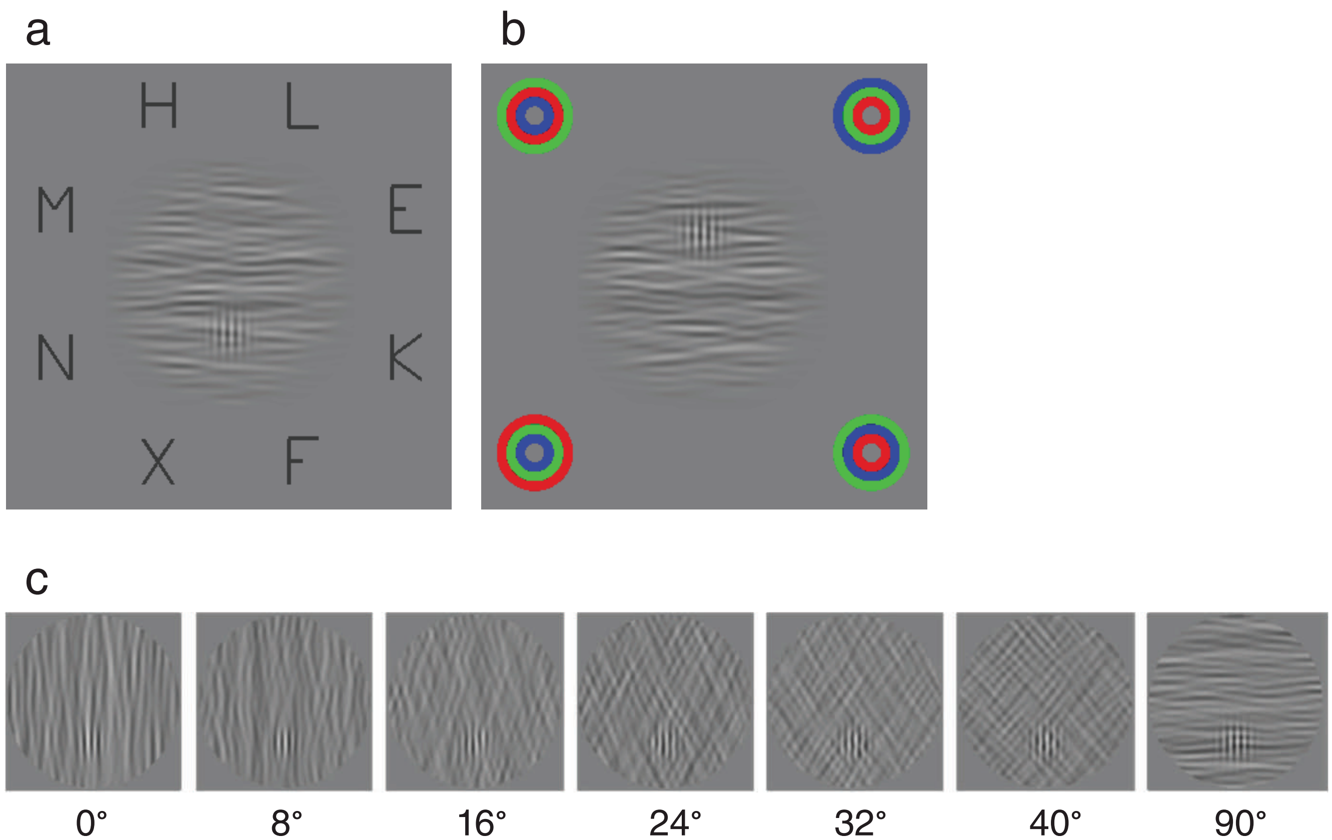

Figure 1. Schematic illustration of stimulus displays in the high-load conditions of Experiments 1 and 2. (a) In Experiment 1 observers performed a dual task, searching for a target letter (Z or N) among either heterogeneous nontarget letters (high-load condition, shown) or homogenous nontarget letters (all Vs, low-load condition) while detecting the location of a small Gabor probe presented in orientation band-passed noise. (b) In Experiment 2 observers performed a color-conjunction search task instead of the letter-search task. The target was always one of two predefined color conjunctions and appeared either among heterogeneous nontarget discs (high-load condition shown) or among homogeneous discs (low-load condition). (c) The central frequency of the orientation band-passed noise varied from being identical in orientation (0°) to being orthogonal in orientation (90°) to that of the target. The target orientation remained constant throughout the experiment at 0° (vertical).

pointing to search efficiency as one of the determining factors of perceptual load (Lavie & Cox, 1997; Roper, Cosman, & Vecera, 2013).

Procedure

At the beginning of each trial a fixation cross was presented at the center of the screen for 1200 ms followed by simultaneous presentation of all stimuli for 160 ms. Subsequently, participants responded first to the letter search and then to the orientation discrimination task, indicating whether the Gabor patch had been detected above or below fixation. Note that the orientation of the Gabor patch was fixed at 0° (vertical) across all trials. Noise band-pass orientations (0°–90°) and load levels (high vs. low) were blocked and their order counterbalanced across participants and sessions. Observers completed four sessions of 14 blocks each (resulting in four contrast thresholds obtained for each load condition and noise orientation; 40 trials per threshold estimate). Different sessions were conducted on separate days and observers rested for 2 min after each block.

Psychophysics

In all experiments, an adaptive staircase procedure (QUEST; Watson & Pelli, 1983) was employed to estimate contrast thresholds at 75% performance for the target patch at each noise band-pass orientation. Staircases for each noise orientation and load condition were blocked and their order pseudorandomized and counterbalanced across sessions and participants. In each of four sessions, a single threshold was obtained for each of the seven noise band-pass orientations under high and low perceptual load.

For each observer, Gaussian functions were fit to the data obtained from averaging the four contrast thresholds measured at each noise level. The functions were centered on 0° and assumed to be mirror

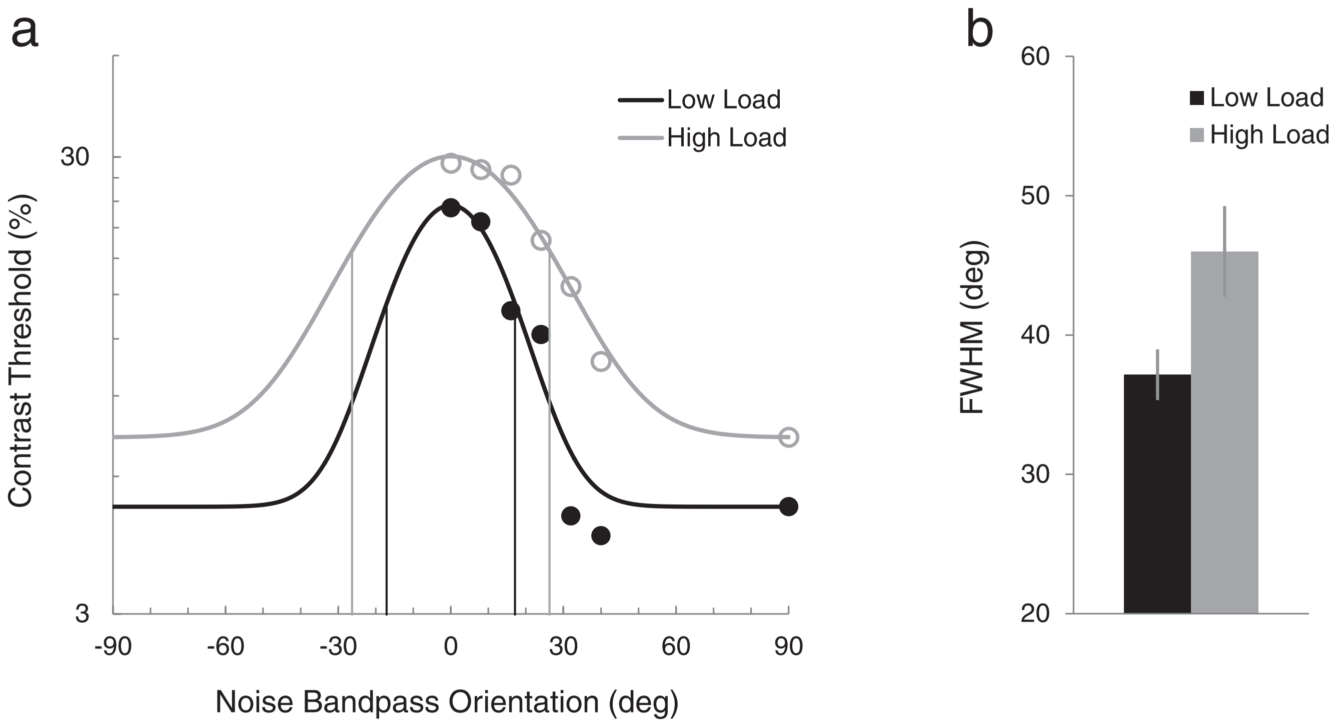

Figure 2. The effect of perceptual load on orientation tuning. (a) Example orientation tuning curves from one observer under low and high perceptual load in the letter-search task in Experiment 1. Contrast thresholds in the orientation detection task were fit with a modified Gaussian function. The vertical lines delineate the full width of the curve at half maximum (FWHM). (b) Mean bandwidth across 12 observers (FWHM). Error bars correspond to ± 1 *SE*.

symmetric. We then compared bandwidth (full width at half maximum, FWHM) parameters and contrast elevation from each fitted curve obtained under low and high perceptual load. Paired *t* tests were used to reveal significant parameter differences between the two attention conditions.

Results

High load in the letter-search task resulted in both reduced visual search speed, low load $M = 692$ ms, high load $M = 837$ ms, $t(11) = 8.299$, $p < 0.001$, and accuracy, low load $M = 93\%$, high load $M = 83\%$, $t(11) = 7.217$, $p < 0.001$, compared to low load, confirming the efficacy of our attentional manipulation.

In the orientation detection task, contrast thresholds steadily increased, indicating reduced sensitivity, when the difference between the target and mean noise orientation became smaller (Figure 2a). This confirms the efficacy of our noise-masking procedure. The orientation tuning curves showed a robust increase in contrast threshold across all noise orientations with high compared to low load (Figure 2a) and the averaged thresholds showed a significant increase from the low-load ($M = 10.4\%$) to the high-load ($M = 15.0\%$) condition, $t(11) = 4.017$, $p < 0.01$.

Importantly, the threshold elevation under high load was not uniform across the different noise orientations, indicating a change in the tuning bandwidth (Figure 2a, b). A paired *t* test on the estimated bandwidth parameters (FWHM) confirmed that high perceptual load significantly increased the tuning bandwidth by 8.9° on average, $t(11) = 3.480$, $p < 0.01$.

Experiment 2

The results of the first experiment suggest that reduced perception or inattentional blindness under high load is due to both reduced gain and broadening of the tuning. However, the manipulation of perceptual load through letter similarity in the letter search task may have involved added orientation content and thus additional external noise content in high-compared to low-load processing (since the target search among the more similar heterogeneous nontarget letters required discrimination of more orientations than the less similar and homogenous nontarget search in the low-load condition). The added noise in the orientation detectors could directly affect orientation tuning (see Dosher & Lu, 2000a, 2000b; Lu & Dosher, 1998). To test whether the effects of perceptual load on tuning can also be found in a load manipulation that neither varies the level of orientation information content nor the level of noise relevant for orientation perception, in Experiment 2 we replaced the letter search task with a color-conjunction disc search task. Observers searched for a uniquely colored target among homogeneous (low load) or heterogeneous colored discs (high load; Figure 1b).

Method

Ten observers (two of whom were male, 20–29 years old) participated in the second experiment. All had normal or corrected to normal vision and were naïve to the purpose of the experiment. None had participated in Experiment 1.

The procedure and stimuli were identical to Experiment 1, except that observers performed a color-conjunction task instead of the letter-search task: Four discs subtending 2° of visual angle were presented surrounding the Gabor patch and noise mask at four fixed locations equidistant from the center. The discs consisted of three concentric circles which were colored red, blue, or green. All three colors always appeared in a single disc but colors applied to specific circles varied, creating a total of six possible combinations. In both load conditions, participants searched the display for one of two predefined targets with a unique color combination. One of the two targets was presented on a random half of the trials while the other target appeared in the remaining trials. Three distractors were presented in the other locations. In the low-load condition the distractors were identical within each individual trial, while in the high-load condition each distractor had a unique color combination. The distractors in both conditions were randomly selected from the nontarget discs on each trial (with the constraint that in the high-load condition distractors could not be identical).

Results

The results showed that high load significantly reduced search accuracy, low load $M = 94\%$, high load $M = 81\%$, $t(9) = 6.890$, $p < 0.001$, and response speed, low load $M = 836$ ms, high load $M = 990$ ms, $t(9) = 8.787$, $p < 0.001$, demonstrating that this attentional manipulation was effective. As in Experiment 1, contrast thresholds were significantly increased under high perceptual load, averaged thresholds for high and low load were 15.2% and 11.2%, respectively, $t(9) = 4.140$, $p < 0.01$. More importantly, as illustrated in Figure 3, under high perceptual load in the search task the tuning bandwidth (FWHM) in the orientation discrimination task was again significantly increased, 13.9° on average, $t(9) = 3.147$, $p = 0.012$; thus, replicating the effects of perceptual load on gain and tuning with a load manipulation that involves no added orientation content.

Experiment 3

Previous research has demonstrated that in addition to increases in perceived contrast at attended locations, contrast sensitivity is reduced at unattended locations (e.g., Pestilli & Carrasco, 2005). The results of Experiments 1 and 2 lend support to this claim by showing increased contrast thresholds for target orientation detection under high compared to low load. This raises the possibility that a reduction in perceived contrast may mediate the effects of load we established. Indeed, a reduction in the perceived contrast can clearly explain the finding of reduced gain (higher contrast thresholds) under high load. It may also provide a plausible account for the observed change in tuning width under load. For example, the different mask orientations might be less discriminable at lower perceived contrast, leading to a broader tuning curve.

Although it has been shown previously that orientation discrimination thresholds remain unchanged within the 5% to 30% contrast range (e.g., Caelli, Brettel, Rentschler, & Hilz, 1983; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987) and changes in stimulus contrast have typically no effect on the orientation tuning curves of single neurons (e.g., Sclar & Freeman, 1982) it is unclear how this may translate precisely to the perceptual tuning curves obtained by employing the noise masking technique used here.

In Experiment 3 we, therefore, tested whether a reduction in the apparent noise mask contrast affects the width of the orientation tuning curve. To this end, the contrast of the noise mask was halved to emulate the reduction in apparent mask contrast under high perceptual load. Furthermore, in order to isolate the effect of reduced mask contrast on the tuning curve, and provide a powerful test for the effects of mask contrast to emerge unhindered by any additional task demands, observers performed the orientation discrimination task alone without any additional load task.

Method

Eight observers participated in Experiment 3 (five females, 21–29 years old), four of whom had also

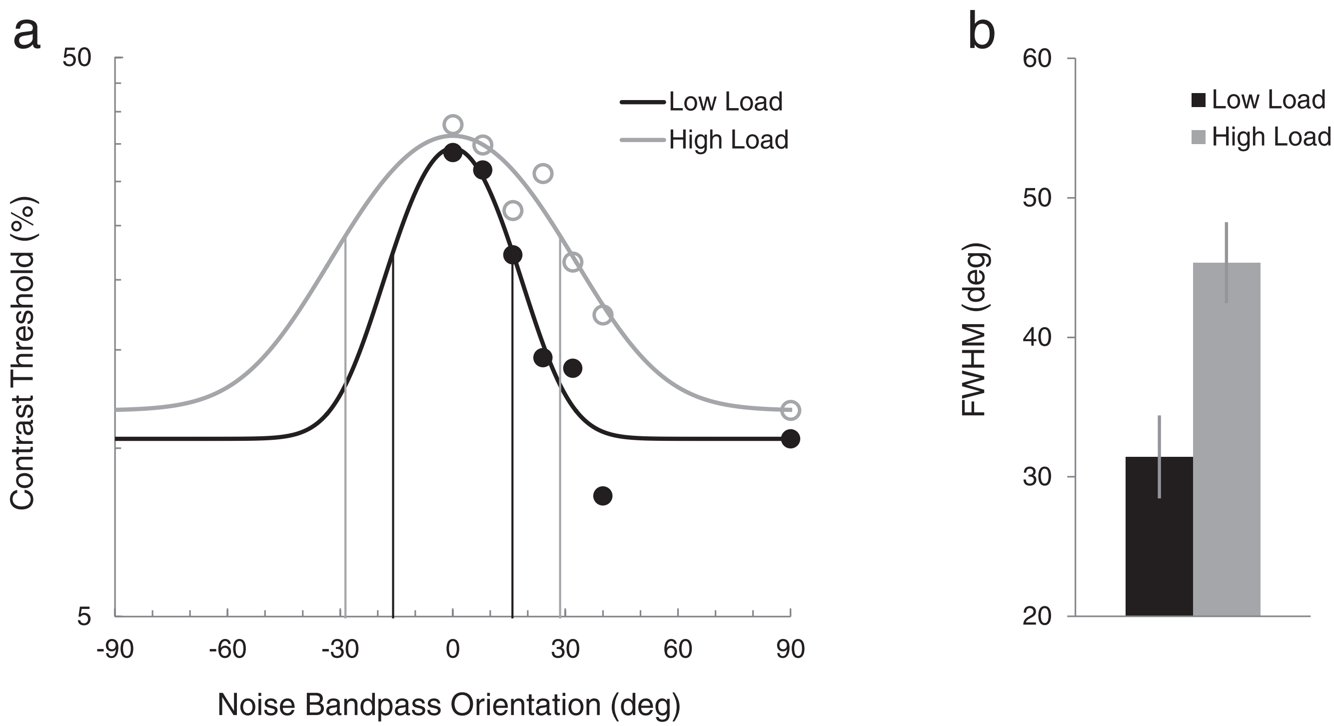

Figure 3. The effect of perceptual load on orientation tuning when orientation content in the search task was constant. (a) Example orientation tuning curves from one observer under low and high perceptual load in the color-conjunction search task in Experiment 2. The vertical lines delineate the full width of the curve at half maximum (FWHM). (b) Mean bandwidth (FWHM) across 10 observers. Error bars correspond to ±1 *SE*.

participated in Experiment 2. All observers had normal or corrected to normal vision and were naïve to the purpose of the experiment.

The stimuli and procedure were identical to those used in Experiment 1 except that observers now performed the orientation discrimination task in isolation (without any additional load task) and the mask contrast was either the same as before (15% RMS contrast) or half the level (7.5% RMS contrast). Mask contrast levels were blocked and their order counterbalanced across participants. Four thresholds were obtained for each noise mask contrast and noise orientation.

Results

As expected, the amplitude of the tuning curve increased significantly with higher mask contrast, threshold under high mask contrast $M = 11\%$, low mask contrast $M = 5\%$, $t(7) = 12.074$, $p < 0.001$. However, tuning bandwidth remained the same, high mask contrast $M = 30°$, low mask contrast $M = 34°$, $t(7) = 0.828$, $p = 0.435$. This result rules out a change in the effective contrast as a possible explanation for the change in tuning under load.

Discussion

Overall the present research establishes perceptual load as an important determinant of both neural sensory gain and tuning. These combined effects suggest a compelling explanation for the robust modulations of neural activity: High perceptual load has been shown to virtually eliminate neural response to unattended information over a wide range of tasks, stimuli, and cortical areas (see Lavie, 2005, 2010, for review). The present results provide a powerful likely mechanism that can explain the elimination of neural signals related to unattended information seen in previous studies. With both reduced signal and increased noise due to imprecise tuning in conditions of inattention under load, visual cortex response can no longer be discriminated from baseline levels of activity.

At the cellular level, neural response to orientation is determined not only by which orientation columns are stimulated but also by the strength of lateral interactions between the cell columns (Ferster & Miller, 2000). Although higher perceptual load is unlikely to modulate the response bandwidth of individual neurons (this appears to be determined simply by anatomical position, see also McAdams & Maunsell, 1999) high perceptual load could reduce the gain of individual neurons, thus leading to a modulation of lateral inhibitory interactions. Reduced lateral inhibition under high load would result in broadening of the population tuning due to reduced inhibitory inputs from neurons tuned to other orientations. Enhanced responses to normally suppressed orientations would broaden the overall population response, effectively increasing the level of noise in the sensory representation of a given orientation. In addition, the taking up of neural capacity in conditions of high perceptual load may lead to a reduced number of neurons responding to the orientation, and thus also reduce the amount of noise cancelation that is achieved through population averaging. With a smaller population of neurons responding, the inherent variability of single neuron responses is not averaged out as well, thus resulting in a noisier response showing as broadened tuning (Gilbert & Li, 2013).

Other manipulations of attention

Previous studies of the effects of attention on orientation perception have typically used spatial cueing to vary the allocation of attention. This research indicated a clear effect of spatial cuing on gain (Baldassi & Verghese, 2005; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Eckstein, Shimozaki, & Abbey, 2002; McAdams & Maunsell, 1999) but has typically failed to show any effects on tuning, even when using similar noise masking techniques as that reported here (Baldassi & Verghese, 2005; Eckstein et al., 2002; Murray, Sekuler, & Bennett, 2003). Our findings raise the possibility that spatial cuing effects on tuning may require a higher level of perceptual load.

Indeed our study conclusion is consistent with Lu and Dosher's (1998; Dosher & Lu, 2000a, 2000b) suggestion that the effects of spatial cuing depend on a noise exclusion mechanism with a limited capacity. However the previous support for this suggestion may not necessarily indicate broadening of orientation tuning with higher perceptual load because the effects on noise exclusion were shown only for orientation discrimination from among white noise, and thus cannot inform about the overall orientation tuning profile, unlike the present study procedure. Moreover, our results have generalized the effects of perceptual load across a color-based manipulation that does not vary at all the level of external noise directly involved in orientation perception (Experiment 2). Our findings of broadened tuning under higher perceptual load are therefore not due to an increase in the level of external noise presented under higher load.

Notice that our findings also generalized across more sparse displays with a smaller number of elements that were more widely spaced in Experiment 2 as compared to Experiment 1, as well as in many other previous load in visual search studies (e.g., Carmel, Saker, Rees & Lavie, 2007; Forster & Lavie, 2008; Lavie & Cox, 1997; Macdonald & Lavie, 2008) while our task required local binding of color and position over the small scale of each ring-made disc shape presented (see Figure 1b). Moreover, the effects of perceptual load on tuning were if anything larger in this design (e.g., the average increase in the tuning curve width was 13.9° in Experiment 2 compared to 8.9° average increase in Experiment 1). This makes it unlikely that the effects of perceptual load on tuning could be due to increased lateral inhibition among more dense and proximal arrays or to greater competitive interactions between more adjacent stimuli (e.g., Torralbo & Beck, 2008). Instead, these findings provide further support for the notion of limited perceptual capacity as originally stipulated in Lavie's load theory (1995). However, as the two tasks used in Experiments 1 and 2 likely involved different neural substrates, a direct test of whether the spacing between the search items within each task would have any effect on the tuning (as measured in the fovea) could prove an interesting future direction.

Another previous report indicating that orientation detection is less precise in dual- versus single-task conditions (Lee, Itti, Koch, & Braun, 1999) is also consistent with the present findings. However, in Lee et al.'s (1999) study attention had to be divided between two sets of orientations in the dual task but not in the single-task condition. The single and dual task comparison therefore did not only involve increased attentional load but also increased orientation noise, as well as added demands on memory and response.

Our manipulation of the level of perceptual load in dual-task conditions only, together with our generalization of results across manipulations of perceptual load that involved no change in the level of orientation noise, avoids these pitfalls and clearly demonstrates that it is the level of perceptual load per se that is critical for the effect of attention on tuning. Moreover, we have shown that engaging attention in a high perceptual load task leads to changes in gain and tuning without relying on spatial cueing or target location uncertainty. Our findings thus clarify that while high perceptual load is a necessary condition for the effect of attention on tuning, spatial cueing is neither necessary nor sufficient for an effect on tuning. Furthermore, an account in terms of feature-based attention (Ling, Liu, & Carrasco, 2009; Martinez-Trujillo & Treue, 2004) is not viable either since (a) our manipulation of perceptual load did not involve any cuing of the orientation feature, (b) the orientation of the target was always constant, and (c) if feature based attention was influenced by increased load in the letter-search task in Experiment 1, high load in the task should lead to increased feature based attention for the target (opposite to our results) as orientation discrimination for the target letter becomes more demanding.

Future research

Due to the invasive nature of cell recording, electrophysiological measures of neural tuning cannot be obtained in the intact human brain. Our findings, however, suggest that conditions that constitute high perceptual load for nonhuman primates would also lead to attentional modulation of orientation tuning. In the human brain this can be indirectly deduced through neuroimaging research using decoding techniques to assess tuning at the neural population (rather than single cell) level (Kamatani & Tong, 2005). Specifically, estimating voxel-based orientation tuning functions (e.g., Serences, Saproo, Scolari, Ho, & Muftuler, 2009) should reveal broadened tuning under high perceptual load and, additionally, allow for quantifying the effects of high perceptual load on the gain and tuning of neural populations in different brain areas. These should prove interesting avenues for future research.

Conclusion

Our results demonstrate that high perceptual load in a letter- or color-based search task leads to both reduced signal gain and broadened tuning for orientation detection. These results suggest that a combined mechanism, involving both reduced neural response gain and reduced precision of tuning, underlies the reduced sensory processing and accompanying inattentional blindness found under high perceptual load.

All authors contributed to developing the study concept and design as well as to data interpretation. M. S. performed implementation, testing, data collection, and analysis. B. B. contributed to the data analysis. N. L. and M. S. wrote the manuscript.

Keywords: perceptual load, attention, orientation, tuning, gain

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