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Attention enhances contrast sensitivity at cued and impairs it at uncued locations

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Abstract

Transient covert attention increases contrast sensitivity at the target location with an informative spatial cue. Here we explored whether an uninformative spatial cue (50% valid with two possible locations) also increases contrast sensitivity and whether contrast sensitivity is altered at the uncued location as compared to the neutral condition. For all four observers, transient covert attention had both a benefit and a cost: it enhanced contrast sensitivity at the cued location and impaired contrast sensitivity at the uncued location at both parafoveal and peripheral positions. These results are consistent with the idea of limited resources, and indicate that transient attention helps control the expenditure of cortical computation.

Keywords: Transient covert attention; Contrast sensitivity; Cue automaticity; Limited resources

1. Introduction

Our capacity to process visual information is limited by the high-energy cost of the neuronal activity involved in cortical computation. The limited energy expenditure that the brain can afford necessitates machinery for the system to allocate energy according to task demand (Lennie, 2003). This limited capacity entails a selective process—attention—that enables us to process effectively vast amounts of visual information by selecting relevant information from noise. In this study we investigated the possibility that covert attention helps to control the expenditure of cortical computation by trading contrast sensitivity across attended and unattended areas of the visual field, even with impoverished displays and simple tasks. Specifically, we assessed contrast sensitivity at both attended and unattended locations.

Attention can be allocated overtly, by directing one's gaze towards a location of the visual scene, or covertly, by attending to an area in the periphery without actually directing gaze towards it. Spatial covert attention enhances visual performance in a specific area of the visual field, without eye movements to that location (Posner, 1980). There is consensus that performance is improved at the attended area; however there is less agreement regarding the fate of information that is not directly attended (Eriksen & Hoffman, 1974; Kinchla, 1992; Rock & Gutman, 1981). Some have proposed that information beyond the focus of attention is barely perceived (Pashler, 1998) and most hypotheses regarding the distribution of attention in the visual field assume that information outside the attended area is not processed (e.g., Cheal, Lyon, & Gottlob, 1993; Eriksen & Hoffman, 1973; Eriksen & St. James, 1986; Posner, 1980). However, several studies have shown that information

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beyond the focus of attention affects performance, indicating that it is processed to a certain degree (Cameron, Tai, Eckstein, & Carrasco, 2004; Carrasco & Yeshurun, 1998; Cave & Cepeda, 1995; Eriksen, 1990).

A growing body of behavioral evidence demonstrates that there are two systems of covert attention: 'sustained' (endogenous) and 'transient' (exogenous). The former corresponds to the common intuition that we can monitor information at a given location at will, whereas the latter corresponds to an automatic, involuntary orienting response to a location where sudden stimulation has occurred. Experimentally, these systems can be differentially engaged by using distinct cues: central symbolic cues direct attention in a goal or conceptually driven fashion in ~300 ms, whereas peripheral transient cues (hereafter called *peripheral cue*) do so in a stimulus driven, automatic manner in ~100 ms. This involuntary shift may occur even when the cues are uninformative or impair performance (Cheal & Lyon, 1991; Jonides, 1981; Nakayama & Mackeben, 1989; Yantis, 1996).

A cue is considered valid when it indicates the target location, and it is considered invalid when it indicates a non-target location. For both sustained and transient attention reaction time (RT) is faster at valid-cued target locations and slower at invalid-cued ones (Chastain & Cheal, 1997; Eriksen & Hoffman, 1972; Theeuwes, Kramer, & Atchley, 2001). However, RT data indicating benefits and costs could result from changes in speed of processing, discriminability, or decision criteria (Carrasco & McElree, 2001; Dosher & Rosedale, 1997; Reed, 1973) and do not directly reveal information regarding the quality of the signal. It has also been shown that accuracy is higher at the valid-cued than at the invalid-cued locations (Bashinski & Bacharach, 1980; Henderson, 1991). Although assessing the effects of attention by comparing performance at the valid and invalid conditions is useful for distinguishing between sensitivity-based and decision-based explanations of the cueing effect, this comparison cannot determine whether such an effect is due to an enhanced (or faster) signal at the cued location, to a diminished (or slower) signal at the uncued location, or to both. To pinpoint the source of the attentional effect, it is necessary to compare performance in both the valid and invalid conditions with a neutral condition, in which the cue does not indicate a stimulus location but only the timing of the display onset (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Hawkins et al., 1990; Lu & Dosher, 1998; Luck et al., 1994).

In this study, we evaluate the effect of transient attention on contrast sensitivity at both the attended and unattended locations. We know that at the attended area transient attention increases sensitivity in an orientation discrimination task with an informative cue, i.e., when the cue indicates target location but not its orientation (Cameron, Tai, & Carrasco, 2002; Carrasco et al., 2000; Dosher & Lu, 2000; Lu & Dosher, 1998). When a peripheral cue is always valid in terms of location, it is possible that some of its effect could be due to a conceptually-driven, voluntary component of attention. To eliminate this possible contamination, we ensured cue unpredictability by cueing the target only 50% of the time, and by asking observers to report the orientation of the stimulus indicated by a response cue (a line displayed after stimuli offset). Indeed, observers could have entirely disregarded the cue and based their responses only on the information accumulated during stimulus presentation and still attained the same overall performance level. The use of the unpredictive cue and the response cue enabled us to isolate the purely automatic orienting of attention. Given that the transient peripheral cue is thought to be automatic (Jonides & Yantis, 1988; Yantis & Jonides, 1984), even an uninformative cue (which indicates neither target location nor orientation) should exert an effect. If an uninformative cue were to increase sensitivity, it should benefit performance in a task that improves with contrast, such as orientation discrimination (Cameron et al., 2002; Nachmias, 1967; Skottun, Bradley, Sclar, Ohzawa, & Freeman, 1987).

To investigate the effect of transient covert attention on contrast sensitivity at both the attended and unattended locations, we assessed the effects of an uninformative peripheral cue by comparing the stimulus contrast necessary for observers to perform an orientation discrimination task at a given performance level. Generally, with invalid cue trials, although attention is diverted away from the target location at stimulus onset, observers have information regarding the target location because its identity differs from the distracter. In contrast, in this study, observers did not know where the target was, and to perform the task they had to process the identity of the stimuli presented at both locations.

Previous studies have examined the effect of attention on contrast sensitivity at parafoveal locations (Cameron et al., 2002; Carrasco et al., 2000; Dosher & Lu, 2000; Lee, Koch, & Braun, 1997; Lu & Dosher, 1998, 2000; Solomon, 2004; Solomon, Lavie, & Morgan, 1997). We investigated the effects of transient attention at both parafoveal and peripheral locations to assess whether the benefit and cost varied as a function of the distance between the attended and unattended stimuli.

Observers were asked to discriminate the orientation of one of two Gabor patches simultaneously presented left and right of fixation (at either 4 or 9° of eccentricity). Contrast sensitivity was measured at the cued (valid cue) and uncued (invalid cue) locations, and compared with the contrast sensitivity obtained at the same locations when the target was preceded by a cue presented at fixation (neutral cue). Based on models of signal enhancement, which propose that attention directly improves the quality of the stimulus representation (Bashinski & Bacharach, 1980; Cameron et al., 2002;

Carrasco et al., 2000; Liu, Pestilli, & Carrasco, 2005; Lu & Dosher, 1998; Muller et al., 1998), we hypothesize that sensitivity will be increased at the cued location. Based on models of distracter exclusion, which propose that attention allows us to exclude distracters from the signal by narrowing the filter processing the stimulus (Baldassi & Burr, 2000; Davis, Kramer, & Graham, 1983; Foley & Schwarz, 1998; Morgan, Ward, & Castet, 1998; Palmer, 1994; Solomon et al., 1997), we hypothesize that sensitivity will be reduced at the uncued location.

2. Method

2.1. Observers

Four observers with normal or corrected-to-normal vision participated in this experiment. All observers but one (FP) were naive as to the purpose of the study; two (FP & JG) were trained psychophysical observers.

2.2. Apparatus

Stimuli were displayed on a gamma-corrected P260 IBM 21″ Multiscan color monitor in a dark environment. A video attenuator drove the green gun of the monitor to increase rendering precision at low contrast levels from 8 bits to 12 bits (Pelli & Zhang, 1991). The background luminance was set to the middle of the monitor range, 18 cd/m^2.

2.3. Stimuli

The stimuli were generated and presented on a Power Macintosh computer using MATLAB 5.2.1 and the *Psychophysics Toolbox* (Brainard, 1997; Pelli, 1997). A small dark circle of 0.1° of visual angle in diameter was used as a fixation point. Two Gabor patches (2° of visual angle in diameter and σ of 1.1°) were presented on the horizontal meridian either at 4° or 9° eccentricity to the left and right side of the central fixation point. Each Gabor had an independent, randomly chosen tilt of ±4° from vertical and spatial frequency of 4 c/deg. The cue, a 0.4° diameter dark filled circle, appeared either 1.5° above the center of one of the Gabor patches (peripheral cue), or at the center of the screen (neutral cue). The response cue, a 0.5° horizontal line was equally likely to appear to the left or the right of fixation, indicating to the observer which Gabor's orientation should be discriminated.

2.4. Procedure and design

All observers viewed the display binocularly, fixating at the center of the screen throughout the entire block. Fig. 1a illustrates a trial sequence. In each trial, a 40 ms cue appeared either above one of the two stimulus locations (peripheral) or at fixation (neutral). After a 60 ms ISI the two tilted Gabor patches were simultaneously presented to the left and right of the fixation point on the horizontal meridian for 100 ms. Given that about 250 ms are needed to execute goal directed saccades (Mayfrank, Kimmig, & Fischer, 1987), no eye

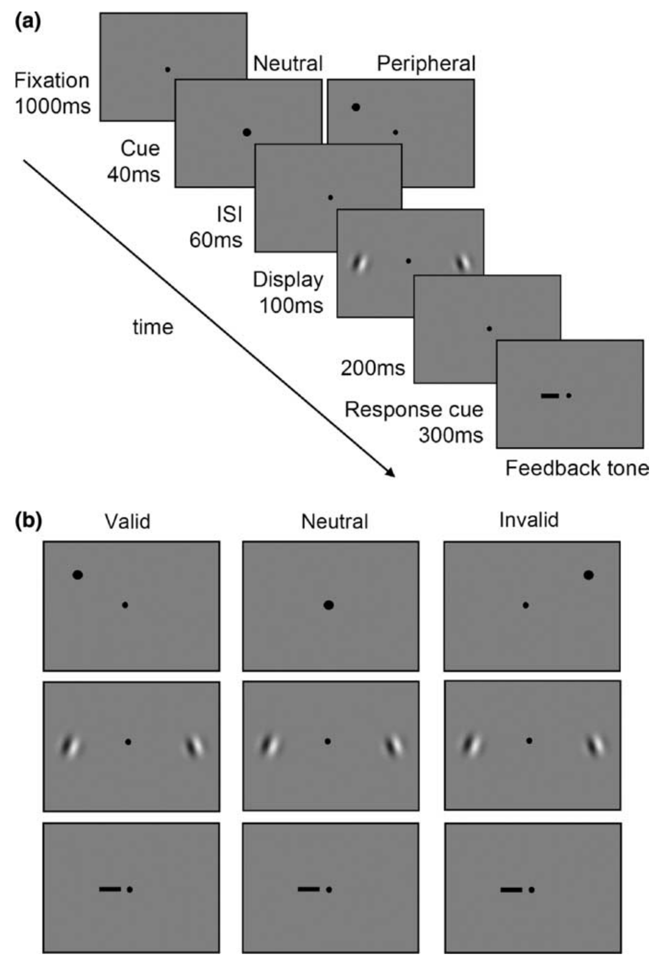


Fig. 1. (a) *A trial sequence*. Following a fixation point, a cue appeared either above one of the two Gabor locations (peripheral cue) or at fixation (neutral cue). After an interstimulus interval (ISI), two Gabors were simultaneously presented (randomly oriented to the left or to the right) on the horizontal meridian for 100 ms. After a 200 ms interval, a response cue appeared at fixation to indicate the target Gabor for which the observer had to report the orientation. On one third of the trials the response cue pointed to a precued Gabor. On another third of the trials it pointed to the Gabor that was not precued. In the remaining trials the precue was presented in the center of the screen and the response cue was equally likely to indicate the Gabor to the right or to the left of fixation. (b) *Examples of types of trials*. In a *valid* trial the locations indicated by the peripheral cue and by the response cue matched. In an *invalid* trial the locations indicated by the peripheral cue and by the response cue did not match. In a *neutral* trial the cue was presented at fixation and the response cue indicated the left Gabor in half of the trials and the right Gabor in the other half.

movements could occur between cue onset and stimulus offset. After 200 ms, a 300 ms response cue was presented at fixation indicating the location of the target. A feedback tone sounded only after correct responses.

Observers performed the 2AFC orientation discrimination task responding with the index and middle finger of their dominant hand. There were three experimental conditions (Fig. 1b): (a) In the *valid-cue* condition the observer was to discriminate the tilt of the Gabor preceded by the peripheral cue, i.e., the cue and the response cue indicated the same location; (b) in the *invalid-cue* condition the observer was to discriminate the tilt of the Gabor not preceded by a cue, i.e., the peripheral cue and the response cue indicated the opposite locations; (c) in the *neutral-cue* condition neither of the two stimulus locations was indicated by the cue and the observer was to discriminate the tilt of the Gabor indicated by the response cue. In both valid-cue and invalid-cue conditions the cue preceded one of the two Gabor patches, but its presence did not provide information regarding either target orientation or its location, because the validity of the cue was determined by the response cue.

Contrast thresholds were measured using a modified QUEST staircase procedure (Watson & Pelli, 1983) with an 82% performance criterion and ß of 3.5 for 50-trial runs. Three QUEST runs were interleaved in each block to ensure that observers could not adopt a different strategy for the three different cue conditions—valid, invalid and neutral. Following 250 practice trials per condition, each observer performed 3750 experimental trials, which contributed to 25 contrast threshold estimations per condition at each eccentricity.

3. Results

Contrast thresholds were obtained for the valid-, invalid-, and neutral-cue conditions at 4° or 9° eccentricity. To quantify the magnitude of the attentional effect, we calculated the ratio of the contrast sensitivity (1/median threshold) for valid vs. neutral cue, and invalid vs. neutral cue at both eccentricities (Fig. 2a). No difference between the two cue conditions would yield a ratio = 1. A benefit in contrast sensitivity would result in values >1; a cost would yield values <1. The average across observers is reported in the left-most columns (gray background). The valid:neutral cue ratio shows a benefit (First and third bars for 4° and 9° eccentricity, respectively), whereas the invalid:neutral cue ratio shows a cost (Second and fourth bars for 4° and 9° eccentricity, respectively). This pattern of results was consistent for all observers: values >1 for valid:neutral and <1 for invalid:neutral ratios (except FP at 9° eccentricity).

By directly comparing contrast sensitivity at cued and uncued locations, we found a relatively high and constant attentional effect. We assessed the overall attentional effect (black vertical lines) and found that on average, the valid:invalid ratio was 1.23 at parafovea (ranges 1.14–1.33 for individual observers) and 1.21 at periphery (ranges 1.19–1.26 for individual observers). The attentional effect results from both a benefit (valid:neutral ratio) and a cost (invalid:neutral ratio); with the average benefit greater than the cost.

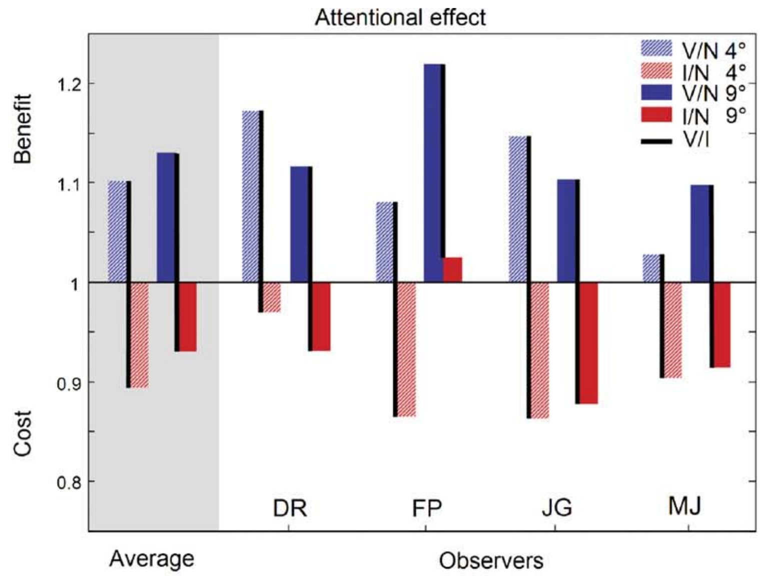
Fig. 2b illustrates that the data for individual observers were consistent with the overall frequency distributions. The histograms represent the threshold values obtained for individual observers in each cue condition at 4° and 9° of eccentricity. Although the absolute contrast threshold and the spread of the distribution varied across observers, the valid cue (first and fourth row histograms) improved performance and the invalid cue (third and sixth row histograms) impaired performance with respect to the neutral cue for each individual observer at both eccentricities (except FP, who had no cost at 9° eccentricity).

A within-subjects 2-way analysis of variance (*cueing condition*: neutral vs. valid vs. invalid; *eccentricity*: 4° vs. 9°) on the log-transformed contrast thresholds confirmed these results. Both main effects were significant: cueing condition ($p < 0.001$) and eccentricity ($p < 0.001$). Contrast thresholds were lower for the valid than neutral condition ($p < 0.001$), which in turn were lower than for the invalid condition ($p < 0.001$). They were also lower for the parafoveal than peripheral locations. The lack of a significant interaction between these two variables ($p > 0.2$) indicates that the cueing effect was similar at both eccentricities and independent of contrast threshold.

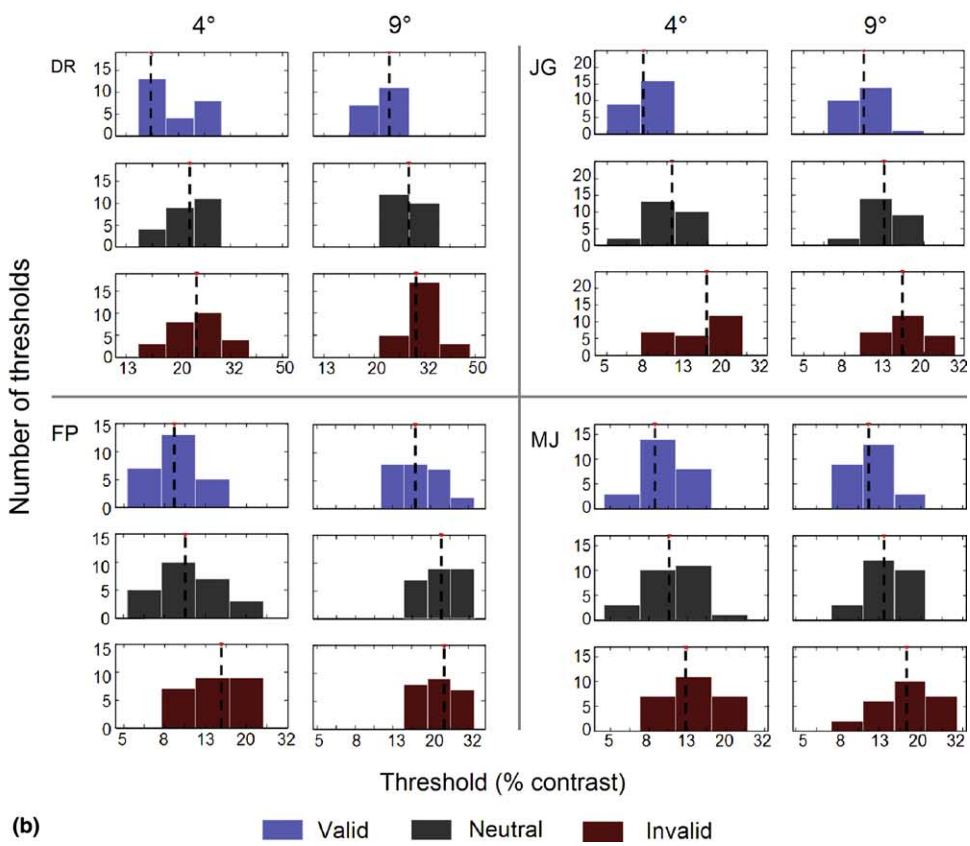
4. Discussion

In this study we investigated the effects of transient attention on contrast sensitivity at both parafoveal and peripheral locations. Comparing valid and invalid trials provides an estimation of the absolute effect of attention, but only by using a neutral cue can one assess whether contrast sensitivity is enhanced at the target location, diminished at the distracter location, or both.[1] The present data indicate that transient attention causes both a benefit and a cost in contrast sensitivity, and that the former is slightly greater than the latter. The same pattern of results, and of comparable magnitude, was obtained at both parafoveal and peripheral locations. The neutral cue used here is an appropriate baseline to

[1] Dosher and Lu (2000) manipulated *sustained* attention and mentioned that "neutral cues yielded accuracies intermediate between those for valid and invalid cues [...]. This result suggests that the [sustained] attentional effect in high external noise reflects both costs and benefits relative to neutral performance." (p. 142, footnote 1).



(a)



(b)

Fig. 2. (a) *Attentional effect*. This figure depicts the ratios of the medians of the sensitivity (1/median threshold) in each condition. The valid:neutral (*V*/*N*) ratio indicates the magnitude of the benefit resulting from allocating attention to the target location. The invalid:neutral (*I*/*N*) ratio indicates the magnitude of the cost resulting from allocating attention to the non-target location. A ratio of one would indicate no effect of attention on contrast sensitivity. A ratio >1 indicates a benefit (sensitivity in the valid condition is higher than sensitivity in the neutral condition). A ratio <1 indicates a cost (sensitivity in the invalid condition is lower than sensitivity in the neutral condition). Black vertical lines indicate the overall attentional effect, i.e., the valid:invalid ratio (*V*/*I*). First and second bars represent the benefit and cost at 4° of eccentricity. Third and fourth bars represent the benefit and cost at 9° of eccentricity. The gray shaded area highlights the averaged data. Data for individual observers are reported on a white background. (b) *Distributions of the measured thresholds*. The histograms represent the thresholds obtained for each individual observer in each cue condition at 4° and 9° of eccentricity. First- and fourth-row histograms represent the threshold obtained for the valid condition. Second- and fifth-row histograms represent the thresholds obtained in the neutral cue condition. Third- and sixth-row histograms are the thresholds obtained in the invalid cue condition. Dashed vertical lines indicate the median values.

assess benefit and cost at the cued and uncued locations, respectively.[2] We found that compared to a neutral cue, a peripheral cue adjacent to an upcoming stimulus improves contrast sensitivity at that location and reduces contrast sensitivity at another location, even though the cue is uninformative with regard to both identity and target location. This result shows that transient attention automatically enhances contrast sensitivity at an attended location and decreases it at the unattended location. Whereas information at the attended location is processed to a greater degree than in the neutral condition, information processed outside of the focus of attention is processed to a lesser degree. These results are discussed with regard to the ideas of cue automaticity, attentional mechanisms, and limited resources.

4.1. Automaticity of the peripheral cue

Previous studies have shown that transient attention increases contrast sensitivity when the cue is informative with regard to target location (Cameron et al., 2002; Carrasco et al., 2000; Foley & Schwarz, 1998; Lu & Dosher, 1998, 2000; Solomon et al., 1997). In the present study the cue was not predictive at all (see also, Carrasco, Ling, & Read, 2004; Liu et al., 2005; Solomon, 2004). Observers could have not attempted to differentially process the stimuli because the role of the stimuli—target vs. distracter—was only revealed by the response cue. Moreover, because staircases for the three cue conditions—valid, neutral and invalid—were interleaved, observers could not have adopted a different strategy for each cue condition.

When a peripheral cue is always valid in terms of location, it is possible that some of its effect could be due to a conceptually-driven, voluntary component of attention. The comparable magnitude of the benefit of transient attention on contrast sensitivity obtained here and when the peripheral cue is always valid (Cameron et al., 2002; Carrasco et al., 2000), supports the notion that transient attention is stimulus driven and automatic (Jonides, 1981; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Yantis, 1996). It is worth noting that threshold differences of this magnitude have been shown to improve performance significantly in orientation discrimination tasks (Cameron et al., 2002; Carrasco et al., 2004).

Recently, Solomon (2004) conducted a study in which he measured contrast sensitivity when either one (predictive cue) or multiple (non-predictive cue) locations were simultaneously precued. His results are consistent with the present findings regarding the enhanced sensitivity at the cued location, as well as the overall attentional effect, computed by comparing sensitivity at valid- and invalid-cue locations. Moreover, comparing valid- vs. invalid-cue trials, he found that a single-peripheral cue and multiple cues enhanced contrast sensitivity to a similar degree. This finding differs from other studies in which performance was compared for single and multiple cues (Cameron et al., 2002; Talgar et al., 2004; Yeshurun, 2004; Yeshurun & Levy, 2003).[3] In contrast to Solomon's results, all these studies indicate that the spatial specificity of the cue matters.

4.2. Attentional mechanisms

The overall attentional effect is consistent across observers and eccentricities. Previous studies have shown that performance is enhanced at cued locations in conditions of suprathreshold single target displays, without any local or global mask or distracters, and when there is no location uncertainty regarding the target location. Under such conditions, signal enhancement is the most likely mechanism to account for the improved contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2000; Carrasco, Williams, & Yeshurun, 2002). Other studies have found external noise reduction as the main mechanism of attentional benefit in the presence of external noise, such as distracters or masks (Cameron et al., 2004; Foley & Schwarz, 1998; Lu & Dosher, 2000; Smith, 2000; Smith, Ratcliff, & Wolfgang, 2004). The existence of both benefit and cost is consistent with models of signal enhancement and distracter exclusion, and suggests that these mechanisms affect contrast sensitivity concurrently. On the one hand, the finding that the benefit at the cued location is of similar magnitude to the one when the target was presented by itself in the absence of added external noise (Cameron et al., 2002; Carrasco et al., 2000) suggests that the benefit is due to an effect restricted to the cued location. On the other hand, the diminished sensitivity at the invalidly cued location indicates that transient attention also exerts its effect by diminishing the signal outside the

[2] In a letter identification task contingent on contrast sensitivity, the performance difference between a single-peripheral cue and a distributed-neutral cue (the same peripheral cue at all locations) was comparable to the difference between a single-peripheral cue and a central-neutral cue (Talgar, Pelli, & Carrasco, 2004). These findings ruled out the possibility that the benefit in performance brought about by transient attention could be due to a reduction of the attentional spread by the central-neutral cue (e.g., Pashler, 1998). The same pattern of results emerged in an acuity task (Cameron et al., 2002).

[3] The performance difference between a single-peripheral cue and a distributed-neutral cue (the same peripheral cue at all locations) was comparable to the difference between a single-peripheral cue and a central-neutral cue in a letter identification task contingent on contrast sensitivity (Talgar et al., 2004) as well as in an acuity task (Cameron et al., 2002). Similarly, transient attention degrades temporal resolution regardless of whether the neutral cue is composed of either two long horizontal lines appearing above and below the entire display (Yeshurun & Levy, 2003) or several small horizontal bars appearing all possible target locations (Yeshurun, 2004).

attended area (Davis et al., 1983; Lu & Dosher, 1998, 2000; Morgan et al., 1998; Shiu & Pashler, 1995; Solomon et al., 1997). Thus, consistent with previous research, the present study supports the concurrent effects of signal enhancement and external noise reduction, particular by distracter exclusion (Cameron et al., 2004; Lu & Dosher, 1998).

4.3. Limited resources

The idea that stimuli compete for limited resources has been long proposed (Broadbent, 1958; Desimone & Duncan, 1995; Neisser, 1967; Treisman, 1960) and it has been supported by electrophysiological (Luck, Chelazzi, Hillyard, A, & Desimone, 1997; Moran & Desimone, 1985; Reynolds, Pasternak, & Desimone, 2000), neuroimaging (Holcombe, Kanwisher, & Treisman, 2001; Luck et al., 1994; Pinsk, Doniger, & Kastner, 2004), and behavioral (Eriksen & Schultz, 1977; Yantis & Jonides, 1990) studies. For instance, the biased-competition hypothesis, which states that target and non-targets compete for processing capacity in visual search, is based on the limited capacity and selectivity assumptions.

Single unit recording studies in awake, behaving macaque monkeys have shown that attention can increase the response of neurons as early as V1 (Gilbert, Ito, Kapadia, & Westheimer, 2000; Motter, 1993; Reynolds & Chelazzi, 2004; Reynolds et al., 2000). By presenting two stimuli simultaneously and having the monkey detect the presence of a grating at the cued location (attended) while ignoring the other (unattended) grating, Reynolds et al. (2000) tested the biased-competition hypothesis with single cell recording in macaque monkeys. The effect of attention was comparable to a $\sim$50% increase in effective stimulus contrast, with a $\sim$25–30% increase in firing rate in the dynamic range. This supports the view that attention acts not only in cluttered displays, but also in conditions of reduced display complexity, to meet the demands imposed by the brain's limited capacity to process information. Moreover, both single cell recordings with macaque monkeys (Martinez-Trujillo & Treue, 2002) and fMRI studies with humans (Pinsk et al., 2004) have found such competitive interaction when the two stimuli are presented close together or at distant locations in the visual field.

Some authors have supported the view of an unlimited capacity perceptual process (Eckstein, Thomas, Palmer, & Shimozaki, 2000; Palmer, Verghese, & Pavel, 2000; Solomon, 2004). Others have asserted that attentional selection is required only once the perceptual load exceeds the capacity limit of the system (Lavie, 1995; Lavie & Tsal, 1994). The present findings—enhanced contrast sensitivity at the attended location and reduced sensitivity at the unattended location—question these ideas. The findings that cueing the target location reduces, but does not eliminate, either the set size effect (performance decreases with increasing number of distracters), the eccentricity effect (performance decreases as target eccentricity increases), or the effect of distracters in search tasks, have been considered to indicate that covert attention is not completely effective in excluding the processing of the unattended, nonrelevant items (Cameron et al., 2004; Carrasco & Yeshurun, 1998; Foley & Schwarz, 1998). A model that assumes limited capacity with parallel processing (Cameron et al., 2004; Carrasco & Yeshurun, 1998; McElree & Carrasco, 1999) would yield improved target processing at the attended location, as well as diminished processing of unattended items. A selective process does not necessarily entail *exclusion*; perceptual efficiency may simply result from an improved control of the expenditure of cortical computation. *More* processing for the attended information and *less* for the unattended or distracting information is indeed efficient also in conditions of low visual load, as in the case of our impoverished displays.

Given that the brain's energy consumption does not change with normal variations in mental activity (Clarke & Sokoloff, 1994), the high bioenergetic cost of spikes requires the brain not only use representational codes that rely on very few active neurons (Barlow, 1972), but also to allocate its energy resources flexibly according to task demand. The energy limitations, which require that only a small fraction of the machinery can ever be engaged concurrently, provide a neurophysiological basis to the idea that selective attention arises from the brain's limited capacity to process information (Lennie, 2003).

5. Conclusion

It has been established that transient attention enhances contrast sensitivity at the attended location (Cameron et al., 2002; Carrasco et al., 2004; Carrasco et al., 2000; Lu & Dosher, 1998), and that the higher the contrast the higher the neuronal firing rate (Campbell, Maffei, & Piccolino, 1973; Fiorentini & Maffei, 1973; Tolhurst, Movshon, & Thompson, 1981). By manipulating transient attention in an orientation discrimination task that depends on contrast sensitivity, this study is the first to show that relative to the neutral condition differences in sensitivity at attended and unattended locations are due to a benefit at the attended and a cost at the unattended locations. This finding indicates a processing trade-off even in a simple task with an impoverished display: the benefit brought about at the attended location has a concomitant cost at the unattended location. This result is consistent with the limited bioenergetic resources of the system, and lends support to the idea that transient attention aids to control the expenditures of cortical computations according to task demand.

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