et al., 2011a; El-Shamayleh & Movshon, 2011; Landy & Oruç, 2002; Larsson et al., 2006).

Procedure

Figure 3 depicts the trial sequence for the exogenous- and endogenous-attention experiments. Each trial began with a 300-ms fixation cross at the center of the screen. Observers were instructed to fixate the cross throughout each trial. Next, exogenous or endogenous attention was manipulated either via peripheral or central precues, respectively, which induced observers to direct their attention to the cued location. The order of the attention experiments (exogenous or endogenous) was counterbalanced across observers. Within each attention experiment, each experimental session only contained one of the two different stimulus conditions (i.e., low or high spatial frequency); the order was counterbalanced.

Exogenous attention was manipulated by a peripheral cue presented adjacent to the target location. In two-thirds of the trials (cued trials), one black rectangle (width: 0.3°, length 1.6°, orientation: 45°) was flashed for 60 ms 3.5° from one stimulus location (i.e., 1.5° border-to-border from the upcoming stimulus). In the remaining one-third of the trials (neutral trials), four black rectangles were presented next to the four possible stimulus locations, distributing observers' attention across space. After an inter-stimulus-interval (ISI) of 40 ms, two second-order texture stimuli were presented simultaneously for 100 ms. The two stimuli

could be presented at any two of the four possible locations. Orientation and phase of the second-order modulator were independently randomized across trials for each second-order stimulus in a pair. Then, 100 ms after stimulus display, a white response cue was presented near the fixation cross, pointing to one of the two stimuli (the target). Response cues considerably reduce location uncertainty by indicating the exact target location (Kinchla, Chen, & Evert, 1995; Lu & Dosher, 2004; Luck et al., 1994; Pestilli & Carrasco, 2005; Yeshurun et al., 2008).

The task was a two-alternative, forced-choice, second-order-orientation-discrimination task. Observers were instructed to report the orientation (vertical or horizontal) of the second-order sine wave grating presented at the target location indicated by the response cue. Auditory feedback was given. About 2,530 trials per stimulus condition were collected for each observer in 16 blocks (in approximately four experimental sessions)—an equal number of trials for each of nine second-order modulator contrast levels.

For the endogenous-attention experiment, the procedure and the task were the same as for the exogenous condition except that attention was manipulated via symbolic, central cues presented at fixation preceding stimulus presentation. In two-thirds of the trials (cued trials), a black line pointing at one possible location was presented for 300 ms near the fixation cross. In the remaining one-third of the trials (neutral trials), four black lines were presented near fixation, pointing at the four possible stimulus locations. After an ISI of 300 ms, the two second-order texture stimuli were presented
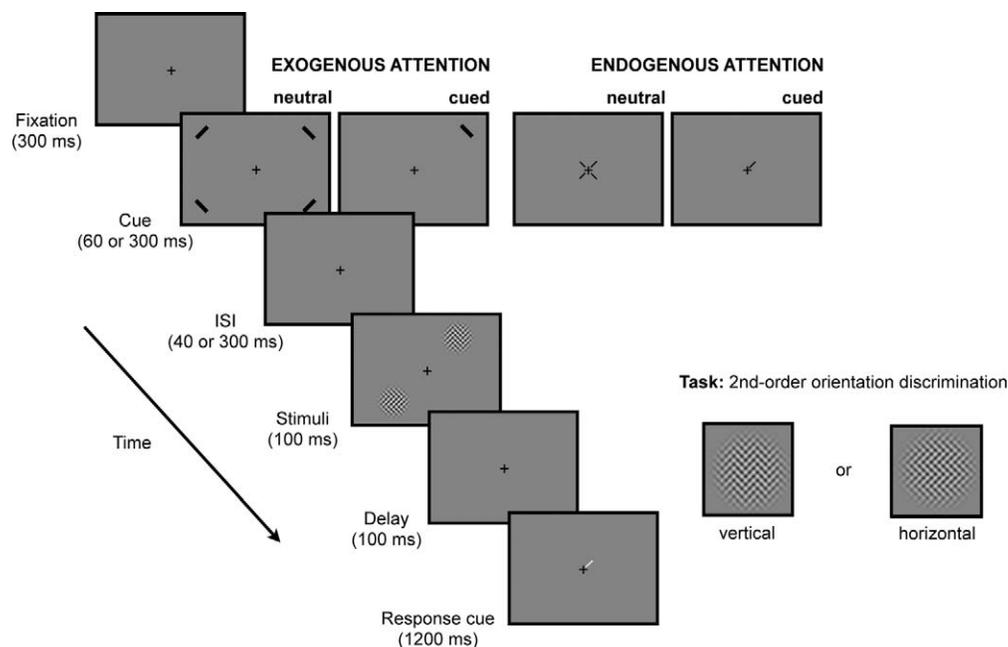

Figure 3. Trial sequence. The trial sequence was identical for the exogenous and endogenous attention conditions except for the location and timing of the peripheral and central cues, which differed to maximize the effects of each type of attention.

simultaneously for 100 ms, and then a response cue was presented 100 ms after stimulus display. About 1,620 trials per stimulus condition were collected for each observer in 12 blocks (in approximately three experimental sessions)—an equal number of trials for each of nine second-order modulator contrast levels.

As illustrated in Figure 4, the relationship between the attentional cue and the response cue defined the validity of the precue (Downing, 1988; Lu & Dosher, 2004; Luck et al., 1994; Montagna et al., 2009; Pestilli & Carrasco, 2005). On valid trials, the location indicated by the precue and the response cue matched, and observers reported the orientation of the cued ('attended') stimulus. On invalid trials, the precue and response cue did not match, and observers reported the orientation of the uncued ('unattended') stimulus. On neutral trials, all four potential stimulus locations were precued.

For exogenous attention, we used non-predictive precues. The target was equally likely to be the cued (a *valid* trial) or uncued (an *invalid* trial) stimulus, and the precue gave no information about target orientation; the precue only indicated stimulus onset, as was the case in the neutral trials (Lu & Dosher, 2004; Lu, Liu, & Dosher, 2000; Montagna et al., 2009; Pestilli & Carrasco, 2005; Pestilli et al., 2007). Observers were told that the precue was uninformative and that it would not be advantageous to move their eyes to the cued location. Note that goal-directed saccades require about 250 ms (Leigh & Zee, 1991; Mayfrank, Kimmig, & Fischer, 1987). Thus, no eye movements to the stimulus could occur between precue onset and stimulus onset (100 ms). Peripheral cues cannot be voluntarily ignored, even if observers are instructed to do so (Jonides & Irwin, 1981), and their effect is not influenced by cue validity (Giordano et al., 2009), given that the peripheral cue automatically draws attention to the cued location (Jonides & Yantis, 1988; Yantis & Jonides, 1984).

For endogenous attention, we used informative precues. Effects of central cues depend on cue validity and might not occur when the central cues are uninformative (Giordano et al., 2009; Jonides & Irwin, 1981; Jonides & Yantis, 1988; Kinchla, 1980; Sperling & Melchner, 1978). In two-thirds of the cued trials, the cued location corresponded to the target location (*valid* trials). In one-third of the cued trials, the cued location corresponded to the distractor location (*invalid* trials). Observers were told that the precue was informative and that it would be advantageous to deploy their attention to the cued location without moving their eyes. Eye position was monitored to ensure that observers were not breaking fixation at any time from the precue onset to the stimulus offset.

Analysis

For each observer, performance was assessed separately for each stimulus condition (i.e., low or high second-order spatial frequency), second-order modulation contrast and cueing condition (valid, invalid and neutral). We used signal detection theory, treating the vertical second-order stimulus as a signal-present and the horizontal second-order stimulus as a signal-absent trial. Performance was evaluated as $d' = z$(hit rate) − z(false alarm rate). d' values were averaged over observers. The data were fit with a Naka-Rushton function:

Figure 4. Cue validity for exogenous and endogenous attention.

$$d'(c) = d'_{max} \frac{c^n}{c^n + c_{50}^n} \qquad (2)$$

using a least-squares criterion, where $d'(c)$ represents performance as a function of contrast, d'_{max} is the asymptotic performance at high contrast values, c_{50} is the contrast at which the observer achieves half the asymptotic performance, and n determines the slope of the psychometric function. For each stimulus condition, we fit the data from the three attention conditions, allowing distinct values of d'_{max}, c_{50} and n for each attention condition.

Confidence intervals and p-values were computed by bootstrapping. Specifically, individual psychophysical trials were randomly resampled with replacement to generate resampled data sets, which were refitted using the same procedure. We repeated this procedure of resampling and refitting 10,000 times to generate bootstrap distributions of the fitted parameters. Confidence intervals for the fitted parameters and p-values were based on these bootstrap distributions, e.g., to test if there was a benefit for valid and a cost for invalid cues, compared to neutral cues either in d'_{max}, c_{50} or n. We assembled the bootstrap distribution of the differences between the conditions (e.g., valid minus neutral trials) and performed statistical tests by assessing the percentage of the values in the tail of the distribution of the differences greater than zero for changes in d'_{max} or n, or lower than zero for changes in c_{50}. Performance in this orientation-discrimination task improves with increasing second-order contrast. Thus, if attention increases second-order contrast sensitivity at the attended location and decreases it at unattended locations, it should improve performance at the attended location and performance should be degraded at unattended locations.

For endogenous attention, eye positions were measured using an infrared eye tracker (EyeLink CL, SR Research, Kanata, Ontario, Canada) with 1000 Hz sampling rate in the main experimental sessions. Eye positions were analyzed offline. For analysis, raw data were converted to eye position in degrees of visual angle. Eye position samples around the time of blinks (100 ms preceding and following a blink) were excluded from further analysis. The mean eye position during the fixation interval at the beginning of each trial served as a baseline and was subtracted from the mean eye position in each following interval (cue presentation, ISI, stimulus presentation) to compensate for any slow drift in the measurements during each block. We used the standard Eyelink detection algorithm (combined velocity [$30°/s$] and acceleration [$8000°/s^2$] criteria to detect saccades; below, we report their frequency for each condition).

Results

Exogenous attention

Figure 5 shows the performance data and psychometric function fits averaged across observers ($N = 8$) for the exogenous-attention experiment. The effects of exogenous attention depended on the spatial frequency of the second-order modulator, as previously reported (Barbot et al., 2011a). When the spatial frequency of the second-order modulator was low (Figure 5A), the three psychometric functions (valid, neutral and invalid) were indistinguishable and no effect of cueing was observed on d'_{max} ($p_{valid-invalid} > 0.1$), c_{50} ($p_{valid-invalid} > 0.1$) or n ($p_{valid-invalid} > 0.1$). However, when the spatial frequency of the second-order modulator was high (Figure 5B), performance was consistent with response gain, i.e., attention modulated the value of d'_{max} ($p_{valid-invalid} < 0.01$), but not c_{50} ($p_{valid-invalid} > 0.1$). Compared to the neutral condition, a valid cue to the target enhanced second-order contrast sensitivity, as indicated by an increase in d'_{max}, whereas an invalid cue decreased sensitivity, reducing d'_{max}. No change of n ($p_{valid-invalid} > 0.1$) was observed.

Figure 5C and D shows the values of c_{50} and d'_{max} for individual observers in the valid and invalid attention conditions in which each value is normalized by (i.e., divided by) the corresponding parameter values from the neutral attention condition. The effect of attention on second-order contrast sensitivity was consistent across observers. For the low second-order spatial frequency condition (Figure 5C), there was no clear pattern across valid and invalid conditions, reflecting the absence of attentional modulation. In contrast, for the high second-order spatial frequency condition (Figure 5D), valid d'_{max} values were higher than the neutral d'_{max} values (i.e., red squares above the unity line), and invalid d'_{max} values were lower than the neutral d'_{max} values (i.e., blue squares below the unity line). These results show that exogenous attention affects contrast sensitivity for second-order, orientation-defined patterns in a manner that depends on second-order spatial frequency.

Endogenous attention

Figure 6 shows the performance data and psychometric function fits averaged across observers ($N = 7$) for the endogenous-attention experiment. Although the effects of exogenous attention depended on the spatial frequency of the second-order modulator, endogenous attention affected performance independent of the second-order spatial frequency content. For the low second-order spatial frequency condition (Figure 6A),
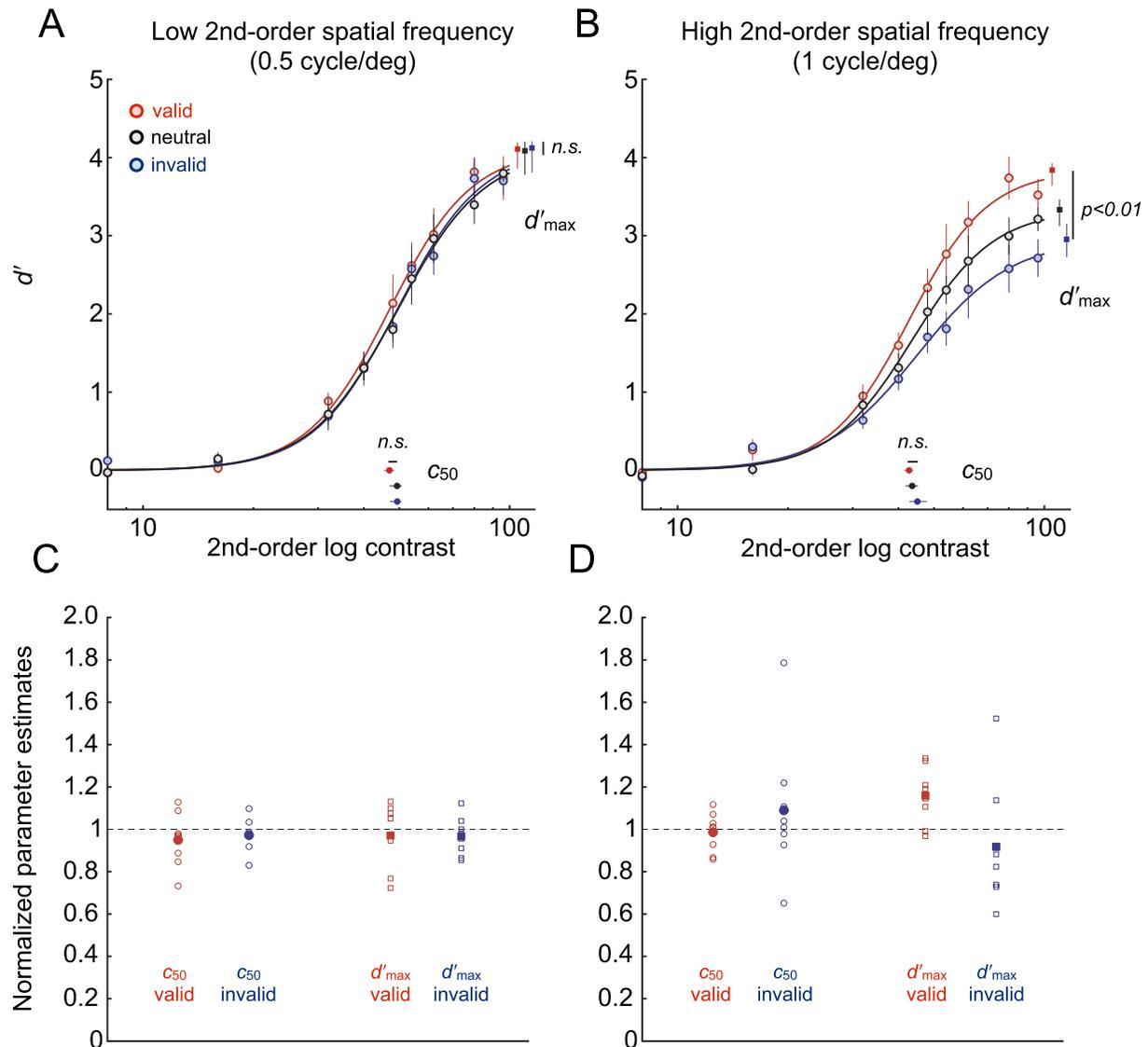
Figure 5. **(A,B)** Effects of exogenous attention on performance (d') as a function of second-order modulator contrast for the low (A) and high (B) second-order spatial frequency conditions (Figure 2). Each panel shows psychometric functions and parameter estimates (c_{50}: second-order contrast yielding half-maximum performance; d'_{max}: asymptotic performance) for each cueing condition (valid, neutral and invalid). Each data point represents the mean across observers ($N = 8$). Error bars correspond to ± 1 SEM for data points and 68%-confidence intervals obtained by bootstrapping for parameter estimates. All $r^2 > .98$. **(C, D)** Effects of exogenous attention on individual observers' parameter estimates in the low (C) and high (D) second-order spatial frequency conditions (c_{50}: open circles; d'_{max}: open squares). Each plot displays individual observers' parameter estimates in the valid (red symbols) and invalid (blue symbols) cue conditions normalized by the corresponding values in the neutral-cue condition. Filled symbols indicate mean across observers.

changes in performance were consistent with a mixture of contrast gain and response gain, as indicated by a decrease in c_{50} ($p_{valid\text{-}invalid} < 0.05$) and by an increase in d'_{max} ($p_{valid\text{-}invalid} < 0.05$) with attention. For the high second-order spatial frequency conditions (Figure 6B), changes in performance were consistent with response gain, as indicated by an increase in d'_{max} ($p_{valid\text{-}invalid} < 0.05$) with attention. A marginal increase in c_{50} was also observed ($p_{neutral\text{-}invalid} = 0.058$). No change in n was observed for either the high- or the low-frequency stimulus condition ($p_{valid\text{-}invalid} > 0.1$).

Figure 6C-D shows the values of c_{50} and d'_{max} for individual observers in the valid and invalid attention conditions in which each value is normalized by (i.e., divided by) the corresponding parameter values from the neutral attention condition. For both second-order spatial frequency conditions, valid d'_{max} values were higher than the neutral d'_{max} values (i.e., red squares above the unity line), and invalid d'_{max} values were lower than the neutral d'_{max} values (i.e., blue squares below the unity line). In addition, we observe that valid c_{50} values were generally lower and invalid c_{50} values
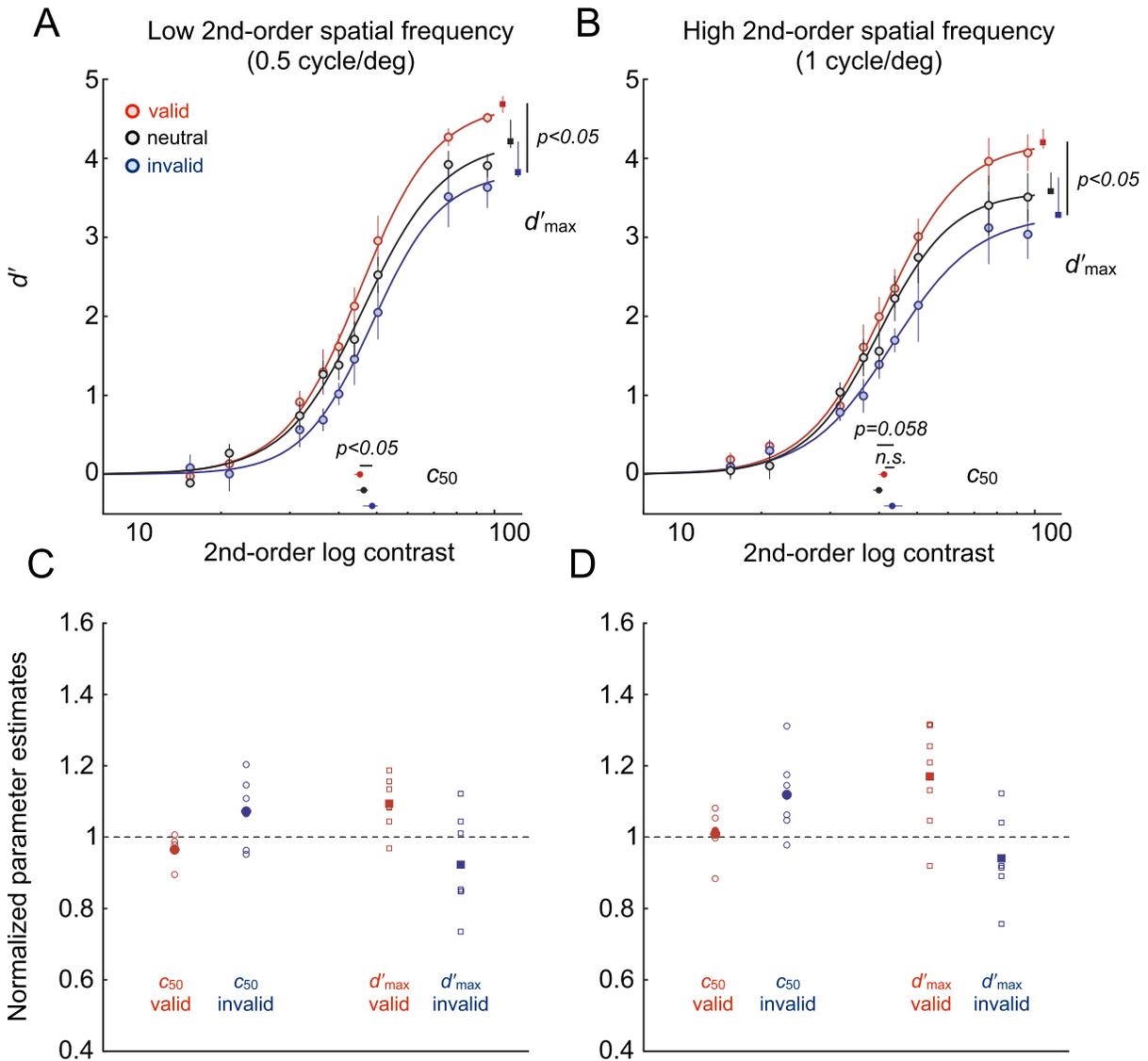
Figure 6.   Effects of endogenous attention on performance (d') as a function of second-order modulator contrast for the low (A) and high (B) second-order spatial frequency conditions ($N = 7$). All $r^2 > .98$. All plotting conventions as in Figure 5.

higher than the neutral c_{50} values for both stimulus conditions. These results indicate that unlike exogenous attention, endogenous attention can increase second-order contrast sensitivity regardless of the spatial frequency content.

Eye tracking

Observers were able to voluntarily deploy their attention to the cued location without breaking fixation. Less than 5% of the eye-movement data were missing or unable to be analyzed due to problems with the calibration. Less than 1% of all recorded gaze positions were outside the central fixation area subtending 2° of visual angle. Observers did not move their eyes toward the cued location during cued trials. For each cued trial, we computed average gaze position from cue onset to stimulus offset. We rotated the coordinate system trial-by-trial to one in which the fixation point was at the origin and cued location was displaced 5° to the right. In this coordinate system, in the low second-order spatial frequency condition, the horizontal and vertical gaze positions averaged over cued trials were 0.049° ± 0.29° and 0.004° ± 0.36° respectively, and the x-value was not significantly greater than zero (one-tailed t-test, $p > 0.4$); i.e., gaze stayed at the fixation mark. The corresponding values for the high second-order spatial frequency condition were 0.039° ± 0.27° and 0.0002° ± 0.28° (x-value: one-tailed t-test, $p > 0.4$). Saccade frequency during the interval between cue onset and stimulus offset was also extremely low (0.23% and 0.32% in the low and high

second-order spatial frequency conditions respectively). Thus, our results are not due to eye movements toward the cued location.

Discussion

We measured attentional trade-offs in second-order contrast sensitivity at parafoveal locations (5° eccentricity). We compared the effects of exogenous and endogenous attention for second-order orientation-defined patterns of either relatively high or low second-order spatial frequency. The results show that both types of attention affect contrast sensitivity to second-order texture-defined information, increasing sensitivity at the attended location and decreasing it at unattended locations. Moreover, these findings reveal that exogenous attention and endogenous attention differentially affect second-order contrast sensitivity.

Covert attention enhances second-order processing

Previous work has shown that attention increases contrast sensitivity to first-order information (Carrasco, 2006, 2011; Reynolds & Chelazzi, 2004). The present findings indicate that spatial covert attention can enhance sensitivity to second-order information as well. This finding challenges the idea that second-order processing is purely pre-attentive and does not benefit from attention (Braun & Sagi, 1990). Although attention is not necessary for texture segmentation to occur, texture perception can benefit from the allocation of attentional resources. Performance in our second-order orientation-discrimination task is unaffected by modest changes in first-order carrier contrast (Barbot et al., 2011a). Thus, the attentional effect cannot be due to an effect of attention on effective first-order contrast. Moreover, had the attention effects been due to changes in first-order contrast sensitivity, they should have been the same regardless of the second-order frequency in the exogenous attention experiment. The changes in sensitivity with attention observed in the present study can only be attributed to a change in second-order contrast sensitivity. When covert attention is directed to a given location, our ability to discriminate patterns defined by changes in either first-order luminance or second-order textural attributes improves at that location and worsens elsewhere.

Attentional trade-offs for both exogenous and endogenous attention emerged for simple and non-cluttered displays in which only two stimuli were competing for processing, supporting the notion of limited resources. This finding challenges the idea that

perceptual processes are of unlimited capacity (Palmer, Verghese, & Pavel, 2000) or that selective attention is required only once the perceptual load exceeds the capacity limit of the system (Lavie, 1995). Attention helps manage metabolic consumption in the brain between attended and unattended locations by biasing competition in favor of information at the attended area, at the cost of information processing at other unattended areas. Our findings support the notion that trade-offs are a ubiquitous property of attentional selection that can affect various visual attributes (Abrams, Barbot, & Carrasco, 2010; Carrasco, 2011; Montagna et al., 2009; Pestilli & Carrasco, 2005; Pestilli, Carrasco, Heeger, & Gardner, 2011; Pestilli et al., 2007).

Segmentation of the visual scene into distinct perceptually coherent regions is crucial for the reliable detection and identification of objects. Object segmentation begins with the detection of discontinuities representing boundaries between adjacent regions, rather than immediate detection of objects per se (Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008; Li, 2003). Access to multiple visual cues, such as first- and second-order contours, considerably improves performance. When both first- and second-order cues are present, texture segmentation improves (Smith & Scott-Samuel, 2001), but this benefit only occurs when the two cues are correlated in an ecologically valid manner (Johnson, Prins, Kingdom, & Baker, 2007). Perceived contour location is a compromise between the position signaled by second-order texture-defined cues and by other cues such as luminance or motion (Rivest & Cavanagh, 1996). When an edge is defined by multiple cues, the cues are combined using a weighted average, with greater weight given to the more reliable cues (Landy & Kojima, 2001). Considering that many first-order luminance cues originate from non-uniform surface illumination, second-order information appears to represent a more reliable signal of discontinuities between adjacent surfaces (Kingdom, 2003; Schofield et al., 2006; Schofield et al., 2010; Sun & Schofield, 2011). By enhancing sensitivity to first-order cues, but more importantly to the more reliable second-order cues, attention can efficiently improve segmentation of visual scenes into distinct regions, significantly improving object detection and identification.

On the flexibility and automaticity of covert attention

Exogenous attention increases second-order contrast sensitivity as a function of the second-order spatial frequency content; it affects sensitivity for patterns with relatively high, but not low, second-order spatial frequency. These results for exogenous attention are consistent with our previous findings (Barbot et al., 2011a). As in the

present study, for stimuli at parafoveal locations, exogenous attention improved performance only for the high-spatial frequency patterns, but at more eccentric locations, it also improved performance for the low-spatial frequency patterns. Thus, the effects of exogenous attention on second-order contrast sensitivity were a function of both the second-order spatial frequency of the stimulus and its eccentricity. We interpreted these findings in terms of the *resolution hypothesis*, whereby exogenous spatial attention increases resolution by increasing the sensitivity of the smallest second-order filters at a particular eccentricity (Carrasco, 2011; Carrasco & Yeshurun, 2009). Given that the average filter size, and thus the resolution, decreases with eccentricity, the results were consistent with the fact that the smallest filters at parafovea mediate the high but not the low spatial frequency condition. Conversely, at more eccentric locations, the filters with highest spatial resolution are larger and coarser, and thus are used for the low second-order spatial frequency. Hence, a mechanism affecting the sensitivity of the smallest filters at a given eccentricity could explain why the effect of exogenous attention depended on the modulator frequency of the second-order texture and its eccentricity.

In the present study, however, endogenous attention increased second-order contrast sensitivity regardless of the second-order spatial frequency content. Taken together, the present findings reveal that both exogenous attention and endogenous attention modulate second-order contrast sensitivity, but via different mechanisms, and that endogenous attention is more flexible.

Whereas endogenous attention and exogenous attention often modulate perception in similar ways, this study provides further evidence that they can differentially affect perception. Endogenous attention is more flexible, being able to adjust its operation depending on goals and task demands (Carrasco, 2011). For instance, in a texture segmentation task, constrained by spatial resolution, exogenous attention improves performance at peripheral locations but impairs it at central locations (Carrasco et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2000, 2008). In contrast, endogenous attention improves performance at all eccentricities (Yeshurun et al., 2008), by adjusting the sensitivity of selective second-order spatial frequency filters to optimize spatial resolution based on task demands (Barbot, Montagna, & Carrasco, 2011b), consistent with a more flexible endogenous-attention system.

There are also differences in the effects of endogenous and exogenous attention on temporal processing. For instance, endogenous allocation of attention improves temporal order judgments, whereas exogenous allocation of attention impairs judgments (Hein et al., 2006). Furthermore, exogenous attention and endogenous attention have different effects when cue validity is manipulated, consistent with a more flexible endogenous-attention system. Whereas both the benefits (valid trials) and costs (invalid trials) due to endogenous attention increase with cue validity, the effects of exogenous attention are similar across cue-validity conditions (Giordano et al., 2009). Whereas endogenous attention can be flexibly allocated according to cue validity, exogenous attention is automatic and unaffected by cue validity.

Conclusion

Exogenous and endogenous attention can affect one's ability to discriminate second-order information: Contrast sensitivity to second-order texture-defined patterns increases at the attended location, while decreasing elsewhere. Together with the effects of covert attention on first-order contrast sensitivity, our study suggests that attention aids in the segmentation of the retinal image by increasing both first- and second-order sensitivity at the attended location. Moreover, this study revealed that whereas the effects of exogenous attention are a function of the second-order spatial frequency content, endogenous attention affected second-order contrast sensitivity regardless of the second-order spatial frequency content. These findings support the idea that exogenous and endogenous attention affects perceptual processing via different mechanisms. Endogenous attention is under the observer's voluntary control and can flexibly adjust to optimize performance depending on goals and task demands.

Acknowledgments

Commercial relationships: none.
Corresponding author: Antoine Barbot.
Email: antoine.barbot@nyu.edu.
Address: Department of Psychology, New York University, New York, NY, USA.

Footnote

[1]Data of three of the eight observers for the exogenous attention experiment were published previously (Barbot et al., 2011a).

References

Abrams, J., Barbot, A., & Carrasco, M. (2010). Voluntary attention increases perceived spatial frequency. *Attention, Perception, & Psychophysics, 72*, 1510–1521.

Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. *Vision Research, 52*, 70–78.

Appelbaum, L. G., Wade, A. R., Pettet, M. W., Vildavski, V. Y., & Norcia, A. M. (2008). Figure-ground interaction in the human visual cortex. *Journal of Vision, 8*(9):8, 1–19, http://www.journalofvision.org/content/8/9/8, doi:10.1167/8.9.8. [PubMed] [Article]

Arsenault, A. S., Wilkinson, F., & Kingdom, F. A. (1999). Modulation frequency and orientation tuning of second-order texture mechanisms. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 16*, 427–435.

Ashida, H., Lingnau, A., Wall, M. B., & Smith, A. T. (2007). fMRI adaptation reveals separate mechanisms for first-order and second-order motion. *Journal of Neurophysiology, 97*, 1319–1325.

Baker, C. L., Jr. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology, 9*, 461–466.

Barbot, A., Landy, M. S., & Carrasco, M. (2011a). Exogenous attention enhances 2nd-order contrast sensitivity. *Vision Research, 51*, 1086–1098.

Barbot, A., Montagna, B., & Carrasco, M. (2011b). Endogenous attention optimizes spatial resolution depending on task demands [Abstract]. *Perception, 40*, 191.

Braun, J., & Sagi, D. (1990). Vision outside the focus of attention. *Perception & Psychophysics, 48*, 45–58.

Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the 'spotlight' of visual attention. *Nature Neuroscience, 2*, 370–374.

Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research, 42*, 949–967.

Carrasco, M. (2006). Covert attention increases contrast sensitivity: Psychophysical, neurophysiological and neuroimaging studies. *Progress in Brain Research, 154*, 33–70.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research, 51*, 1484–1525.

Carrasco, M., Loula, F., & Ho, Y. X. (2006). How attention enhances spatial resolution: Evidence from selective adaptation to spatial frequency. *Perception & Psychophysics, 68*, 1004–1012.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research, 40*, 1203–1215.

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision, 15*, 61–75.

Carrasco, M., & Yeshurun, Y. (2009). Covert attention effects on spatial resolution. *Progress in Brain Research, 176*, 65–86.

Casco, C., Grieco, A., Campana, G., Corvino, M. P., & Caputo, G. (2005). Attention modulates psychophysical and electrophysiological response to visual texture segmentation in humans. *Vision Research, 45*, 2384–2396.

Cheal, M., & Lyon, D. R. (1991). Central and peripheral precuing of forced-choice discrimination. *Quarterly Journal of Experimental Psychology A, 43*, 859–880.

Cheal, M., Lyon, D. R., & Hubbard, D. C. (1991). Does attention have different effects on line orientation and line arrangement discrimination? *Quarterly Journal of Experimental Psychology A, 43*, 825–857.

Dakin, S. C., Williams, C. B., & Hess, R. F. (1999). The interaction of first- and second-order cues to orientation. *Vision Research, 39*, 2867–2884.

DeValois, R. L., & DeValois, K. K. (1988). *Spatial Vision*. New York: Oxford University Press.

Dosher, B. A., & Lu, Z. L. (2000). Mechanisms of perceptual attention in precuing of location. *Vision Research, 40*, 1269–1292.

Downing, C. J. (1988). Expectancy and visual-spatial attention: Effects on perceptual quality. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 188–202.

Dumoulin, S. O., Baker, C. L., Jr., Hess, R. F., & Evans, A. C. (2003). Cortical specialization for processing first- and second-order motion. *Cerebral Cortex, 13*, 1375–1385.

El-Shamayleh, Y., & Movshon, J. A. (2011). Neuronal responses to texture-defined form in macaque visual area V2. *Journal of Neuroscience, 31*, 8543–8555.

Ellemberg, D., Allen, H. A., & Hess, R. F. (2004). Investigating local network interactions underlying first- and second-order processing. *Vision Research, 44*, 1787–1797.

Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 96,* 3314–3319.

Giordano, A. M., McElree, B., & Carrasco, M. (2009). On the automaticity and flexibility of covert attention: A speed-accuracy trade-off analysis. *Journal of Vision, 9*(3):30, 1–10, http://www.journalofvision.org/content/9/3/30, doi:10.1167/9.3.30. [PubMed] [Article]

Graham, N. (1989). *Visual pattern analyzers.* New York: Oxford University Press.

Graham, N., & Wolfson, S. S. (2001). A note about preferred orientations at the first and second stages of complex (second-order) texture channels. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 18,* 2273–2281.

Hallum, L. E., Landy, M. S., & Heeger, D. J. (2011). Human primary visual cortex (V1) is selective for second-order spatial frequency. *Journal of Neurophysiology, 105,* 2121–2131.

Hein, E., Rolke, B., & Ulrich, R. (2006). Visual attention and temporal discrimination: Differential effects of automatic and voluntary cueing. *Visual Cognition, 13,* 29–50.

Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size matters: Attention affects performance by contrast or response gain. *Nature Neuroscience, 13*(12), 1554–1559.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research, 33,* 1219–1240.

Huk, A. C., & Heeger, D. J. (2000). Task-related modulation of visual cortex. *Journal of Neurophysiology, 83,* 3525–3536.

Johnson, A. P., & Baker, C. L., Jr. (2004). First- and second-order information in natural images: A filter-based approach to image statistics. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 21,* 913–925.

Johnson, A. P., Kingdom, F. A., & Baker, C. L., Jr. (2005). Spatiochromatic statistics of natural scenes: First- and second-order information and their correlational structure. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 22,* 2050–2059.

Johnson, A. P., Prins, N., Kingdom, F. A., & Baker, C. L., Jr. (2007). Ecologically valid combinations of first- and second-order surface markings facilitate texture discrimination. *Vision Research, 47,* 2281–2290.

Jonides, J. (1981). Voluntary vs automatic control of the mind's eye's movement. In J. B. Long & A. Baddeley (Eds.), *Attention and Performance IX.* (pp. 187–204). Hillsdale, NJ: Erlbaum.

Jonides, J., & Irwin, D. E. (1981). Capturing attention. *Cognition, 10,* 145–150.

Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics, 43,* 346–354.

Julesz, B. (1981, March 12). Textons, the elements of texture perception, and their interactions. *Nature, 290,* 91–97.

Kinchla, R. A. (1980). The measurement of attention. In R. Nickerson (Ed.), *Attention and performance VIII.* (pp. 213–238). Princeton, NJ: Psychology Press.

Kinchla, R. A., Chen, Z., & Evert, D. (1995). Precue effects in visual search: Data or resource limited? *Perception & Psychophysics, 57,* 441–450.

Kingdom, F. A. (2003). Color brings relief to human vision. *Nature Neuroscience, 6,* 641–644.

Landy, M. S., & Kojima, H. (2001). Ideal cue combination for localizing texture-defined edges. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 18,* 2307–2320.

Landy, M. S., & Oruç, I. (2002). Properties of second-order spatial frequency channels. *Vision Research, 42,* 2311–2329.

Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and second-order patterns in human visual cortex. *Journal of Neurophysiology, 95,* 862–881.

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 451–468.

Leigh, R. J., & Zee, D. S. (1991). *The neurology of eye movements.* Philadelphia: Davis.

Lennie, P. (2003). The cost of cortical computation. *Current Biology, 13,* 493–497.

Li, Z. (2003). V1 mechanisms and some figure-ground and border effects. *Journal of Physiology - Paris, 97,* 503–515.

Ling, S., & Carrasco, M. (2006a). Sustained and transient covert attention enhance the signal via different contrast response functions. *Vision Research, 46,* 1210–1220.

Ling, S., & Carrasco, M. (2006b). When sustained

attention impairs perception. *Nature Neuroscience, 9*, 1243–1245.

Liu, T., Pestilli, F., & Carrasco, M. (2005). Transient attention enhances perceptual performance and fMRI response in human visual cortex. *Neuron, 45*, 469–477.

Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research, 47*, 108–113.

Lu, Z. L., & Dosher, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research, 38*, 1183–1198.

Lu, Z. L., & Dosher, B. A. (2004). Spatial attention excludes external noise without changing the spatial frequency tuning of the perceptual template. *Journal of Vision, 4*(10):10, 955–966, http://www.journalofvision.org/content/4/10/10, doi:10.1167/4.10.10. [PubMed] [Article]

Lu, Z. L., Liu, C. Q., & Dosher, B. A. (2000). Attention mechanisms for multi-location first- and second-order motion perception. *Vision Research, 40*, 173–186.

Luck, S. J., Hillyard, S. A., Mouloua, M., Woldorff, M. G., Clark, V. P., & Hawkins, H. L. (1994). Effects of spatial cuing on luminance detectability: Psychophysical and electrophysiological evidence for early selection. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 887–904.

Mangun, G. R., & Hillyard, S. A. (1990). Allocation of visual attention to spatial locations: Tradeoff functions for event-related brain potentials and detection performance. *Perception & Psychophysics, 47*, 532–550.

Mayfrank, L., Kimmig, H., & Fischer, B. (1987). In J. K. O'Regan & A. Levy-Schoen (Eds.), *Eye movements: From physiology to cognition* (pp. 37–45). New York: Elsevier, North-Holland.

McAdams, C. J., & Reid, R. C. (2005). Attention modulates the responses of simple cells in monkey primary visual cortex. *Journal of Neuroscience, 25*, 11023–11033.

Montagna, B., Pestilli, F., & Carrasco, M. (2009). Attention trades off spatial acuity. *Vision Research, 49*, 735–745.

Montaser-Kouhsari, L., Landy, M. S., Heeger, D. J., & Larsson, J. (2007). Orientation-selective adaptation to illusory contours in human visual cortex. *Journal of Neuroscience, 27*, 2186–2195.

Morgan, M. J., Mason, A. J., & Baldassi, S. (2000). Are there separate first-order and second-order mech-

anisms for orientation discrimination? *Vision Research, 40*, 1751–1763.

Müller, H. J., & Findlay, J. M. (1988). The effect of visual attention on peripheral discrimination thresholds in single and multiple element displays. *Acta Psychology (Amsterdam), 69*, 129–155.

Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 315–330.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research, 29*, 1631–1647.

Palmer, J., Verghese, P., & Pavel, M. (2000). The psychophysics of visual search. *Vision Research, 40*, 1227–1268.

Pestilli, F., & Carrasco, M. (2005). Attention enhances contrast sensitivity at cued and impairs it at uncued locations. *Vision Research, 45*, 1867–1875.

Pestilli, F., Carrasco, M., Heeger, D. J., & Gardner, J. L. (2011). Attentional enhancement via selection and pooling of early sensory responses in human visual cortex. *Neuron, 72*, 832–846.

Pestilli, F., Ling, S., & Carrasco, M. (2009). A population-coding model of attention's influence on contrast response: Estimating neural effects from psychophysical data. *Vision Research, 49*, 1144–1153.

Pestilli, F., Viera, G., & Carrasco, M. (2007). How do attention and adaptation affect contrast sensitivity? *Journal of Vision, 7*(7):9, 1–12, http://www.journalofvision.org/content/7/7/9, doi:10.1167/7.7.9. [PubMed] [Article]

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*, 3–25.

Prinzmetal, W., McCool, C., & Park, S. (2005). Attention: Reaction time and accuracy reveal different mechanisms. *Journal of Experimental Psychology: General, 134*, 73–92.

Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience, 27*, 611–647.

Rivest, J., & Cavanagh, P. (1996). Localizing contours defined by more than one attribute. *Vision Research, 36*, 53–66.

Schofield, A. J. (2000). What does second-order vision see in an image? *Perception, 29*, 1071–1086.

Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and contrast in visual

white noise: Separate mechanisms with similar behaviour. *Vision Research, 39*, 2697–2716.

Schofield, A. J., Hesse, G., Rock, P. B., & Georgeson, M. A. (2006). Local luminance amplitude modulates the interpretation of shape-from-shading in textured surfaces. *Vision Research, 46*, 3462–3482.

Schofield, A. J., Rock, P. B., Sun, P., Jiang, X., & Georgeson, M. A. (2010). What is second-order vision for? Discriminating illumination versus material changes. *Journal of Vision, 10*(9):2, 1–18 http://www.journalofvision.org/content/10/9/2, doi:10.1167/10.9.2. [PubMed] [Article]

Schubö, A., & Meinecke, C. (2007). Automatic texture segmentation in early vision: Evidence from priming experiments. *Vision Research, 47*, 2378–2389.

Scott-Samuel, N. E., & Georgeson, M. A. (1999). Does early non-linearity account for second-order motion? *Vision Research, 39*, 2853–2865.

Smith, A. T., & Scott-Samuel, N. E. (2001). First-order and second-order signals combine to improve perceptual accuracy. *Journal of the Optical Society of America A: Optics, Image Science, and Vision, 18*, 2267–2272.

Sperling, G., & Melchner, M. J. (1978). The attention operating characteristic: Examples from visual search. *Science, 202*, 315–318.

Störmer, V. S., McDonald, J. J., & Hillyard, S. A. (2009). Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 22456–22461.

Sun, P., & Schofield, A. J. (2011). The efficacy of local luminance amplitude in disambiguating the origin of luminance signals depends on carrier frequency: Further evidence for the active role of second-order vision in layer decomposition. *Vision Research, 51*, 496–507.

Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: An attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance, 23*, 443–463.

Talgar, C. P., & Carrasco, M. (2002). Vertical meridian asymmetry in spatial resolution: Visual and attentional factors. *Psychonomic Bulletin & Review, 9*, 714–722.

Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance, 10*, 601–621.

Yantis, S., & Jonides, J. (1996). Attentional capture by abrupt onsets: New perceptual objects or visual masking? *Journal of Experimental Psychology: Human Perception and Performance, 22*, 1505–1513.

Yeshurun, Y. (2004). Isoluminant stimuli and red background attenuate the effects of transient spatial attention on temporal resolution. *Vision Research, 44*, 1375–1387.

Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature, 396*, 72–75.

Yeshurun, Y., & Carrasco, M. (2000). The locus of attentional effects in texture segmentation. *Nature Neuroscience, 3*, 622–627.

Yeshurun, Y., & Carrasco, M. (2008). The effects of transient attention on spatial resolution and the size of the attentional cue. *Perception & Psychophysics, 70*, 104–113.

Yeshurun, Y., & Levy, L. (2003). Transient spatial attention degrades temporal resolution. *Psychological Science, 14*, 225–231.

Yeshurun, Y., Montagna, B., & Carrasco, M. (2008). On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Research, 48*, 80–95.

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision, 10*(10):16, 1–12, http://www.journalofvision.org/content/10/10/16, doi: 10.1167/10.10.16. [PubMed] [Article]