

Attention alters spatial resolution by modulating second-order processing

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Endogenous and exogenous visuospatial attention both alter spatial resolution, but they operate via distinct mechanisms. In texture segmentation tasks, exogenous attention inflexibly increases resolution even when detrimental for the task at hand and does so by modulating second-order processing. Endogenous attention is more flexible and modulates resolution to benefit performance according to task demands, but it is unknown whether it also operates at the second-order level. To answer this question, we measured performance on a second-order texture segmentation task while independently manipulating endogenous and exogenous attention. Observers discriminated a second-order texture target at several eccentricities. We found that endogenous attention improved performance uniformly across eccentricity, suggesting a flexible mechanism that can increase or decrease resolution based on task demands. In contrast, exogenous attention improved performance in the periphery but impaired it at central retinal locations, consistent with an inflexible resolution enhancement. Our results reveal that endogenous and exogenous attention both alter spatial resolution by differentially modulating second-order processing.

Introduction

The visual system's spatial resolution varies systematically with eccentricity: Resolution peaks at the fovea and declines toward the periphery. As a consequence of this inhomogeneity, closely spaced visual objects are best discriminated at the fovea but are cluttered and blurred in the periphery. Covert spatial attention, the selection of visuospatial information in the absence of eye movements, can alleviate this eccentricity-dependent limitation by enhancing spatial resolution (for reviews, see Anton-Erxleben & Carrasco, 2013; Carrasco & Barbot, 2014; Carrasco & Yeshurun, 2009).

Conversely, when high-resolution information is sparse or when a global assessment of the scene is required (e.g., viewing the forest rather than individual trees), attention can improve discriminability (Barbot & Carrasco, 2017; Yeshurun, Montagna, & Carrasco, 2008) by reducing spatial resolution (Barbot & Carrasco, 2017).

Attention's role in modifying spatial resolution has been demonstrated with tasks that benefit from enhanced resolution: visual search (Carrasco & Yeshurun, 1998; Giordano, McElree, & Carrasco, 2009), acuity and hyperacuity (Carrasco, Williams, & Yeshurun, 2002; Montagna, Pestilli, & Carrasco, 2009; Yeshurun & Carrasco, 1999), and crowding (Grubb et al., 2013; Montaser-Kouhsari & Rajimehr, 2005; Yeshurun & Rashal, 2010). However, enhanced resolution is not always beneficial as illustrated by texture segmentation tasks in which performance is constrained by the visual system's spatial resolution. In texture segmentation tasks, observers detect a texture target of a fixed spatial scale that is embedded at various eccentricities within a larger background texture (Gurnsey, Pearson, & Day, 1996; Kehrner, 1989; Morikawa, 2000; Potechin & Gurnsey, 2003). Performance typically varies nonmonotonically with eccentricity, peaking when resolution is optimal and declining when resolution is too high or too low for the texture's spatial scale. For instance, the discriminability of a large-scale texture is poor at the fovea where resolution is high, peaks in the midperiphery where resolution is optimal, and declines farther in the periphery where resolution is low. The advantage of the midperiphery over more central locations is referred to as the central performance drop (CPD), and its magnitude varies with the texture's spatial scale: the larger the scale of the texture, the farther the eccentricity at which performance peaks and the more pronounced the CPD (Gurnsey et al., 1996; Joffe &

Citation: Jigo, M., & Carrasco, M. (2018). Attention alters spatial resolution by modulating second-order processing. *Journal of Vision*, 18(7):2, 1–12, <https://doi.org/10.1167/18.7.2>.

<https://doi.org/10.1167/18.7.2>

Received March 14, 2018; published July 2, 2018

ISSN 1534-7362 Copyright 2018 The Authors



Scialfa, 1995; Kehrner, 1989; Yeshurun & Carrasco, 1998; Yeshurun, Montagna et al., 2008).

The effects of attention on texture segmentation depend on the type of spatial attention that is manipulated. Exogenous covert attention—the stimulus-driven and transient orienting response to a given location (for a review, see Carrasco, 2011)—automatically and inflexibly enhances resolution even if detrimental to the task. When engaged by brief peripheral cues, exogenous attention improves texture segmentation in the periphery where resolution is low but impairs it at central locations where resolution is already high—a pattern referred to as the central attentional impairment (Carrasco, Loula, & Ho, 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2008). In contrast, endogenous covert attention—the voluntary and sustained prioritization of information at a given location (Carrasco, 2011)—improves texture segmentation at both peripheral and central locations, suggesting a more flexible mechanism that can either increase or decrease resolution depending on resolution constraints (Barbot & Carrasco, 2017; Yeshurun, Montagna et al., 2008; for reviews, see Carrasco & Barbot, 2014; Carrasco & Yeshurun, 2009).

The resolution account of texture segmentation performance has been ascribed to the degree of overlap between the spatial extent of the texture pattern and the spatial characteristics of second-order filters (Kehrner & Meinecke, 2003; Yeshurun & Carrasco, 2000). These filters comprise models of early visual processing that postulate two successive stages of linear filtering: a first stage that detects luminance-defined (first-order) boundaries and a second stage that pools across space to detect texture-defined (second-order) boundaries (e.g., variations in contrast, orientation, or spatial frequency; for reviews, see Landy, 2013; Victor, Conte, & Chubb, 2017). Second-order filters are tuned to orientation and spatial frequency (SF) and mediate the sensitivity to texture patterns of various spatial scales (Elleberg, Allen, & Hess, 2006; Graham, Sutter, & Venkatesan, 1993; Landy & Oruç, 2002; Sutter, Sperling, & Chubb, 1995).

The SF tuning of these filters is related to receptive-field (RF) size. At central locations, RFs are predominantly small, which allows information to be integrated across narrow regions of space and mediates high-SF tuning (DeValois & DeValois, 1988; Jones & Palmer, 1987). At more peripheral locations, RFs increase in size and are, consequently, tuned to lower SFs (Freeman & Simoncelli, 2011; Gattass, Gross, & Sandell, 1981; Gattass, Sousa, & Gross, 1988; Hess, Baker, May, & Wang, 2008). Such changes in SF tuning across space have also been linked to performance in texture segmentation tasks (Gurnsey et al., 1996; Kehrner, 1997; Kehrner & Meinecke, 2003; Yeshurun & Carrasco, 2000).

Normally, both first- and second-order filters simultaneously contribute to task performance, and therefore, their separate influences cannot be disentangled. Thus, to isolate the influence of second-order filters, texture stimuli have been designed to contain only texture-defined (second-order) boundaries, rendering them invisible to luminance-based (first-order) mechanisms. This has been achieved for both dynamic and static stimuli. For instance, Chubb and Sperling (1988, 1989, 1991) constructed second-order motion stimuli devoid of first-order motion by ensuring that stimuli contained equal Fourier energy (i.e., the output of first-order spatiotemporal mechanisms) in opposite motion directions, thereby precluding first-order filters from signaling any apparent motion. Static second-order stimuli can be constructed by arranging high-frequency Gabor elements (first-order content) in low-frequency patterns (second-order content; Graham et al., 1993) or by modulating the luminance contrast of carrier noise (first-order content) with a Gabor pattern at a particular SF (Sutter et al., 1995); both methods yield second-order textures that are invisible to first-order mechanisms and activate a narrow band of second-order filters. Yeshurun and Carrasco (2000) used these two kinds of static stimuli to investigate whether exogenous attention automatically enhances spatial resolution by modulating first- or second-order filters. They found that manipulating first-order content did not alter the attentional effect whereas increasing the SF of second-order content diminished the central attentional impairment and shifted peak performance closer to the fovea.

An open question is whether endogenous attention also modifies spatial resolution by modulating second-order filters. Addressing this question could reveal important mechanistic differences between endogenous and exogenous attention and could help identify potential cortical loci that underlie these attentional effects. In particular, if both endogenous and exogenous attention acted on the same second-order filters, their distinct effects on behavior would suggest distinct attentional mechanisms. Moreover, because the striate cortex is capable of extracting second-order boundaries (Hallum, Landy, & Heeger, 2011; Lamme, 1995; Lamme, van Dijk, & Spekreijse, 1993; Larsson, Landy, & Heeger, 2006; Purpura, Victor, & Katz, 1994), these attentional effects could be mediated by cortical processing in V1.

Recently, Barbot and Carrasco (2017) investigated the mechanism by which endogenous attention improves performance across eccentricity (Yeshurun, Montagna et al., 2008). Observers detected the presence of a texture target comprising oriented lines with first- and second-order boundaries after selectively adapting to second-order filters of high or low SF. They found that when observers selectively adapted to a low SF, the

attentional effect remained. In contrast, after adaptation to a high SF, the benefit at central locations disappeared. These results suggest that endogenous attention operates by modulating sensitivity to high SFs but do not reveal whether these modulations impact first- or second-order processing.

Here, we directly investigate endogenous attention's effects on second-order filters by using *second-order stimuli* in a texture segmentation task. In addition, given that the effects of exogenous and endogenous attention differ for texture targets with first-order content (Yeshurun, Montagna et al., 2008), we assessed whether this difference extends to second-order stimuli. Thus, by independently manipulating both types of attention while keeping the observers, task, and stimuli constant, we provide the first direct comparison of attentional effects on second-order texture processing.

Methods

Participants

Nine New York University (NYU) students (two females, seven males, age range: 23–32) with normal or corrected-to-normal vision participated in this study. All participants were naïve to the purpose of the study (except the author, M.J.) and gave written informed consent under the protocol approved by the Institutional Review Board at NYU. Five participants volunteered, and four participants were remunerated at a rate of \$10/hour. Data from one participant were excluded due to below-chance performance in all experimental conditions. Thus, the results reported here are based on eight participants.

We based our sample size on previous studies of visual attention and texture segmentation that used a similar experimental design and analytical approach (Yeshurun & Carrasco, 2000, experiment 3, exogenous cueing; Yeshurun, Montagna et al., 2008, experiments 1 and 2, endogenous and exogenous cueing, respectively). We estimated the power in each experiment for a range of sample sizes (two to 10 participants) by drawing random samples from two-dimensional normal distributions. Each dimension's mean and standard deviation were determined from the group-averaged mean and standard error in each cueing condition (neutral, valid) from each experiment. Separate distributions were generated for each eccentricity. For each sample size, we drew a corresponding number of samples at each eccentricity and performed a two-way (cue \times eccentricity) repeated-measures ANOVA. This process was repeated 10,000 times, and separate p -value distributions were constructed for the main effects and their interaction. Power was computed as the propor-

tion of significant ($p < 0.05$) effects in each p -value distribution, and power greater than 0.8 was considered sufficient (Cohen, 1988). Assuming that our study would yield similar cueing effects, we found that a sample size of eight yielded sufficient power for the main effect of cue (endogenous cueing) and the interaction effect with eccentricity (exogenous cueing).

Apparatus

Visual stimuli were generated using MGL (<http://justingardner.net/mgl>), a set of OpenGL libraries running in MATLAB (MathWorks, Natick, MA), and displayed on a 21-in. CRT monitor (1,024 \times 768 resolution, 60 Hz). The display was calibrated using a Konica Minolta LS-100 (Ramsey, NJ) to produce linearized look-up tables. Participants sat in a dark and quiet room with their head stabilized by a chin rest placed 57 cm from the monitor. The position of the left eye was monitored at 1000 Hz with an Eyelink 1000 eye tracker (SR research, Ottawa, Ontario, Canada).

Stimuli

Second-order texture stimuli (30.5° \times 10°) were generated by modulating the luminance contrast of a noise carrier pattern (Figure 1A). The carrier was generated by filtering zero mean random noise (with values ranging from -1 to 1) with an isotropic band-pass filter that had a center spatial frequency of 2 c/deg and a bandwidth of one octave. Pixel values were constrained within ± 3 standard deviations of the mean and were normalized to span the maximum range of the CRT display (i.e., zero to one). To create the target, the carrier was multiplied with a Gabor function, $G(x, y)$,

$$G(x, y) = 1 + \alpha \times \cos(2\pi\omega y + \rho) \times \exp\left(\frac{-(x - \rho)^2 - y^2}{2\sigma^2}\right),$$

whose amplitude, α , was constrained between zero and one to ensure that the function was always positive and, thus, could be rendered on the display. The spatial frequency of the grating, ω , was set to 0.25 c/deg, and its orientation was always vertical. The grating was windowed by a two-dimensional Gaussian whose standard deviation, σ , was 0.8° vertically and horizontally. The location parameter, ρ , determined the phase of the grating and the center of the Gaussian distribution along the horizontal meridian such that the center of the Gaussian function coincided with peak luminance in the grating; this ensured that the appearance of the Gabor modulation was constant at all eccentricities. By constructing the texture stimuli in this way, we ensured that the luminance (first-order

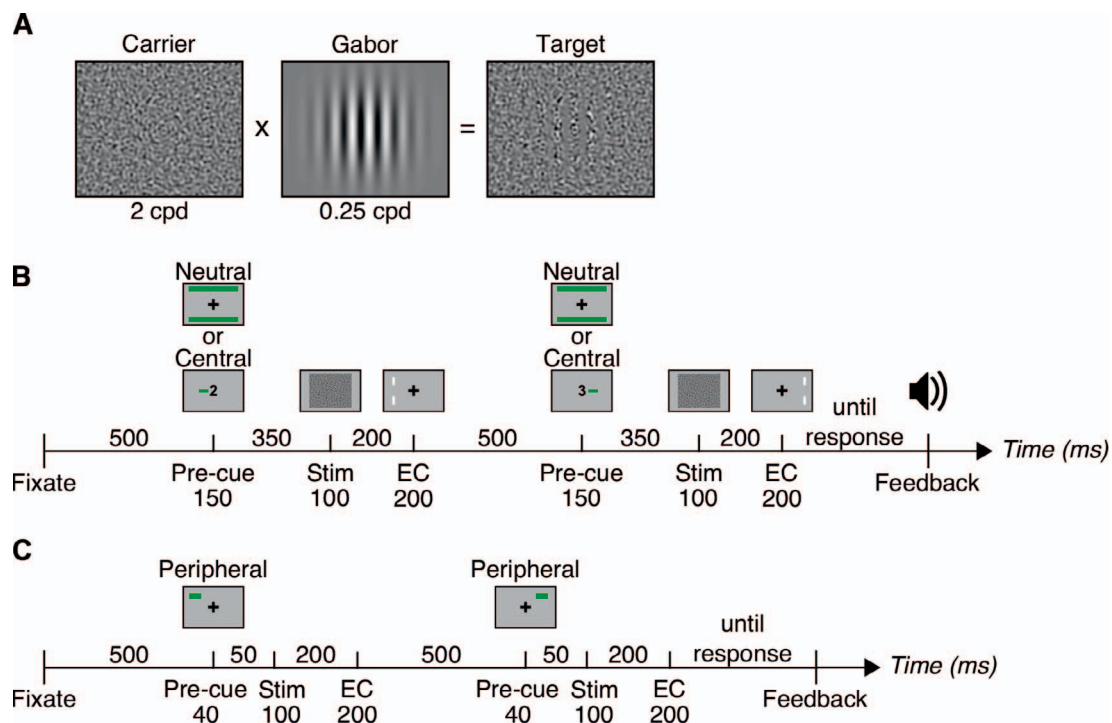


Figure 1. Schema of stimuli and trial sequence for the 2IFC texture segmentation tasks. (A) Schematic of second-order texture construction. The luminance contrast of isotropic carrier noise was modulated by a Gabor function, yielding a second-order texture target. (B) Endogenous attention task trial sequence. Texture stimuli (stim) differed in each interval; one interval contained noise while the other contained the target. Texture stimuli were followed by an eccentricity cue (EC). (C) Exogenous attention task trial sequence. Duplicate images from panel B were omitted.

content) of the Gabor modulation and the carrier were equivalent while their contrast (second-order content) could differ.

At the beginning of each trial, two unique textures were generated: One was unmodulated ($\alpha = 0$, carrier) whereas the other contained a Gabor modulation (target) that was centered at the fovea (0°) or one of six possible eccentricities along the horizontal meridian (1.2° , 2.4° , 3.6° , 4.8° , 6° , 7.2°) to the left or right of fixation (13 total possible locations). All stimuli were displayed on a gray background (31.2 cd/m^2).

Texture segmentation tasks

Endogenous attention task

We used a two-interval, forced-choice (2IFC) task, during which two temporal intervals containing texture stimuli were preceded and followed by a cue (Figure 1B). This procedure was based on previous studies (Barbot & Carrasco, 2017; Yeshurun, Montagna et al., 2008). Prior to each interval, participants fixated on a black central cross ($0.5^\circ \times 0.5^\circ$) for 500 ms. Following the fixation period, a precue was presented for 150 ms. On neutral trials, the cue was composed of two long green bars ($30.5^\circ \times 0.1^\circ$, 68.8 cd/m^2) that were located 5° above and below the horizontal meridian, respec-

tively. This cue informed participants of the temporal onset of the texture but provided no prior information about the location of the target. On valid trials, endogenous attention was manipulated by a central symbolic cue consisting of a black digit ($0.5^\circ \times 0.5^\circ$) and a green horizontal bar ($0.7^\circ \times 0.1^\circ$) presented on the horizontal meridian.¹ This cue provided information about the texture's temporal onset *and* its location. In the interval containing the target, the digit indicated the target's eccentricity: zero represented the fovea, and one through three represented progressively more eccentric locations (1.2° , 3.6° , and 6° or 2.4° , 4.8° , and 7.2° ; see Procedure below). The bar indicated the visual hemifield (left or right) where the target would be displayed; no bar accompanied the cue for the fovea. For nontarget intervals, the cue indicated another possible target location. The precue was followed by a 350-ms interstimulus interval (ISI). A texture stimulus was then presented for 100 ms. Following a 200-ms ISI, an eccentricity cue composed of two white vertical lines ($0.03^\circ \times 0.7^\circ$, 121.2 cd/m^2 , presented 1.6° above and below the horizontal meridian, respectively) was displayed for 200 ms. In the target interval, the eccentricity cue was centered on the target location whereas in the nontarget interval, the eccentricity cue was centered on another possible target location. This cue eliminated location uncertainty in both cueing

conditions. During valid trials, the location of the precue and eccentricity cue was identical in each interval. Following the second interval, the fixation cross turned green, and participants used their right hand to press “1” or “2” on a numeric keyboard to report whether the first or second interval contained the target. Participants were instructed to respond as accurately as possible, without time stress, and auditory feedback was provided for correct and incorrect responses.

Exogenous attention task

To allow a direct comparison between exogenous and endogenous attention manipulations, the task design was identical to that described above with the following exceptions regarding the spatial and temporal characteristics of the cue. Such changes were necessary to appropriately manipulate exogenous attention (Figure 1C). Following the fixation period in each temporal interval, the precue was presented for 40 ms followed by a 50-ms ISI. On valid trials, the precue was a short horizontal green bar ($0.7^\circ \times 0.1^\circ$) located 1.6° above the horizontal meridian and centered on a possible target location. The precue was centered on the target location when the interval contained a target and appeared at another possible target location during the nontarget interval. This procedure and cue characteristics were similar to those used in previous studies (e.g., Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2000).

Procedure

Within each block, cueing condition (neutral or valid), target interval (first or second), target eccentricity, and target hemifield were randomly interleaved. Each participant performed 24 blocks of 56 trials each (total: 1,344 trials) across four experimental sessions that were completed on separate days. Task order was counterbalanced across participants; half completed the exogenous task first and then the endogenous task, and the other half followed the opposite order.

In each session and as in previous studies (Barbot & Carrasco, 2017; Yeshurun, Montagna et al., 2008), target eccentricity was constrained to one of two sets of eccentricities: 0° , 1.2° , 3.6° , and 6° or 0° , 2.4° , 4.8° , and 7.2° . Because the central location (0°) was common to both sets, the eccentric locations were tested twice as often as the central location within a session. At the beginning of each block, participants were shown an unmodulated carrier with the tested locations indicated by their respective symbolic digits (zero through three). This informed participants of the possible target locations in the upcoming block and allowed them to

readily associate each symbolic cue with a specific target location during the endogenous attention task.

For each task, the Gabor’s modulation amplitude was adjusted using performance on neutral trials via best PEST—an adaptive staircase procedure as implemented in the Palamedes toolbox (Prins & Kingdom, 2009)—to maintain an average performance of 75% across the three central eccentricities (0° , 1.2° , and 2.4°). Prior to the first experimental session, participants performed an average of 14 practice blocks, during which the staircase was initialized with a uniform prior between modulation amplitudes 0.1 and 1, in steps of 0.02 (46 total levels). On each trial, the posterior probability for a participant’s modulation threshold was updated based on task performance. When participants reached equivalent thresholds (defined as the final threshold estimate on each block) on at least three blocks, their final posterior distribution was saved and served as the prior probability distribution used to initialize the staircase in the main experiment. During the main experiment, the modulation amplitude was updated on each trial to account for any further learning effects and/or fatigue. Although the modulation amplitude was allowed to vary, the narrow prior distribution prevented large changes across trials (average $SD = 0.03$, approximately one step). A repeated-measures ANOVA revealed that modulation amplitude did not vary systematically with eccentricity, cue or their interaction (all $F_s \leq 0.2$).

Data analysis

Psychophysics

Performance, $d' = z(\text{hit rate}) - z(\text{false-alarm rate})$, was computed for each observer across experimental sessions and separately for each eccentricity and cue (neutral, peripheral, and central). A hit was (arbitrarily) defined as a first-interval response to a target occurring in the first interval and a false alarm as a first-interval response to a second-interval target. Performance was averaged across hemifields, and repeated-measures ANOVAs were used to assess the effects of cue condition and eccentricity. In all cases in which Mauchly’s test of sphericity indicated a violation of the sphericity assumption, Greenhouse–Geisser corrected values were used. ANOVA effect sizes were reported in terms of generalized eta-squared (η_G^2 ; Bakeman, 2005; Olejnik & Algina, 2003). In our formulation of d' , we opted to ignore the $\sqrt{2}$ relation between performance in 2IFC and yes–no tasks because this relation is predicated on the assumption that performance is equal in each interval of a 2IFC task (e.g., Egan, 1975; Green & Swets, 1973; Macmillan & Creelman, 2005). This assumption, however, has been shown to be invalid for many data sets from different labs (Yeshurun, Carrasco, & Maloney, 2008). To verify our d' results, we also evaluated

performance as proportion correct; our results were not impacted by the performance measure used. Results using d' are reported below.

Although participants were instructed to be as accurate as possible without any time constraint, reaction times (RTs) were analyzed to rule out any speed–accuracy trade-offs. To assess RTs when the target was correctly detected, we collapsed across hit and correct rejection trials (i.e., a second-interval response to a second-interval target), computed geometric means, and performed a two-way, repeated-measures ANOVA with cue condition and eccentricity as factors.

Group-averaged performance was fitted with the best-fitting polynomial as determined by a leave-one-out cross-validation approach. For each cueing condition, we removed one data point (i.e., one eccentricity), fit polynomials (orders one through four) to the remaining six data points, and computed the residual sum of squares for the excluded value. This process was repeated seven times with a unique eccentricity excluded each time. We used the mean squared error across iterations as an index of the goodness of fit and observed that performance in both tasks was best fit by third-order polynomials. Individual observer data were then fit with third-order polynomials, which provided an estimate of the peak eccentricity. Within each task, paired t tests were used to compare the peak eccentricity between neutral and valid conditions; effect sizes were reported in terms of Cohen's d (Cohen, 1988; Lakens, 2013).

Eye tracking

Participants were instructed to maintain fixation until they made their response. If a blink or an eye movement $\geq 1.5^\circ$ occurred before the response, the trial was immediately aborted and a tone was played, reminding participants to maintain fixation. These trials were rerun at the end of the block. To verify that participants maintained fixation, off-line eye-position analysis was performed. Raw eye data were converted to eye position in degrees of visual angle. For each temporal interval, the mean eye position during the fixation period served as a baseline and was subtracted from the stimulus presentation interval to compensate for any slow drift within the trial. The average eye position during stimulus presentation was within 1° on 99.9% of trials.

Results

Endogenous attention uniformly improves performance

Performance on the endogenous attention task (Figure 1B) is depicted in Figure 2 for discriminability

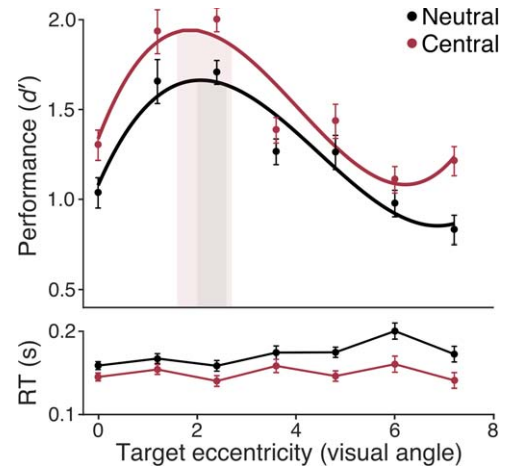


Figure 2. Average performance (top) and reaction time (bottom) as a function of target eccentricity and cue type (neutral vs. central) when endogenous attention was manipulated. In the neutral condition (black), performance peaked at the midperiphery ($\sim 2^\circ$ of eccentricity) and declined toward more central and peripheral locations, replicating the CPD. Precueing the target location with a central cue (red) improved performance at all eccentricities. Error bars represent \pm within-subject SEM (Cousineau, 2005). Performance data were fit with third-order polynomials (solid lines), and shaded regions represent 95% confidence intervals for peak eccentricity estimates as determined by a bootstrapping procedure.

(top panel) and RT (bottom panel). The effects of cue (neutral vs. central) and eccentricity (seven eccentricities) were assessed with a two-way, repeated-measures ANOVA.

There was a significant main effect of eccentricity, $F(2.13, 14.88) = 4.41$, $p < 0.05$; $\eta_G^2 = 0.24$, with performance peaking in the midperiphery and declining at both central and peripheral locations (Figure 2). This pattern is consistent with texture segmentation studies using oriented line stimuli (e.g., Gurnsey et al., 1996; Kehrer, 1989; Morikawa, 2000; Yeshurun & Carrasco, 1998) and extends the occurrence of the CPD to second-order textures. Importantly, there was a significant main effect of attention, $F(1, 7) = 18.04$, $p < 0.005$; $\eta_G^2 = 0.043$, which did not interact with eccentricity ($F < 1$). That is, endogenous attention uniformly increased performance at all eccentricities for second-order textures. This pattern is consistent with reported effects of endogenous attention on texture segmentation with first-order textures (Barbot & Carrasco, 2017; Yeshurun, Montagna et al., 2008).

Group-averaged performance was well described by third-order polynomials (neutral: $R^2 = 0.90$; central: $R^2 = 0.86$). To assess whether attention altered the eccentricity of the performance peak, third-order polynomials were fit to individual participant data, and estimates of peak eccentricity were obtained. The location of the peak did not differ between cue

conditions (neutral: $2.59^\circ \pm 0.80^\circ$, central: $2.69^\circ \pm 0.76^\circ$), $t(7) = 0.09$, $p = 0.9$, as depicted by the overlapping 95% confidence intervals (Figure 2, shaded regions).

Analysis of RT confirmed that there were no speed–accuracy trade offs (Figure 2, bottom). A significant main effect of cue, $F(1, 7) = 26.40$, $p < 0.005$; $\eta_G^2 = 0.015$, revealed faster RTs with the central cue (mean: 0.15 s) than the neutral cue (mean: 0.17 s). Thus, participants were more sensitive and responded faster with the central cue, ruling out speed–accuracy trade offs. The main effect of eccentricity and the interaction were nonsignificant (all $F_s < 2.5$, $p > 0.06$).

Exogenous attention yields eccentricity-dependent effects on performance

Performance on the exogenous attention task (Figure 1C) is depicted in Figure 3 for discriminability (top panel) and RT (bottom panel). The effects of cue (neutral vs. peripheral) and eccentricity (seven eccentricities) were assessed with a two-way, repeated-measures ANOVA.

There was a significant main effect of cue, $F(1, 7) = 48.38$, $p < 0.001$; $\eta_G^2 = 0.10$, and eccentricity, $F(6, 42) = 3.13$, $p < 0.05$; $\eta_G^2 = 0.19$. Critically, there was a significant cue \times eccentricity interaction, $F(2.82, 19.73) = 7.73$, $p < 0.005$; $\eta_G^2 = 0.084$; peripheral cues improved performance at peripheral locations but impaired it at central locations (Figure 3, top). This central attentional impairment is consistent with previously reported effects of exogenous attention on texture segmentation with first-order (Carrasco et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998) and second-order textures (Yeshurun & Carrasco, 2000).

Group-averaged performance was well described by third-order polynomials (neutral: $R^2 = 0.90$; peripheral: $R^2 = 0.76$), which were used to estimate peak eccentricities for individual participants. Peripheral cues shifted peak eccentricity toward the periphery (neutral: $1.13^\circ \pm 0.33^\circ$, peripheral: $3.80^\circ \pm 0.98^\circ$), $t(7) = 2.50$, $p < 0.05$, Cohen's $d = 0.89$ (Figure 3, shaded regions), consistent with an increase in spatial resolution relative to the fixed scale of the texture target (Carrasco et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998). Moreover, this result indicates that the peak eccentricity shift by exogenous attention extends to second-order textures.

Analysis of RT ruled out speed–accuracy trade offs (Figure 3, bottom). A significant main effect of cue, $F(1, 7) = 12.17$, $p < 0.05$; $\eta_G^2 = 0.014$, revealed that RTs were faster with the peripheral cue (mean: 0.15 s) than the neutral cue (mean: 0.18 s), ruling out speed–accuracy trade-offs. The main effect of eccentricity and

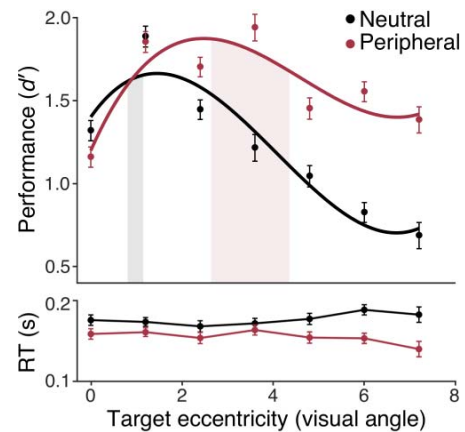


Figure 3. Average performance (top) and reaction time (bottom) as a function of target eccentricity and cue type (neutral vs. peripheral) when exogenous attention was manipulated. Precueing the target location with a peripheral cue (red) improved performance in the periphery but impaired performance at central locations. Error bars represent \pm within-subject SEM. Performance data were fit with third-order polynomials (solid lines), and shaded regions represent the 95% confidence interval for peak eccentricity estimates as determined by a bootstrapping procedure.

the interaction were nonsignificant (all $F_s < 1.3$, $p > 0.3$).

Spatial covert attention yields distinct effects on texture segmentation

Because exogenous and endogenous attention both were within-subject manipulations, their effects on texture segmentation could be directly compared. Cueing effects (valid minus neutral) were computed for each observer, and the group average was fit with straight lines to aid visualization (Figure 4).

Whereas endogenous attention produced an approximately uniform benefit across eccentricity, the effect of exogenous attention scaled with eccentricity: Costs became larger toward the fovea, and benefits increased toward the periphery. In accordance with this crossover in cueing effects, a two-way, repeated-measures ANOVA (2 attention types \times 7 eccentricities) revealed a significant interaction, $F(2.79, 19.54) = 3.53$, $p < 0.05$; $\eta_G^2 = 0.18$. In addition, we observed a main effect of eccentricity, $F(6, 42) = 2.41$, $p < 0.05$; $\eta_G^2 = 0.13$, and attention, $F(1, 7) = 8.26$, $p < 0.05$; $\eta_G^2 = 0.03$, due to a larger benefit of exogenous attention at peripheral locations. These results highlight the distinct mechanisms of both types of attention: an inflexible exogenous mechanism whose resolution enhancement is most beneficial in the periphery (Carrasco et al., 2002; Carrasco & Yeshurun, 1998; Yeshurun &

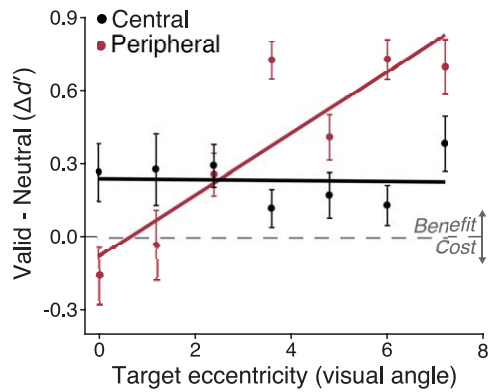


Figure 4. Cueing effects (valid minus neutral) as a function of target eccentricity and cue type (central vs. peripheral). Precuing with peripheral cues impaired performance at central locations and improved performance in the periphery. Central cues yielded a performance improvement that was independent of eccentricity. Straight-line fits (solid lines) were used to aid in data visualization.

Carrasco, 1999) and a flexible endogenous mechanism that modifies resolution according to task demands.

Discussion

Using a second-order texture-segmentation task, this study shows that endogenous attention improves performance at all attended locations, suggesting that it is an adaptive mechanism that can flexibly modulate second-order filters. Such an adaptive mechanism has been suggested (Yeshurun, Montagna et al., 2008) and demonstrated (Barbot & Carrasco, 2017) before. However, this is the first study to isolate second-order processing while comparing the effects of exogenous and endogenous attention on texture segmentation. Our results reveal that second-order filters mediate the differential effects of exogenous and endogenous attention. Exogenous attention impairs performance at central locations and improves it at peripheral locations, consistent with an automatic resolution enhancement. In contrast, endogenous attention improves performance across eccentricity, consistent with a flexible modulation of resolution.

Such flexible control of spatial resolution by endogenous attention could be explained in terms of interfrequency inhibition; small RFs tuned to high SFs inhibit large RFs tuned to low SFs at the same spatial location (Foley & McCourt, 1985; Gurnsey et al., 1996; McCourt, 1982; Yeshurun & Carrasco, 2000). According to this hypothesis, the CPD is the consequence of greater high-SF sensitivity at the fovea inhibiting sensitivity to low SFs, thereby narrowing spatial filters and yielding a spatial resolution that is too high for the

texture target. Thus, to alleviate the CPD and improve performance at central locations, endogenous attention reduces sensitivity to high SFs, which effectively reduces the resolution at central locations. Conversely, to improve performance in the periphery, endogenous attention increases high-SF sensitivity and effectively narrows spatial filters to increase resolution. Interfrequency inhibition is consistent with the finding that endogenous attention operates primarily on high-SF filters (Barbot & Carrasco, 2017).

In addition, we provide further evidence that exogenous attention inflexibly increases spatial resolution. The improved performance in the periphery but impaired performance in central locations is consistent with studies that demonstrate this effect with oriented line stimuli (Carrasco et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2008) and second-order textures (Yeshurun & Carrasco, 2000). Thus, our results support the notion that exogenous attention automatically modulates second-order processing by inflexibly narrowing spatial filters, which increases resolution. As described by Yeshurun and Carrasco (2000), this narrowing could be explained in terms of interfrequency inhibition. That is, exogenous attention automatically increases high-SF sensitivity and consequently inhibits low SFs, leading to an enhanced spatial resolution at the attended location. Consistent with this hypothesis, selective adaptation to high SFs diminishes the detrimental effects of exogenous attention on texture segmentation (Carrasco et al., 2006).

Because both endogenous and exogenous attention operate on second-order filters tuned to high SFs, their distinct effects on spatial resolution highlight their different modes of operation. Whereas endogenous attention enhances or reduces resolution depending on the resolution constraints of the visual system, exogenous attention inflexibly enhances resolution. Our findings provide converging evidence for an automatic exogenous mechanism whose effects are invariant to the predictability of the cue (Giordano et al., 2009) and have been attributed to modulations of high-SF neurons that enhance spatial resolution and reduce temporal resolution (Carrasco et al., 2006; Megna, Rocchi, & Baldassi, 2012; Yeshurun & Levy, 2003; Yeshurun & Sabo, 2012). Our findings also provide further evidence for a more adaptive endogenous mechanism that improves both spatial and temporal discriminability (Barbot & Carrasco, 2017; Barbot, Landy, & Carrasco, 2012; Giordano et al., 2009; Hein, Rolke, & Ulrich, 2006; Yeshurun, Montagna et al., 2008).

It is unlikely that the effects of attention were mediated by our stimuli's first-order content for the following reasons: First, the discriminability of a second-order stimulus is invariant to the contrast of its first-order carrier (Barbot, Landy, & Carrasco, 2011).

Thus, attention-related changes in first-order contrast sensitivity would have a negligible impact on the detection of a second-order target. Second, attentional effects on second-order stimuli are immune to changes in first-order content (Yeshurun & Carrasco, 2000). Taken together, these facts support the interpretation that the attentional effects we report here were mediated by the second-order content of our stimuli.

Our exogenous attention effects paralleled those of Yeshurun and Carrasco (2000) on second-order textures, but the overall pattern of performance differed. Specifically, performance in their study peaked near the fovea whereas our results exhibited a pronounced CPD. Additionally, we observed that exogenous attention shifted the peak eccentricity 2.7° toward the periphery whereas the peak shift in that study was negligible. We attribute these differences in the overall pattern of performance to the differences in performance titration. Whereas we controlled performance by adjusting the modulation amplitude (second-order contrast) of the texture, they adjusted its duration, which does not reliably elicit the CPD (Morikawa, 2000). Moreover, by presenting the second-order texture at contrast threshold, we presumably activated second-order filters narrowly tuned to the target, which provided a better probe for their role in texture segmentation.

Our findings of endogenous attention's effect on spatial resolution are consistent with neurophysiological and human fMRI evidence (review by Anton-Erxleben & Carrasco, 2013). Yet we note that these studies have not investigated second-order textures directly. In macaques, endogenous attention yields changes in RF size and shifts their position toward the attended location. In particular, RFs shrink around the attended location when attention is directed inside the RF and expand when directed outside (Anton-Erxleben, Stephan, & Treue, 2009; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Indeed, recent neurophysiological evidence has shown that when attention is allocated near the RFs, they are elongated toward the attentional locus (Obara, O'Hashi, & Tanifuji, 2017). Similarly, converging evidence from human fMRI shows that attention narrows the spatial overlap in blood-oxygen-level dependent responses between adjacent locations (Fischer & Whitney, 2009) whereas withdrawing attention from the periphery enlarges peripheral population receptive fields (pRFs; de Haas, Schwarzkopf, Anderson, & Rees, 2014). In addition, attention attracts pRFs toward the attended location across the visual field and throughout cortical areas (Klein, Harvey, & Dumoulin, 2014). Likewise, encoding models that extract the spatial selectivity of individual voxels (vRFs) have shown that vRFs shift toward the attended location, improving spatial discriminability (Vo, Sprague, & Serences, 2017).

In sum, the attention-induced shifts and narrowing of spatial selectivity are possible mechanisms by which endogenous attention increases the sensitivity of small RFs at the attended location, leading to enhanced resolution. Conversely, by enlarging RFs, attention could reduce the spatial resolution at the attended location. The neural mechanisms of exogenous attention on spatial resolution, however, have not been well characterized. But given our observed differences between both types of spatial attention, further investigations will likely reveal distinct RF modulations.

Conclusions

Our findings provide novel evidence that endogenous attention alters the visual system's spatial resolution by modulating second-order processing. In particular, endogenous attention flexibly enhances or reduces resolution based on the spatial scale of relevant visual information and the constraints of the visual system. In addition, consistent with a previous study (Yeshurun & Carrasco, 2000), we provide converging evidence that exogenous attention inflexibly enhances resolution via second-order filters. Thus, our results highlight the distinct mechanisms of both types of covert spatial attention.

Keywords: covert attention, spatial resolution, texture segmentation, second-order

Acknowledgments

M. Carrasco was supported by NIH Grants RO1-EY016200 and RO1-EY019693. We want to thank Antoine Barbot as well as the members of the Carrasco lab for constructive comments on the manuscript. The authors declare no conflicts of interest.

Commercial relationships: none.

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Footnote

¹ For one participant, the cue was placed 1.6° above the fixation cross due to an apparent masking effect when the target appeared in the center of the screen.

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