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Frequency-dependent modulation of foveal contrast sensitivity by fine-scale exogenously triggered attention

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This study explores how exogenous attention operates at the finest spatial scale of vision, within the foveola - a topic that has not been previously explored but is of interest to visual neuroscientists. The question is **important** for understanding how attention shapes perception, and how it differs between the periphery and the central regions of highest visual acuity. The evidence indicating that attention near the fovea preferentially enhances low spatial frequencies is **compelling**, as shown by carefully designed experiments with state-of-the-art eye tracking to monitor attended locations just a few tens of minutes of arc away from the fixation target.

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Abstract

Exogenous attention is a rapid, involuntary mechanism that automatically reallocates processing resources toward salient stimuli. It enhances visual sensitivity in the vicinity of the salient stimulus, both in extrafoveal regions and within the high-acuity foveola. While the spatial frequencies modulated by exogenous attention in extrafoveal vision are well characterized, it remains unknown how this mechanism operates within the foveola, which can resolve spatial frequencies up to 30 cycles per degree (CPD). Here, we examined which spatial frequencies were enhanced by fine-grained deployments of exogenous attention within this highest-acuity region of the visual field. Using high-precision eye-tracking to precisely localize gaze during attentional allocation, we found that exogenous attention at the foveal scale selectively enhances contrast sensitivity for low- to mid-range spatial frequencies (4–8 CPD), with no significant benefits for higher spatial frequencies (12–20 CPD). In contrast, attention-related benefits on asymptotic performance at the highest contrast were observed across a wide range of spatial frequencies. These results indicate that, despite the high-resolution capacity of the foveola, exogenous attention remains an inflexible mechanism that, even at this scale, selectively enhances contrast gain for lower spatial frequencies—mirroring its behavior in extrafoveal vision.

Introduction

Visual spatial attention is a fundamental mechanism that enables both humans (Carrasco, 2011) and animals (Saban et al., 2017; Hahner and Nieder, 2025) to selectively process information from their environment. Often, shifts in spatial attention are accompanied by eye movements to focus on a specific location, a process known as overt spatial attention (Kaspar, 2013). However, covert spatial attention, the ability to shift attention independently of eye movements, is equally crucial in daily life. This ability enables us to monitor locations beyond our line of sight, such as when driving and keeping track of peripheral surroundings.

Covert spatial attention is typically categorized into two types: endogenous and exogenous attention. Endogenous attention refers to the voluntary allocation of processing resources to a specific location. While this shift occurs relatively slowly, taking approximately 200–300 ms to reach the target region, it can be sustained for an extended duration (Theeuwes, 1994; Findlay, 2003; Chica and Lupiáñez, 2009; Carrasco, 2011; Chica et al., 2013; Dugué et al., 2020). In contrast, exogenous attention is driven by salient stimuli that automatically capture attention (Theeuwes, 1994; Findlay, 2003; Chica and Lupiáñez, 2009; Carrasco, 2011; Chica et al., 2013; Dugué et al., 2020). This shift is rapid but transient, often followed by a phenomenon known as inhibition of return, moving attention away from the initially attended location (Klein, 2000; Chica and Lupiáñez, 2009). Compared to endogenous attention, exogenous attention is more automatic and less flexible Corbetta and Shulman (2002); Knudsen (2007); Carrasco (2011).

Until recently, research on the effects of covert attention on visual perception has focused primarily on extrafoveal vision. A vast body of literature has demonstrated that covert attention enhances visual contrast sensitivity (Carrasco et al., 2000; Martínez-Trujillo and Treue, 2002; Reynolds and Chelazzi, 2004; Pestilli and Carrasco, 2005; Li et al., 2008; Foster et al., 2021) and increases spatial resolution (Yeshurun and Carrasco, 1998; Carrasco et al., 2002, 2006; Jigo and Carrasco, 2018) at selectively cued locations in the extrafovea. In contrast, attention within the high-acuity 1-deg foveola has often been considered uniform and distributed evenly throughout this small region. Therefore, the effects of attention in the fovea are traditionally studied using large stimuli encompassing one or more degrees of visual angle (Miniussi et al., 2002; Jigo and Carrasco, 2020; Papaioannou and Luck, 2020). However, recent findings showed that even within the 1-degree foveola, both endogenous (Poletti et al., 2017) and exogenous (Guzhang et al., 2021) attention can be covertly allocated in a highly spatially selective manner. For both types of covert attention, observers were better able to discriminate the orientation of fine details at an attended location—cued endogenously or exogenously—compared to nearby uncued locations just 0.26° away. Although these results highlighted the strikingly fine grain of attentional control, they also raised new questions. In particular, it remains unknown which spatial frequencies benefit from fine-grained attentional shifts within the foveola. While Guzhang et al. (2021) demonstrated visual enhancement from exogenous attention at the foveal scale, the orientation discrimination task used in the study was relatively coarse, requiring observers to determine whether a stimulus was tilted ±45°. Despite the small size of the stimulus, such a task does not require high spatial frequencies (*e.g.*, > 10 cycles per degree); in fact, frequencies around 4-8 cycles per degree (CPD) should be sufficient to perform it effectively. Therefore, the perceptual enhancement observed in Guzhang et al. (2021) could be due to an enhancement of only lower or only higher spatial frequencies, or perhaps a broad range of spatial frequencies. The overall improvement in orientation discrimination of fine spatial stimuli is compatible with any of these scenarios.

The effects of *extra*foveal attention have been found to differ across spatial frequencies: while extrafoveal endogenous attention enhances a broad range of spatial frequencies (Lu and Dosher, 2004; Jigo and Carrasco, 2020), extrafoveal exogenous attention selectively enhances high spatial frequencies (Carrasco et al., 2006; Barbot et al., 2011, 2012; Carretié et al., 2012; Jigo and Carrasco, 2020; Fernández et al., 2022), peaking just above the spatial frequency characterized by the highest sensitivity at a given eccentricity (Jigo and Carrasco, 2020). Whether fine spatial exogenous attention at the foveal scale modulates visual discrimination similarly is an open question. Generally, fine control of spatial attention at the foveal scale is required when examining fine spatial details, such as reading small text in a book or noticing subtle changes, like a traffic light switching or unexpected pedestrians from afar while driving (Figure 1*A*). In these tasks, precise allocation of attention likely helps distinguishing and recognizing individual letters and details. It is possible that in the foveola, exogenous attention modulates a narrow range of spatial frequencies, similar to how it operates extrafoveally. However, while humans can resolve spatial frequencies up to 30 cycles per degree (CPD) in the foveola (Intoy and Rucci, 2020; Clark et al., 2022), extrafoveally, spatial frequencies above 10 CPD cannot be resolved. Therefore, even if the perceptual enhancement driven by fine spatial attention is limited to a narrow range of lower spatial frequencies, the enhanced frequency range may shift toward higher spatial frequencies in the foveola compared to what happens extrafoveally (Figure 1*B*). Alternatively, attention at the foveal scale might preserve its enhancement of low spatial frequencies while extending it to high spatial frequencies, leading to a broad, rather than narrow, range of modulation (Figure 1*C*). Any of these scenarios could account for the improvement in orientation discrimination observed in Guzhang et al. (2021).

In the current study, we addressed two main questions. First, does exogenous attention at the foveolar scale enhance visual processing across a narrow or a broader range of spatial frequencies? Second, if the enhancement operated within a narrow frequency band, which range of spatial frequencies benefits the most from such fine-grained shifts of attention? Addressing these questions is crucial because, while it is now established that covert attention can be selectively shifted even within the central fovea, it remains unclear whether it follows the same *modus operandi* foveally and extrafoveally. If a similar range of spatial frequencies is enhanced by exogenous attention in both the foveola and extrafovea, it would suggest that exogenous attention operates similarly across the visual field, regardless of the spatial resolution achievable at different eccentricities. In contrast, if the modulation of spatial frequencies differs, it would indicate that the mechanisms of exogenous attention are flexibly tuned in the foveola and adjusted based on the spatial resolution that can be achieved at this scale.

Studying attentional control in the foveola presents unique challenges. Continuous microscopic eye movements during fixation cause constant displacement of the retinal input (Martinez-Conde et al., 2004; Rucci and Poletti, 2015; Krauzlis et al., 2017), making it difficult to limit visual stimulation to the desired eccentricity at this scale. This poses a significant issue when investigating covert attention in the central foveola. To address these challenges, we employed high-precision eye-tracking (Wu et al., 2023) combined with gaze-contingent display control (Santini et al., 2007) to precisely monitor gaze position throughout each trial to ensure that any effects observed are solely due to covert exogenous attention and are not driven by fixational saccades (Hafed and Clark, 2002; Yuval-Greenberg et al., 2014; Shelchkova and Poletti, 2020; Guzhang et al., 2024).

Results

To examine the effects of high-resolution exogenous attention within the fovea on visual discrimination of stimuli at different spatial frequencies, we employed a 2AFC visual discrimination task in which observers were asked to discriminate the orientation of a small Gabor patch ($30'$ x $30'$ with an overlaying $5.4'$ Gaussian window, tilted ±45°) $30'$ from either left or right of the fixation marker when prompted by a response cue (Figure 2*A*). Note that, the Gabor patches used in the current study were much smaller than those typically used in studies probing extrafoveal attention (Rossi and Paradiso, 1995; Gobell and Carrasco, 2005; Herrmann et al., 2010; Jigo and Carrasco, 2020). On each trial, the orientation and phase of the Gabor patch was randomized at each location independently. Eye movements were monitored at high resolution using a digital Dual Purkinje Image eye tracker (Wu et al., 2023) to ensure that observers maintained the center of gaze within a $10'\times10'$ window around the fixation point throughout the trial (Figure 2*D*). There were no systematic differences in fixation position between valid and neutral conditions, either horizontally (valid: $0.20'\pm0.66'$SD; neutral: $0.21'\pm0.63'$SD; p = 0.53) or vertically (valid: $-0.52'\pm0.84'$SD; neutral: $-0.48'\pm0.82'$SD; p = 0.34).

The experiment included two cueing conditions, valid and neutral, that were randomly interleaved with equal probability within each experimental block. In the valid condition, shifts of exogenous attention were elicited by a small and brief white flash (exogenous cue) presented 100 ms before the target either on the left or the right of the visual field. The cue, with 100% validity, appeared just outside the upcoming target location. In the neutral condition, no exogenous cue was presented.

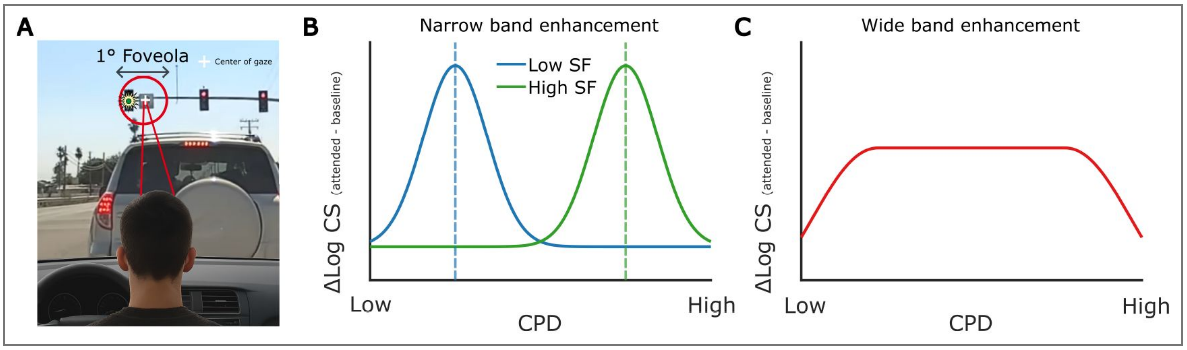

Figure 1. Fine-tuning exogenous attention within the foveola.

(**A**) Fine-tuning of exogenous attention within the foveola occurs, for example, when we are looking at a distant traffic light—occupying less than 1° of our visual field—that suddenly turns green, capturing our attention and prompting us to move forward. As a result of the fine-tuning of exogenous attention, contrast sensitivity could be enhanced for a narrow range of spatial frequencies, centered around lower spatial frequencies (blue) or higher spatial frequencies (green) (**B**). On the other hand, contrast sensitivity may be enhanced uniformly across a wide range of spatial frequencies (**C**).

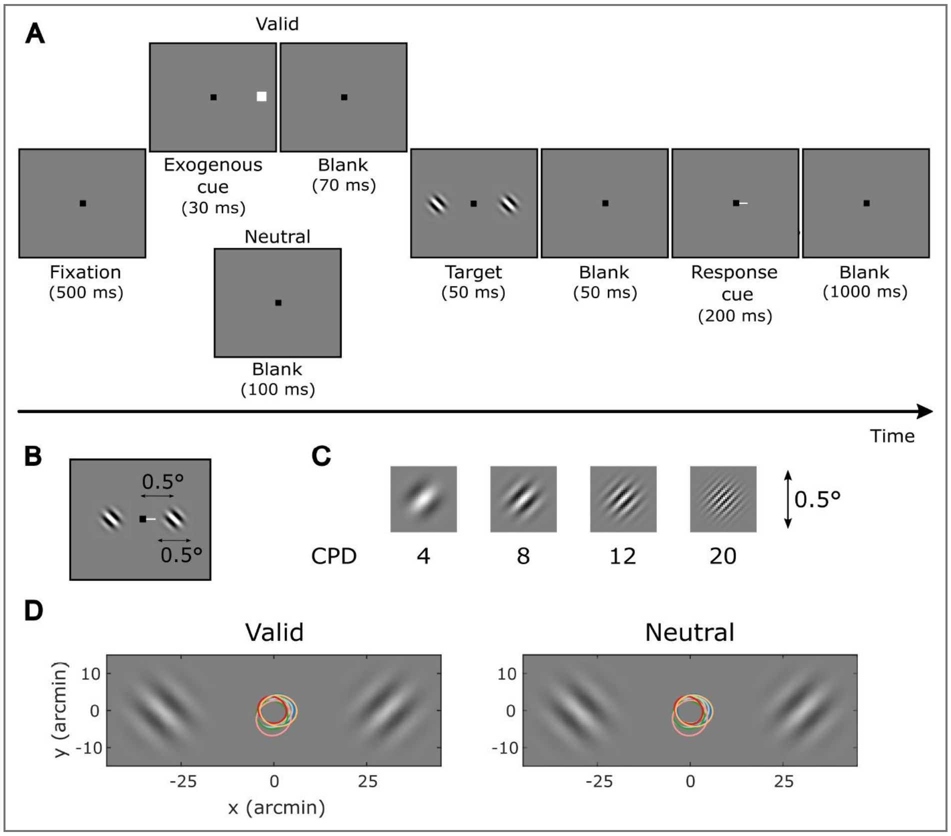

Figure 2. Experimental protocol.

(**A**) Trials started with a fixation marker at the center of the monitor. Observers were instructed to maintain fixation at the center throughout the trial. After a brief flash of the exogenous cue to capture observers' attention, two Gabor patches independently tilted (±45°) were briefly displayed, one on each side of the fixation marker. At the end of the trial, a response cue appeared, and observers had to report the orientation of the stimulus that was previously presented at the cued location. In valid trials, the exogenous cue and response cue indicated the same spatial location. In neutral trials, no exogenous cue was presented. Valid and neutral trials had the same probability of occurrence. (**B**) Size of the stimuli. The Gabor patches had a Gaussian window of 5.4' standard deviation, creating a 30' x 30' visible region. (**C**) Stimuli used in the experiment. Gabor patch of all spatial frequencies tested from 4 to 20 cycles per degree (CPD). (**D**) 68% contour of the gaze probability distribution in valid and neutral conditions during Gabor presentation. Color represents individual observers. Figure 2—figure supplement 1. Number and proportion of trials included in the analysis after filtering. Figure 2—figure supplement 2. Average saccade onset relative to response cue onset.

We tested four spatial frequencies (SFs), 4, 8, 12, and 20 CPDs, Figure 2C), ensuring at least one full cycle of modulation within the Gabor patch even at the lowest SF (4 CPD) (Howell and Hess, 1978). The highest spatial frequency (20 CPD) is close to the limit of visual resolution at the eccentricity tested here. For each spatial frequency tested, an initial threshold contrast was estimated by methods of constant stimuli, then discrimination accuracy was measured at four contrast levels around the initial threshold estimate, and one additional level at the maximum contrast to measure the asymptotic performance (see Methods). The contrast level was kept constant within each experimental block but was randomized across blocks.

To examine how high-resolution exogenous attention influences performance for stimuli at different spatial frequencies, we fitted individual psychometric curves of contrast level versus discrimination accuracy and estimated contrast thresholds for each cueing condition and spatial frequency for each observer (Figure 3A shows the psychometric curves for one example observer with the result of all psychometric curves included in Figure 3—figure Supplement 1).

We first examined the full factorial effects of spatial frequency (SF) and cueing on contrast sensitivity estimated from the observers' psychometric functions by fitting a linear mixed-effects regression to the estimates of log-transformed contrast sensitivity at all 8 conditions (4 SF x 2 cueing) across observers. The contrast sensitivity captures the effects on the intercept and/or slope of the psychometric function.

Consistent with the literature (Howell and Hess, 1978; Bex et al., 2009; Lovegrove et al., 1980; Rovamo et al., 1992, 1993; Pointer and Hess, 1989), we observed a main effect of spatial frequency on contrast sensitivity ($\chi^2(3) = 65.3$, $p < 0.0001$, Figure 3B; see Appendix 1—Table 1 for full model output); contrast sensitivity was highest at 4 CPD and decreased as the spatial frequency increased (post-hoc pairwise comparisons revealed several significant differences between spatial frequencies [post-hoc pairwise comparisons of the estimated marginal means, $ps \leq 0.0001$ for 4 vs. 8 CPD, 4 vs. 12 CPD, 4 vs. 20 CPD, 8 vs. 20 CPD, 12 vs. 20 CPD]). We also observed a significant main effect of attention on contrast sensitivity ($\chi^2(1) = 7.3$, $p < 0.001$; $\text{mean}_{\text{valid}} = 10.1 \pm 7.56\text{SD}$ and $\text{mean}_{\text{neutral}} = 9.03 \pm 6.39\text{SD}$): averaging across all spatial frequencies, the valid cueing condition resulted in higher contrast sensitivity (Figure 3B, C). These findings indicate that exogenous attention led to a contrast gain across spatial frequencies in the attended subfoveolar region.

Notably, the improvement in contrast sensitivity driven by fine-grained attention was not uniform across spatial frequencies (Figure 3D, also visible in Figure 3B, C). We observed a statistically significant interaction between spatial frequency and attention ($\chi^2(3) = 9.3$, $p = 0.0258$), indicating that contrast gains were selective. Specifically, contrast sensitivity exhibited a contrast gain in the valid condition compared to the neutral condition at lower spatial frequencies (4 and 8 CPD) ($\text{mean gain}_{4\text{ CPD}} = 2.62 \pm 2.13$ SD, Cohen's $d = 0.79$ and $\text{mean gain}_{8\text{ CPD}} = 1.36 \pm 1.25$ SD, $d = 0.75$, $ps < 0.004$; see Appendix 1—Table 2 for all pairwise comparisons.). However, the contrast sensitivity gains at higher spatial frequencies (12 and 20 CPD) were smaller and did not reach statistical significance ($\text{mean gain}_{12\text{ CPD}} = 0.09 \pm 0.91\text{SD}$ and $\text{mean gain}_{20\text{ CPD}} = 0.11 \pm 0.13\text{SD}$, $ps > 0.5$). In addition to examining the contrast gain within each spatial frequency, we also compared the amount of contrast gain within each pair of spatial frequencies (see Appendix 1—Table 3 for all pairwise comparisons). Post-hoc pairwise comparisons revealed that attention modulation did not differ between the two low-mid spatial frequencies (4 and 8 CPD, $p > 0.8$) or between the two mid-hight spatial frequencies (12 and 20 CPD, $p > 0.7$). Importantly, attention led to a larger enhancement of contrast sensitivity at the low-mid spatial frequencies (4 and 8 CPD) compared to 12 CPD ($\Delta\text{mean gain}_{4\text{ CPD - }12\text{ CPD}} = 2.53 \pm 2.16\text{SD}$, $d = 0.65$, and $\Delta\text{mean gain}_{8\text{ CPD - }12\text{ CPD}} = 1.27 \pm 0.99\text{SD}$, $d = 0.62$, $ps < 0.025$). When comparing the low-mid spatial frequencies (4 and 8 CPD) to the highest spatial frequency tested (20 CPD), differences in contrast gains were even larger, though these effects were not statistically significant ($\Delta\text{mean gain}_{4\text{ CPD - }20\text{ CPD}} = 3.35 \pm 1.96\text{SD}$, $p = 0.066$ and $\Delta\text{mean gain}_{8\text{ CPD - }20\text{ CPD}} = 1.45 \pm 1.46\text{SD}$, $p = 0.084$). As detailed in Methods, two observers did not have data for the 20 CPD condition. Statistical power might thus have been reduced for comparisons against this condition.

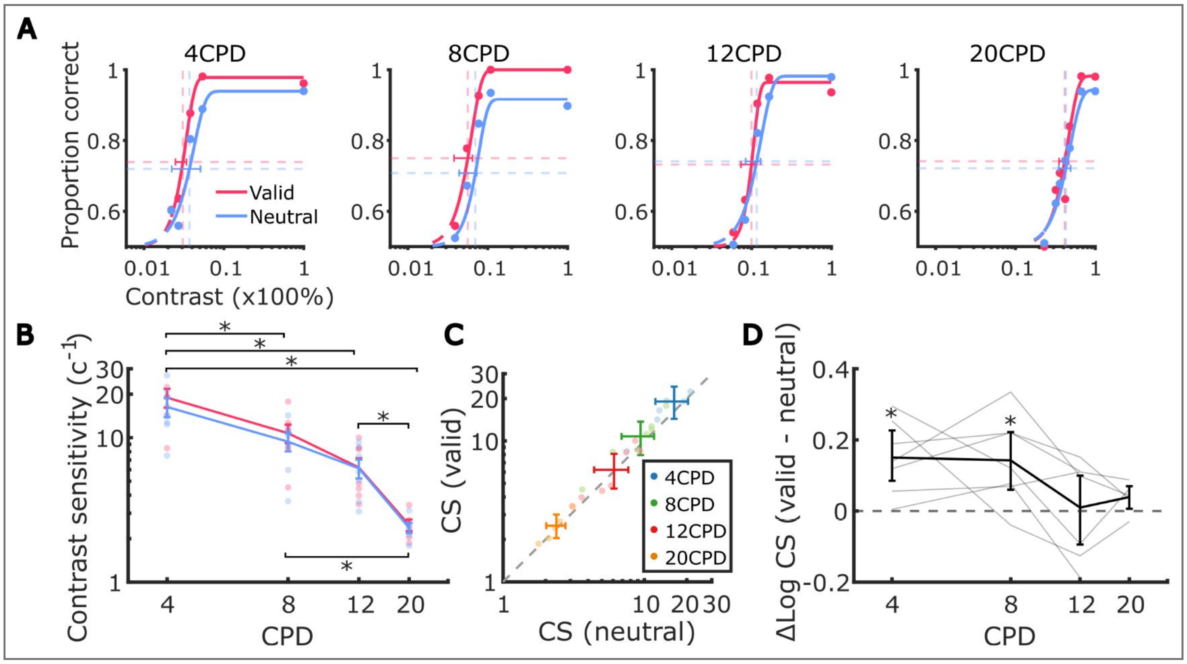

Figure 3. Effect of fine-grained exogenous attention on contrast sensitivity.

(**A**) Psychometric functions illustrating example observers' discrimination accuracy for Gabor patches with spatial frequencies of 4, 8, 12, and 20 cycles per degree (CPD). The size of each dot corresponds to the number of trials included at a specific contrast value. Vertical lines indicate contrast thresholds, while horizontal lines represent the accuracy level midway between chance performance and maximum performance. (**B**) Average contrast sensitivity, calculated as the inverse of the contrast threshold, across spatial frequencies in valid and neutral conditions. Each dot represents an individual observer. Error bars denote the standard error of the mean (SEM). Asterisks mark a significant difference in contrast sensitivity between pairs of spatial frequencies. (**C**) Average contrast sensitivity in neutral condition against that in valid condition at each spatial frequency. Each dot represents an individual observer. Error bars indicate the bootstrapped 95% confidence intervals. (**D**) Average difference in log-scaled contrast sensitivity between valid and neutral conditions across different spatial frequencies. Each line corresponds to the log-scaled contrast sensitivities from each observer. Error bars represent the bootstrapped confidence intervals. Asterisks mark post-hoc pairwise comparison results between valid and neutral conditions within each spatial frequency. Figure 3—figure supplement 1. Psychometric functions for all observers in all conditions. Figure 3—figure supplement 2. Contrast sensitivity results including 2 CPD. Figure 3—figure supplement 3. Relation between mean and variability of contrast sensitivity (CS). Figure 3—figure supplement 4. Attention benefit plotted as ratio of contrast sensitivity between valid and neutral trials.

These results demonstrate that, similar to the selectivity in enhancements in visual periphery, micro-shifts of exogenous attention within the central fovea selectively enhanced contrast sensitivity primarily for low- to mid-range frequencies (4 to 8 CPD).

In addition to contrast sensitivity, we examined the effects of attention on asymptotic performance. Research on *extra*foveal vision has returned mixed results with respect to the effects of exogenous attention on asymptotic performance. It has been found that exogenous attention can enhance both contrast sensitivity (contrast gain) but also asymptotic performance, a phenomenon known as response gain (Morrone et al., 2002, 2004; Ling and Carrasco, 2006; Pestilli et al., 2009; Reynolds and Heeger, 2009; Herrmann et al., 2010). However, some studies have found significant effects only on contrast sensitivity, with no notable impact on asymptotic performance in extrafoveal vision (Cameron et al., 2002; Herrmann et al., 2010; Jigo and Carrasco, 2020). It has been argued that whether covert attention influences contrast gain, response gain, or both, depends on stimulus size, size of the attended area as well as spatial uncertainty(Herrmann et al., 2010; Wu et al., 2021; Reynolds and Heeger, 2009).

To examine how asymptotic performance was impacted by micro-shifts of foveal exogenous attention across spatial frequencies, we fitted a generalized linear mixed-effects regression to the estimated asymptotic performance from all 8 conditions of all observers (see Appendix 2—Table 1 for full model output). Observers' ability to discriminate the orientation at full contrast (asymptotic performance) decreased with increasing frequency (Figure 4*B, C*), but this change was not significant ($\chi^2(3) = 7.6$, $p = 0.0545$) (post-hoc pairwise comparisons revealed significant differences in asymptotic performance only between 8 and 20 CPD [$p = 0.015$] as well as 12 and 20 CPD [$p = 0.048$]). The main effect of attention was significant, with overall higher asymptotic performance in the valid condition compared to the neutral condition ($\chi^2(1) = 11.9$, $p < 0.001$; $\text{mean}_{\text{valid}} = 0.97 \pm 0.03$SD and $\text{mean}_{\text{neutral}} = 0.94 \pm 0.04$SD; see Figure 4*A, C*). These findings suggest that fine-grained attention resulted in a general response gain, enhancing the ability to discriminate the orientation of high-contrast stimuli.

Unlike for contrast sensitivity, we did not observe a significant interaction between spatial frequency and attention on asymptotic performance (Figs.4*D*, $\chi^2(3) = 5.1$, $p > 0.15$). (Post-hoc pairwise comparisons between valid and neutral conditions within each spatial frequency revealed that attention significantly increased asymptotic performance compared to neutral condition at 8 and 12 CPD [mean $\text{gain}_{8\text{ CPD}} = 0.05 \pm 0.04$SD, $p < 0.0001$ and mean $\text{gain}_{12\text{ CPD}} = 0.03 \pm 0.03$SD, $p = 0.0108$] but not at 4 and 20 CPD [mean $\text{gain}_{4\text{ CPD}} = 0.02 \pm 0.03$SD, $p = 0.0819$ and Δmean $\text{gain}_{20\text{ CPD}} = 0.03 \pm 0.04$SD, $p = 0.0501$; see Appendix 2—Table 2 for all pairwise comparisons]. When comparing the attentional benefit on asymptotic performance across pairs of spatial frequencies, we found a significant difference (Δmean gain) only between 4 and 8 CPD [$p = 0.0240$; see Appendix 2—Table 3 for all pairwise comparisons].) Therefore, asymptotic performance exhibited a significant effect of attention alone, with no detected significant effects of spatial frequency or of the interaction between spatial frequency and attention.

Discussion

Whereas attention is often believed to be either uniformly allocated at the center of gaze or selectively shifted to locations outside of the central fovea, recent research has shown that humans are also capable of allocating attention within the central fovea in a spatially selective manner, enhancing our ability to perceive fine spatial stimuli (Poletti et al., 2017; Guzhang et al., 2021). Humans can focus processing resources on a specific region of the central fovea, enhancing visual processing within that small area while suppressing processing at other unattended locations just a few arcminutes away.

These findings raise the question of what spatial frequencies are enhanced by fine-grained shifts of covert attention within the foveola. In our previous work (Guzhang et al., 2021), observers were asked to perform a coarse orientation (±45°) discrimination task. This experiment did not manipulate spatial frequency. Subjectively, however, the stimuli in this task could be distinguished as long as frequency information of more than 3 cycles per degree (CPD) was available to the

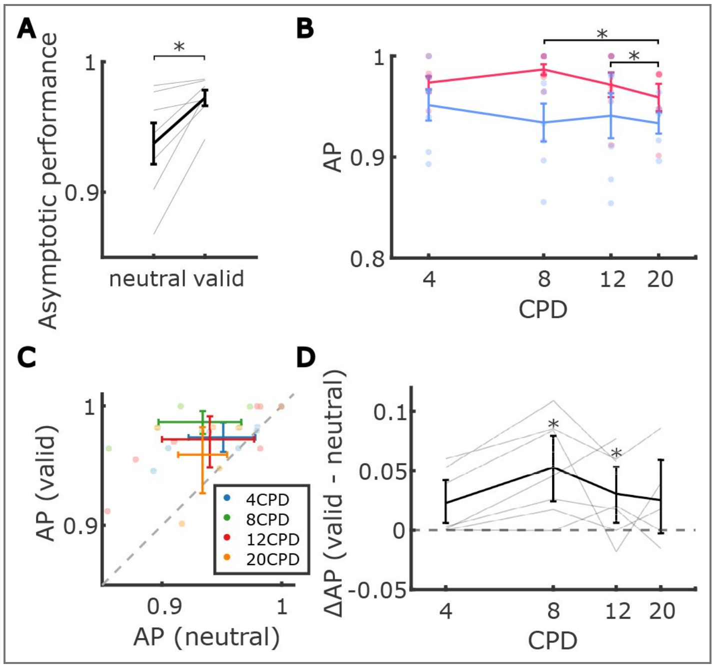

Figure 4. **Effect of fine-grained exogenous attention on asymptotic performance.**

(**A**) Average asymptotic performance, defined as discrimination accuracy at maximum contrast, pooled across spatial frequencies in valid and neutral conditions. Each dot represents an individual observer. Error bars denote the standard error of the mean (SEM). (**B**) Average asymptotic performance across spatial frequencies in valid and neutral conditions. Each dot represents an individual observer. Error bars denote the standard error of the mean (SEM). Asterisks mark a significant difference in asymptotic performance between pairs of spatial frequencies. (**C**) Average asymptotic performance in the neutral condition against that in the valid condition at each spatial frequency. Each dot represents an individual observer. Error bars indicate the bootstrapped 95% confidence intervals. (**D**) Average difference in asymptotic performance between valid and neutral conditions across different spatial frequencies. Each line corresponds to an individual observer. Error bars indicate the bootstrapped confidence intervals. Asterisks mark post-hoc pairwise comparison results between valid and neutral conditions within each spatial frequency. Figure 4—figure supplement 1. Maximum a posteriori (MAP) estimates (points) and 95% confidence intervals for contrast sensitivity (CS) and asymptotic performance (AP).

observer. The attentional gain we observed in the discrimination task could therefore have resulted from foveal exogenous attention enhancing spatial frequencies anywhere above 3 CPD. Thus, it remains unclear which spatial frequencies are enhanced when exogenous attention is allocated at the fine scale within the foveola. Additionally, it is unclear whether fine-grained attention in the foveola is governed by the same principles and is modulated similarly to extrafoveal attention, especially considering the stark differences in spatial resolution between the foveola and the rest of the visual field. The high-acuity foveola can resolve spatial frequencies up to 30 CPD, whereas just five degrees away from the center of gaze, this limit drops to around 10 CPD (Virsu and Rovamo, 1979). Therefore, rather than enhancing the same range of low spatial frequencies as for extrafoveal vision, fine-grained foveal attention may shift or extend its enhancement toward higher frequencies in the foveola.

Our findings indicate that fine-grained shifts of covert exogenous attention in the foveola enhance contrast sensitivity within a narrow range of spatial frequencies, peaking at low to mid frequencies (4–8 CPD). In particular, we found little or no attentional gain at higher spatial frequencies (12–20 CPD), which are closer to the limits of visual resolution at the eccentricity tested (0.3° from the preferred locus of fixation). Whereas enhancements in contrast sensitivity were relatively selective to a narrow band of spatial frequencies, overall asymptotic performance increased as a result of exogenous attention, with no detected dependence on spatial frequency. However, it is worth noting that the statistical power to detect the interaction might differ between analyses of contrast sensitivity and analyses of asymptotic performance, given that the latter tends to involve differences close to its bounds (Bicknell et al., 2025; Jaeger, 2008).

Prior work on coarse exogenous attention shifts between central and peripheral vision has shown that peak attentional benefits for contrast sensitivity occur around 2–4 CPD, with a sizable benefit occurring also at 8 CPD, for a large foveal stimulus (Jigo and Carrasco, 2020). In the present study, the largest attentional gains were observed at the lowest spatial frequency tested (4 and 8 CPD). Because of the small stimulus size required to probe fine-grained attention at the foveal scale, we prioritized testing of spatial frequencies that yielded at least one full cycle within the stimulus aperture. Nevertheless, we conducted a post hoc evaluation at 2 CPD using the same Gabor size (see Figure 3—figure Supplement 2). Because this stimulus contained less than one full cycle, performance may have been compromised (Howell and Hess, 1978). With this caveat in mind, baseline contrast sensitivity was comparable at 2 and 4 CPD and declined at 8 CPD, suggesting a plateau between 2 and 4 CPD. Attention significantly improved contrast sensitivity also at 2 CPD, with contrast gain comparable to that observed at 4 and 8 CPD (see caption of Figure 3—figure Supplement 2).

Thus, the range of spatial frequencies enhanced by fine-grained, exogenously triggered attention closely mirrors that observed when attention is broadly distributed across the fovea. The magnitude of the contrast gain (≈ 20%) was likewise consistent with prior findings (Jigo and Carrasco, 2020) and slightly larger than that reported by (Herrmann et al., 2010) (see Figure 3—figure Supplement 4).

Contrast vs. response gain

Previous studies examining attentional modulation of contrast response functions in extrafoveal vision have reported heterogeneous gain profiles, with some observing predominantly contrast gain (e.g., Cameron et al., 2002; Jigo and Carrasco, 2020) and others reporting a mixture of contrast and response gain (e.g., Ling and Carrasco, 2006; Pestilli et al., 2009). This variability has been attributed to differences in stimulus size and the spatial extent of the attentional field (Reynolds and Heeger, 2009; Herrmann et al., 2010). Within the normalization model of attention, attention multiplicatively scales stimulus drive before normalization and therefore affects both the stimulus drive and, indirectly, the pooled suppressive drive. When the attentional field is small relative to the stimulus, the attended stimulus drive is amplified more than the suppressive drive, producing a multiplicative upward scaling of the contrast response function, with the largest effects at high contrast. On the other hand, when the attentional field is large relative to the stimulus, stimulus and suppressive drive are modulated more proportionally, shifting the effect toward contrast gain. It has also been shown that the effects of endogenous attention manifest as contrast gain, and the effects of exogenous attention can manifest as a mixture between contrast and response gain (Ling and Carrasco, 2006; Pestilli et al., 2009). Hence, the detection of both response and contrast gain in our paradigm, although different from Jigo and Carrasco (2020), is in line with this expectation.

Further, foveal neurons have smaller integration fields and reduced spatial pooling than peripheral neurons. At the retinal level, classic work on macaque midget ganglion cells showed that receptive fields in the central fovea are extremely small and can be dominated by single-cone input, consistent with minimal spatial pooling at the very center of gaze (Dacey and Petersen, 1992; Dacey, 1993). This characterization seems to be maintained at the LGN (Ramsey et al., 2026). More generally, human EEG studies using steady-state visual evoked potentials, as well as behavioral studies, have shown that surround suppression is stronger in the visual periphery than near the fovea (Xing and Heeger, 2000; Petrov et al., 2005; Vanegas et al., 2015). Although there has been relatively little direct electrophysiological work systematically comparing suppressive zone size or normalization strength between central fovea and peripheral neurons in primate visual cortex, the available evidence raises the possibility that the normalization pool engaged at the foveal scale is smaller and less influential than in extrafoveal vision. In the normalization model of attention the resulting attention gain profile depends on the balance between the attended stimulus drive and the pooled suppressive drive (Reynolds and Heeger, 2009). If suppressive interactions are indeed weaker within the foveola, then directing attention to a specific foveal locus may amplify the local stimulus drive more than the pooled suppressive drive, thereby favoring response-gain-like effects over contrast-gain-like effects.

Under this interpretation, the detection of response gain in our data may reflect the unusually small integration and suppressive fields engaged by fine-scale attention within the foveola, in contrast with the seemingly more pronounced contrast-gain effects reported in Jigo and Carrasco (2020). This possibility may also help explain why contrast-gain-like effects were less pronounced at higher spatial frequencies in our study, since high spatial frequency stimuli are expected to engage smaller receptive fields and even less spatial integration, further reducing the contribution of normalization (Teichert et al., 2007; Serrano-Pedraza et al., 2012). This account—based on posthoc between-study comparisons—remains speculative. Future work will be needed to determine whether fine-scale attention within the fovea is mediated by mechanisms distinct from those operating when attention is distributed more broadly across the central fovea, and whether such differences alter the size or influence of the normalization pool.

Alternative explanations for the observed effects

While our primary goal was to examine spatially localized, exogenously triggered fine-grained covert attention within the foveola, one could argue that temporal cueing may have contributed to the observed effects. Specifically, even though the timing of the stimulus onset was fixed across trials, the shorter interval between the additional exogenous cue and the target in valid trials could have acted as a temporal warning signal, potentially enhancing performance relative to neutral trials (Duyar et al., 2023). While we cannot entirely rule out temporal cueing effects, their influence is likely limited. Because stimulus timing was fixed and observers completed many trials, the temporal contingency between the cue and stimulus was likely overlearned. Thus, although a minor temporal benefit may have been present in valid trials, the primary attentional advantage observed here is most attributed to spatially localized attentional engagement at the cued location.

Besides the possible contribution of temporal attention, endogenous attention may also have influenced the results. Although our cue was salient and abrupt in onset, and therefore likely triggered an involuntary exogenous shift of attention, its 100% validity could in principle have supported endogenous maintenance following the initial orienting response (Chica et al., 2013). However, endogenous attentional benefits typically emerge on a slower timescale, with onset latencies of approximately 200 ms or longer (Carrasco, 2011). In contrast, the cue–target SOA in our study was only 100 ms, and the target itself was presented for 50 ms. Under these temporal constraints, any endogenous contribution would be expected to arise only after target offset. Thus, the attentional benefits reported here likely reflect rapid, stimulus-driven exogenous mechanisms.

Future directions

In addition to its perceptual consequences, fine-grained exogenous attention within the foveola may play a preparatory role in oculomotor behavior. When examining the trials that were excluded from main analyses, in which observers happened to perform a saccade following the response cue, we observed a significant reduction in saccade onset latency in valid compared to neutral trials (Figure 2—figure Supplement 2). This effect suggests that exogenous attentional deployment within the foveola not only enhances visual sensitivity but may also facilitate the rapid initiation of gaze shifts toward salient events. Although the present task was deliberately constrained, requiring strict fixation during stimulus presentation, this finding hints at a functional coupling between fine-grained exogenous attention within the foveola and the preparation of subsequent eye movements. Future studies using more naturalistic viewing conditions, in which observers are free to move their eyes, will be critical for determining whether this preparatory mechanism serves to efficiently guide microsaccades or saccades toward behaviorally relevant stimuli in everyday vision.

In everyday life, covert exogenous attention is often engaged when a salient stimulus captures our focus. This evolutionarily important mechanism ensures that we continuously monitor our environment for unexpected events and prepare to respond accordingly (Yantis, 1993; Theeuwes, 2010). Our previous work has demonstrated that attentional shifts can also occur locally within the high-acuity foveola. Here, we show that these fine-grained attention shifts function similarly to those in the extrafoveal region, enhancing visual sensitivity to coarse stimulus features. This mechanism is essential for everyday tasks, such as driving or reading. Our findings not only shed light on the functionality of fine-grained covert attention within the foveola but also reinforce the idea that exogenous attention operates under similar principles as extrafoveal vision. Specifically, exogenous attention remains an inflexible mechanism for selective processing—even in the foveola, where higher spatial frequency information is available, it does not enhance contrast sensitivity of the finer details but instead prioritizes coarser stimulus features. Functionally, this selective enhancement of contrast sensitivity at low to mid spatial frequencies provides a preview of small but salient stimuli located just a few arcminutes from the preferred locus of fixation in everyday tasks. By enhancing contrast sensitivity of these stimuli before direct fixation, this mechanism enables the visual system to rapidly assess their relevance and guide the planning of microsaccades, ensuring efficient and precise shifts of gaze to bring these stimuli into the foveal region for detailed examination.

Methods and Materials

Observers

7 human observers in total, 6 emmetropic observers, and 1 observer with 20/20 corrected vision participated in the experiments (4 females, 3 males; age range 18 - 27 years old). The experiment was approved by the University of Rochester Institutional Review Boards. The experimenter reviewed and explained the material in the consent form to the observers before conducting the experiment. The form was signed only after the participant fully understood the material and voluntarily agreed to take part in the study. Consent was obtained from all observers in the study.

Stimuli and Apparatus

Stimuli were displayed on an LCD monitor (ASUS ROG SWIFT 360Hz PG259QN) at a refresh rate of 360 Hz and spatial resolution of 1920 x 1080 pixels. Observers performed the task monocularly with their right eye while the left eye was patched. A dental-imprint bite bar and a headrest were used to prevent head movements. Eye movements were recorded with high precision using a custom-made digital Dual Purkinje Image (dDPI) eye tracker, which has a sampling rate of 1 kHz

(Wu et al., 2023). The system has an internal noise well below 1' and a spatial resolution of 1' (Ko et al., 2016; Wu et al., 2023). Stimuli were rendered using EyeRIS, a custom-developed system that allows flexible gaze-contingent display control (Santini et al., 2007). This system acquires eye movement signals from the eye tracker, processes them in real time, and updates the stimulus on the display according to the desired combination of estimated oculomotor variables.

Procedure and Experimental Task

Calibration

Every session started with the setup of the bite bar. A magnetized helmet was used to position the observer's head. When accurate localization of gaze position is necessary, calibration represents an important stage of the experimental procedure, which was performed in two phases, automatic calibration followed by manual calibration. During automatic calibration, observers sequentially fixated on each of the nine points of a 3-by-3 grid, as is customary in all oculomotor experiments. After completing automatic calibration, observers were instructed to perform a manual calibration where they refined the pixel-to-pixel mapping, given by the automatic calibration. To this end, observers fixated again on each of the nine points of the grid while the location of the line of sight was displayed in real time on the screen. Observers used a joypad to correct the predicted gaze location, shifting the real-time display to align with the grid point for each fixation, if necessary. These corrections were then incorporated into the transformation of the gaze position as well. This dual-step calibration procedure allows more accurate localization of gaze position than standard single-step procedures. A similar manual calibration procedure was repeated before each trial but only for the central fixation location to compensate for unpreventable head movements.

Experimental task

Observers were instructed to fixate on a central marker (5 by 5 arcminutes) throughout each trial. On valid trials, an exogenous cue—a white square (8-by-8 arcminutes)—appeared 500ms after fixation. The cue appeared for 30 ms at 0.75 deg eccentricity to the left/right of the fixation marker, with each location occurring randomly with equal probability. The smaller exogenous cue, positioned offset from the Gabor patch, was used to prevent forward masking and ensure clear perception of the Gabor patch. Shortly after the cue disappeared (70 ms), two small Gabor patches (0.5 deg visible area), tilted +/- 45 degrees, with a phase of 0 or 90 degrees were shown (50 ms) on the left/right side at 0.5 deg eccentricity. The tilt of the two Gabor patches was randomly and independently chosen on each trial. And the phase was randomly selected on each trial but consistent between the two patches. The spatial frequency of the Gabors was 4, 8, 12, or 20 CPD. After the stimulus offset, a response cue was presented, and observers were instructed to report the orientation of the stimulus previously presented at that location. The trial concluded either when observers responded or automatically after 1000 ms if no response was given following the appearance of the response cue. On valid trials, the response cue always indicated the same location as the exogenous cue, making the cue 100% valid. On neutral trials, no exogenous cue was presented, and the response cue indicated one of the two possible locations randomly.

When observers first arrived for the study, they were given task instructions and completed 50 familiarization trials to become accustomed to the setup and the task. Following this, because contrast sensitivity varies considerably across SF and eccentricity (Rovamo et al., 1992), for each spatial frequency tested, observers underwent a preliminary session in which an initial estimate of contrast threshold, defined as the contrast needed to achieve 70% discrimination accuracy in the neutral condition. It typically took around 50-100 trials to find the target contrast threshold for each spatial frequency. Neither the familiarization trials nor the threshold-estimation trials were included in the final analyses. After the thresholds were obtained, each observer was tested at five different contrast values around the estimated threshold. One of these values included presenting the grating at 100% contrast to obtain a precise estimate for the upper-performance asymptote. The remaining four levels were ±0.075 and ±0.225 $\log_{10}$ units from the initial threshold estimate.

If the initial estimates were within 0.225 $\log_{10}$ units of 100% contrast (i.e., >= 60% contrast), the rest of the four contrast values were -0.6, -0.45, -0.3, and -0.15 $\log_{10}$ units compared to the initial estimate (Prins, 2012). Within each experimental session, a single spatial frequency was tested, and the corresponding contrast levels were presented in a block design. All five contrast levels for a given spatial frequency were tested within a single experimental session. Observers completed 100 trials per contrast level. And each spatial frequency was tested twice on two separate days. Therefore, observers completed approximately 4000 trials in total. The order of spatial frequency tested was randomized across observers.

Two observers were not tested at 20 CPD because their performance remained at chance level even with gratings at maximal contrast. It is possible given that 20 CPD was near the visual resolution limit at the tested eccentricity.

Data Analysis

Eye movements

Only trials with uninterrupted tracking in which the fourth Purkinje image was never eclipsed by the pupil margin, were selected for data analysis. Trials in which the gaze was > 10' away from the center position 50 ms before the onset of the exogenous cue t_0 50 ms after the offset of the target, and trials with blinks, saccades, or microsaccades occurring at any time during the period of interest (50 ms before the onset of the exogenous cue to 200 ms after the offset of the Gabor patches), were discarded. Periods of blinks were automatically detected by the dDPI eye tracker. Eye movements with a minimal amplitude of 30' and a peak velocity higher than 3°/s were categorized as saccades. Saccades with an amplitude of less than 0.5° (30') were defined as microsaccades. Saccade amplitude was defined as the vector connecting the point where the speed of the gaze shift grew greater than 3°/s (saccade onset) and the point where it became less than 3°/s (saccade offset). Periods that were not classified as saccades or blinks were labeled as drifts. Observers had 1000 ms to respond, and trials were excluded from further analysis if observers responded too fast (< 100 ms) or too slow (> 1000 ms), resulting in the exclusion of 0.02% ± 0.02% of the trials. Approximately between 50 and 100 trials per contrast level per cueing condition were retained after filtering. Table 1 summarizes the data remaining for analysis for each condition (see Figure 2—figure Supplement 1 for a detailed breakdown by observer).

Psychometric function fitting

Weibull functions were fitted to the responses of the orientation discrimination task, using the maximum likelihood procedure implemented in the psignifit 4 toolbox (Schütt et al., 2016) for MATLAB. Separate functions were fitted for each combination of observer, attention conditions (attended and neutral), and spatial frequency, for a total of 8 psychometric function fits (2 attention conditions x 4 spatial frequencies) per observer. Each fit resulted in maximum a posteriori (MAP) estimates for the intercept α, slope β, threshold θ, and lapse rate λ of the psychometric function (the guess rate γ was set to .5, given the 2AFC task). Two estimates were extracted from the MAP estimates to examine the effects of fine-grained exogenous attention across spatial frequencies — contrast sensitivity and asymptotic performance. Contrast sensitivity was defined as the inverse of the threshold (the midpoint on the psychometric curve between chance performance and maximum performance). Asymptotic performance was calculated by subtracting the lapse rate from 1, representing the discrimination accuracy at the highest contrast level of the stimuli. In total, this procedure resulted in 52 estimates each of contrast sensitivity and asymptotic performance (5 observers with 4 SFs x 2 cueing conditions, and 2 observers, who did not complete the 20 CPD condition, with 3 SFs x 2 cueing conditions).

Statistical testing

Contrast sensitivity (CS) and asymptotic performance (AP) were both analyzed with (different types of) mixed-effects regressions. Each of the mixed-effects regressions contained cueing, spatial frequency, and their interactions as fixed-effects predictors. Cueing was effect-coded ("attended" = .5 vs. "neutral" = -.5), and frequency was coded using sliding difference, comparing the effects for each spatial frequency against the next highest spatial frequency (4 vs. 8, 8 vs. 12, 12 vs. 20).

	Valid		Neutral	
SF (CPD)	Count	%	Count	%
4	514 [474, 549]	79.1 [66.1, 90.4]	518 [486, 548]	79.6 [67.3, 90.1]
8	491 [417, 551]	82.0 [73.4, 89.3]	489 [418, 553]	81.8 [73.3, 89.6]
12	487 [416, 552]	80.7 [72.9, 88.0]	507 [444, 567]	84.1 [77.5, 90.6]
20	531 [504, 556]	86.8 [82.9, 90.9]	528 [497, 554]	86.4 [81.1, 91.6]

Table 1. Average number and percentage of trials retained for analysis after filtering (mean ± SE across observers) across different spatial frequencies and cueing conditions.

Brackets indicate bootstrapped 95% confidence intervals. Observers who were unable to perform the task at 20 CPD were excluded from the 20 CPD trial counts.

Following the recommended procedure (Lohse, 2022), we included the maximal possible random effect structure: random intercepts by observer, by unique combination of observer and cueing condition, and by unique combination of observer and spatial frequency condition.

CS is a bounded variable with a natural limit in that it cannot be lower than zero. Importantly, the variance of bounded variables tends to systematically decrease as their mean approaches the bound. This violates the assumption of homoskedasticity—the idea that variance should be independent of the mean and thus remain roughly constant across different conditions — an assumption that is shared by widely used statistical methods like *t*-tests, ANOVA (analysis of variance) and linear mixed-effects models (LMMs). When this assumption is violated, it can impact the reliability of statistical conclusions, affecting both Type I errors (false positives) and Type II errors (false negatives) (Jaeger, 2008).

Indeed, we observed a strong positive correlation between the mean and variance of contrast sensitivity: smaller variances for smaller means (Figure 3—figure Supplement 3). To address this issue, we log-transformed CS before analyzing it with an LMM using the lmer function from the lme4 package (Bates et al., 2025) in R (R Core Team, 2024). This largely mitigated the heteroskedasticity, except potentially in the 20 CPD condition (see Figure 3—figure Supplement 3). As a precautionary measure, we verified that all main findings remained unchanged when this condition was excluded. This included the critical interaction between spatial frequency and attention ($\chi^2(2) = 6.6$, $p < .04$), which remained statistically significant.

AP is bounded both at the lower and the upper end (as it cannot be larger than 1, or smaller than the guess rate). Following recommended procedure, we thus normalized asymptotic performance to the range between 0 and 1, and analyzed it with a mixed-effects Beta model (with a logit link) using the `glmmTMB` function of the package `glmmTMB` (McGillycuddy et al., 2025).

Post-hoc pairwise comparisons for both mixed-effects analyses were conducted by estimating the relevant marginal means of the fitted mixed-effects regression, using the `emmeans` package (Lenth et al., 2025) in R. Cohen's d (Cohen, 1988) of the pairwise differences was computed using the function `t_to_d` from the package `effectsize` (Ben-Shachar et al., 2020) in R.

Power analysis

Our initial sample size estimate was an approximation based on our previous study using a similar design to examine exogenous attention during high-acuity stimulus discrimination within the foveola (Guzhang et al., 2021). To formalize this estimate, we conducted a post-hoc power analysis following approaches used in prior work on *extra*foveal attention (Jigo and Carrasco, 2020) to estimate the sample size required to detect attentional effects on contrast gain. We assumed effect sizes comparable to those observed in our previous study (Guzhang et al., 2021). Specifically, we followed a bootstrap approach (McConnell and Vera-Hernández, 2015; Jigo and Carrasco, 2020) in which data from two to twelve observers were randomly sampled with replacement from Guzhang et al. (2021). For each resampled dataset, we conducted a one-way repeated-measures analysis of variance (ANOVA) with attention as a within-subject factor. This procedure was repeated 10,000 times, and a distribution of p-values was constructed for the main effect of attention. Statistical power was estimated as the proportion of iterations yielding a significant main effect ($p < 0.05$) for each sample size. The results indicated that a sample size of five observers was sufficient to achieve statistical power greater than 80% for detecting the main effect of attention. Based on this simulation, the sample size of seven observers used in the present study should provide adequate statistical power.

We conducted additional post-hoc power analyses to evaluate the power of our design to detect main effects and their interactions, using the *simr* function of the package *simr* in R. We estimated statistical power for mixed-effects models through model-based simulation by generating synthetic datasets based on the fixed and random effects structure of the fitted model, preserving the observed effect sizes and variance components. For each simulated dataset, the model was refitted, and the effect of interest was tested. By repeating this procedure 501 times across different sample sizes, power was estimated as the proportion of simulations in which the effect was statistically significant ($p<0.05$). Consistent with the bootstrap power analysis reported above, the results show that our study had high power (>95%) to detect the main effects of attention and spatial frequency, and moderate power (>65%) to detect the interaction. Because classical post hoc power analyses tend to be circular and anti-conservative (Quach et al., 2022; Heinsberg and Weeks, 2022), we also used the same approach while allowing for potential overestimation of effect sizes and underestimation of variance components. Under deliberately conservative assumptions, specifically, effect sizes reduced to 75% of those observed and variance components increased by 25%, power to detect the main effects remained above 85%, while power to detect the interaction (which was nevertheless observed) was approximately 50%.

Below, we summarize the key considerations for interpreting our results.

Limitations

Here, we analyzed log-transformed CS and AP in two separate analyses, each conducted over the observer-level estimates for each condition. We did so both (1) because this approach remains the standard in psychophysics—including in research on the role of covert attention (Cameron et al., 2002; Pestilli and Carrasco, 2005; Herrmann et al., 2010; Li et al., 2021)—and (2) because the alternative would have required fitting mixed-effects *trial-level* psychometric models to the combined data from all conditions and observers (an approach that is computationally demanding, and has not yet been broadly validated). The approach taken here and in prior work on extrafoveal attention does, however, have several known limitations, some of which might be of particular relevance to questions about the effects of attention. We summarize these potential downsides here, so that they can be considered in the interpretation of our results, and addressed in future work.

First, reducing each observer's performance in a given condition to the best-fitting psychometric parameters (*e.g*., sensitivity or asymptotic performance) ignores the uncertainty associated with those estimates. Subsequent repeated-measures ANOVAs or, in our case, mixed-effects regression analyses performed on these point estimates cannot take advantage of the information present in the trial-level data. As a result, two parameter estimates with very different levels of uncertainty (see Figure 4—figure Supplement 1) may have similar influence on the analysis despite substantial differences in precision. Importantly, the precision of psychometric estimates can vary across observers and conditions because the amount and distribution of usable data differ, and because the sampled stimuli may probe different portions of the psychometric function. Ultimately, failure to adequately account for uncertainty can lead to miscalibrated inference, increasing the risk of both Type I and Type II errors.

Second, the standard approach ignores the interdependence among psychometric parameters. In practice, the same data can often be fit nearly equally well by different combinations of parameter values, for example, a steeper slope paired with a lower lapse rate, or a shallower slope paired with a higher asymptote. In particular, when performance fails to adequately constrain the upper asymptote, parameters such as threshold, slope, and lapse or asymptotic performance can become difficult to disentangle. When only the best-fitting parameter values are carried forward, all information about such covariance between parameters is lost. As a result, apparent differences in whether attention affects contrast gain or response gain may partly reflect parameter tradeoffs rather than genuine differences across studies.

Future research could employ alternative analysis approaches. In particular, it is now possible to fit mixed-effects psychometric models to the trial-level data from all conditions and all observers (Prins, 2024; Tan and Jaeger, 2025). While this approach is computationally more demanding and requires familiarity with nonlinear mixed-effects modeling, it allows statistical tests that avoid the downsides described above.

Data Availability

The dataset and analysis code are available on Open Science Framework (OSF): *https://osf.io/pg7hd/overview?view_only=48996efa1f7641b6863b9d6d333ec31d*

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Additional information

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Author Contributions

Y.G. and M.P. designed research; Y.G. performed research; Y.G. and T.J. analyzed data; all authors drafted the paper and approved the final version of the manuscript.

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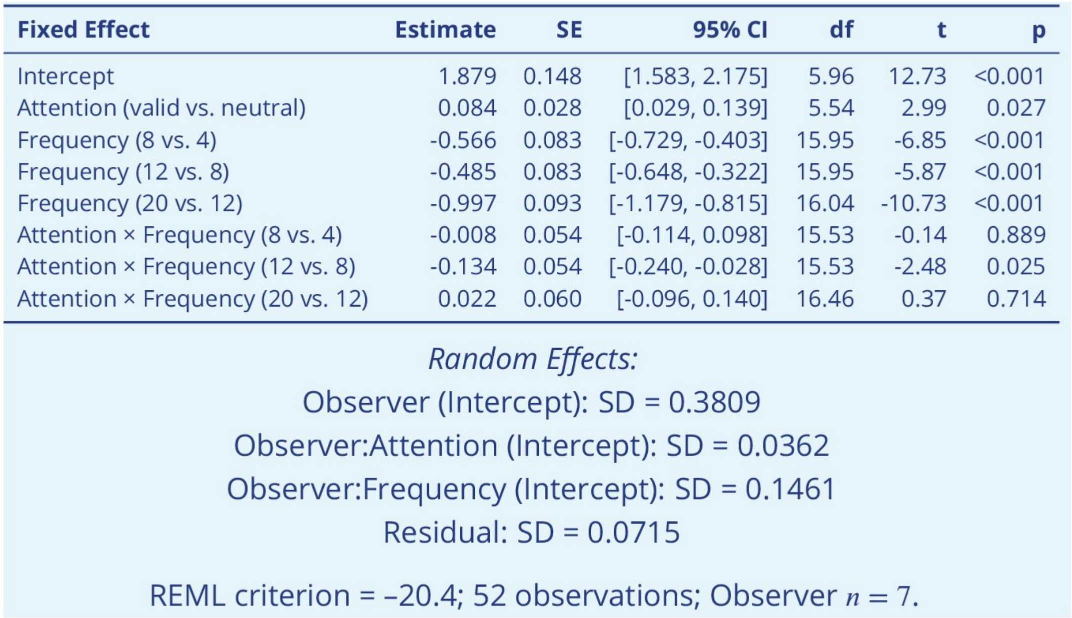
Appendix 1

Effects of attention and spatial frequency on contrast sensitivity

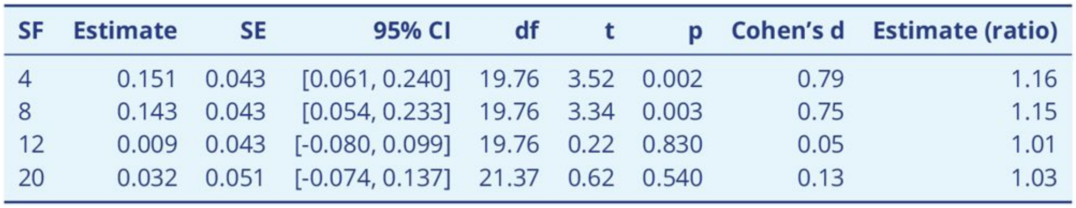


Fixed Effect	Estimate	SE	95% CI	df	t	p
Intercept	1.879	0.148	[1.583, 2.175]	5.96	12.73	<0.001
Attention (valid vs. neutral)	0.084	0.028	[0.029, 0.139]	5.54	2.99	0.027
Frequency (8 vs. 4)	-0.566	0.083	[-0.729, -0.403]	15.95	-6.85	<0.001
Frequency (12 vs. 8)	-0.485	0.083	[-0.648, -0.322]	15.95	-5.87	<0.001
Frequency (20 vs. 12)	-0.997	0.093	[-1.179, -0.815]	16.04	-10.73	<0.001
Attention × Frequency (8 vs. 4)	-0.008	0.054	[-0.114, 0.098]	15.53	-0.14	0.889
Attention × Frequency (12 vs. 8)	-0.134	0.054	[-0.240, -0.028]	15.53	-2.48	0.025
Attention × Frequency (20 vs. 12)	0.022	0.060	[-0.096, 0.140]	16.46	0.37	0.714

Random Effects:
Observer (Intercept): SD = 0.3809
Observer:Attention (Intercept): SD = 0.0362
Observer:Frequency (Intercept): SD = 0.1461
Residual: SD = 0.0715

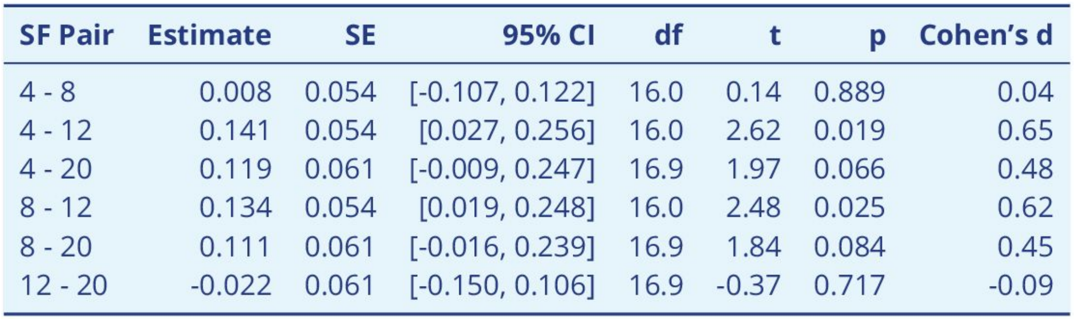
REML criterion = –20.4; 52 observations; Observer $n = 7$.

Appendix 1—table 1. Linear mixed-effects model predicting log-transformed contrast sensitivity from attention, spatial frequency, and their interaction.



SF	Estimate	SE	95% CI	df	t	p	Cohen’s d	Estimate (ratio)
4	0.151	0.043	[0.061, 0.240]	19.76	3.52	0.002	0.79	1.16
8	0.143	0.043	[0.054, 0.233]	19.76	3.34	0.003	0.75	1.15
12	0.009	0.043	[-0.080, 0.099]	19.76	0.22	0.830	0.05	1.01
20	0.032	0.051	[-0.074, 0.137]	21.37	0.62	0.540	0.13	1.03

Appendix 1—table 2. **Simple effects of attention on contrast sensitivity at each spatial frequency (SF) and their effect sizes in Cohen’s d.**

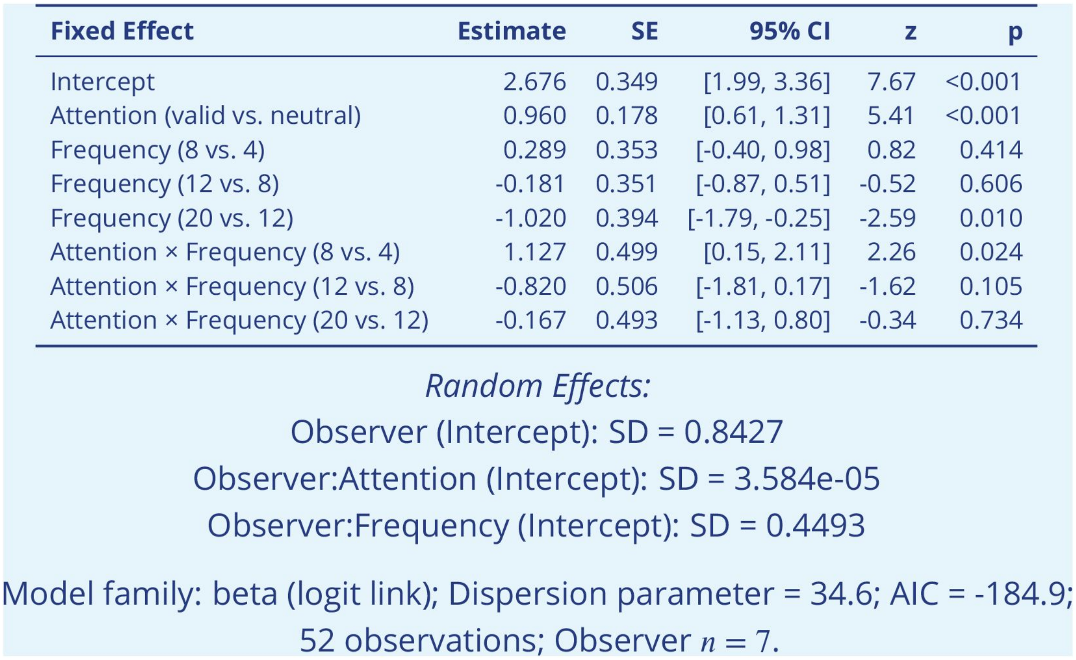


SF Pair	Estimate	SE	95% CI	df	t	p	Cohen’s d
4 - 8	0.008	0.054	[-0.107, 0.122]	16.0	0.14	0.889	0.04
4 - 12	0.141	0.054	[0.027, 0.256]	16.0	2.62	0.019	0.65
4 - 20	0.119	0.061	[-0.009, 0.247]	16.9	1.97	0.066	0.48
8 - 12	0.134	0.054	[0.019, 0.248]	16.0	2.48	0.025	0.62
8 - 20	0.111	0.061	[-0.016, 0.239]	16.9	1.84	0.084	0.45
12 - 20	-0.022	0.061	[-0.150, 0.106]	16.9	-0.37	0.717	-0.09

Appendix 1—table 3. **Interaction contrasts comparing attention effects between spatial frequency (SF) pairs and their effect sizes in Cohen’s d.**

Appendix 2

Effects of attention and spatial frequency on asymptotic performance



Fixed Effect	Estimate	SE	95% CI	z	p
Intercept	2.676	0.349	[1.99, 3.36]	7.67	<0.001
Attention (valid vs. neutral)	0.960	0.178	[0.61, 1.31]	5.41	<0.001
Frequency (8 vs. 4)	0.289	0.353	[-0.40, 0.98]	0.82	0.414
Frequency (12 vs. 8)	-0.181	0.351	[-0.87, 0.51]	-0.52	0.606
Frequency (20 vs. 12)	-1.020	0.394	[-1.79, -0.25]	-2.59	0.010
Attention × Frequency (8 vs. 4)	1.127	0.499	[0.15, 2.11]	2.26	0.024
Attention × Frequency (12 vs. 8)	-0.820	0.506	[-1.81, 0.17]	-1.62	0.105
Attention × Frequency (20 vs. 12)	-0.167	0.493	[-1.13, 0.80]	-0.34	0.734

Random Effects:

Observer (Intercept): SD = 0.8427

Observer:Attention (Intercept): SD = 3.584e-05

Observer:Frequency (Intercept): SD = 0.4493

Model family: beta (logit link); Dispersion parameter = 34.6; AIC = -184.9; 52 observations; Observer $n = 7$.

Appendix 2—table 1. **Generalized linear mixed-effects model predicting normalized asymptotic performance from attention, spatial frequency, and their interaction.**

SF	Estimate	SE	95% CI	z	p	Cohen's d	Estimate (prob. diff.)
4	0.566	0.325	[-0.072, 1.204]	1.74	0.082	0.39	0.030
8	1.693	0.392	[0.925, 2.461]	4.32	<.001	0.97	0.077
12	0.874	0.329	[0.230, 1.518]	2.66	0.008	0.60	0.044
20	0.707	0.361	[0.000, 1.414]	1.96	0.050	0.42	0.081

Appendix 2—table 2. Simple effects of attention on asymptotic performance at each spatial frequency (SF) and their effect sizes in Cohen's d.

SF Pair	Estimate	SE	95% CI	z	p	Cohen's d
4 - 8	-1.127	0.499	[-2.106, -0.149]	-2.26	0.024	-0.56
4 - 12	-0.308	0.460	[-1.209, 0.593]	-0.67	0.503	-0.17
4 - 20	-0.140	0.488	[-1.098, 0.817]	-0.29	0.774	-0.07
8 - 12	0.820	0.506	[-0.173, 1.812]	1.62	0.105	0.40
8 - 20	0.987	0.537	[-0.066, 2.040]	1.84	0.066	0.45
12 - 20	0.167	0.493	[-0.798, 1.133]	0.34	0.734	0.08

Appendix 2—table 3. Interaction contrasts comparing attention effects between spatial frequency (SF) pairs on asymptotic performance and their effect sizes in Cohen's d.

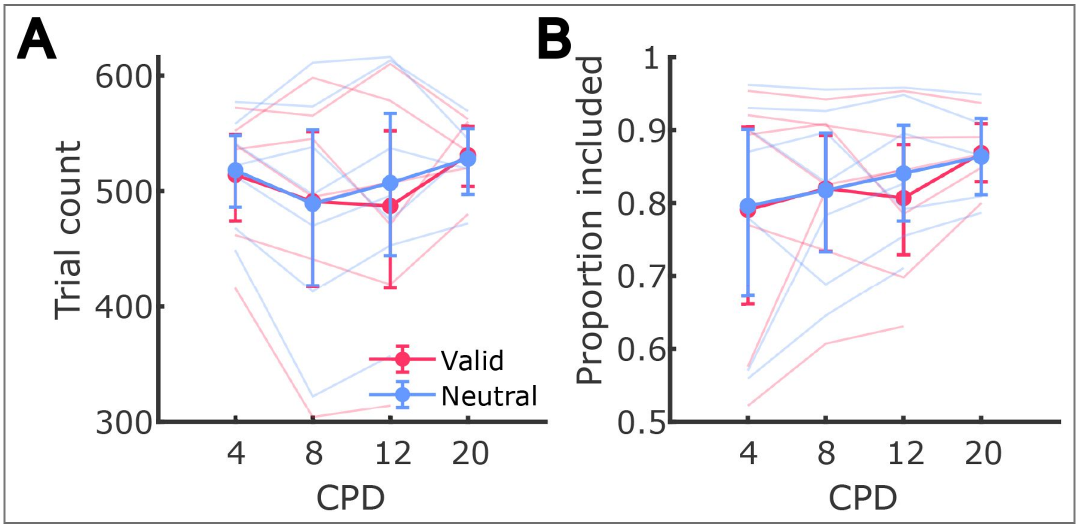


Figure 2—figure supplement 1. Number of trials included for analysis by condition. Each line is an observer. Error bars show the bootstrapped 95% confidence intervals.

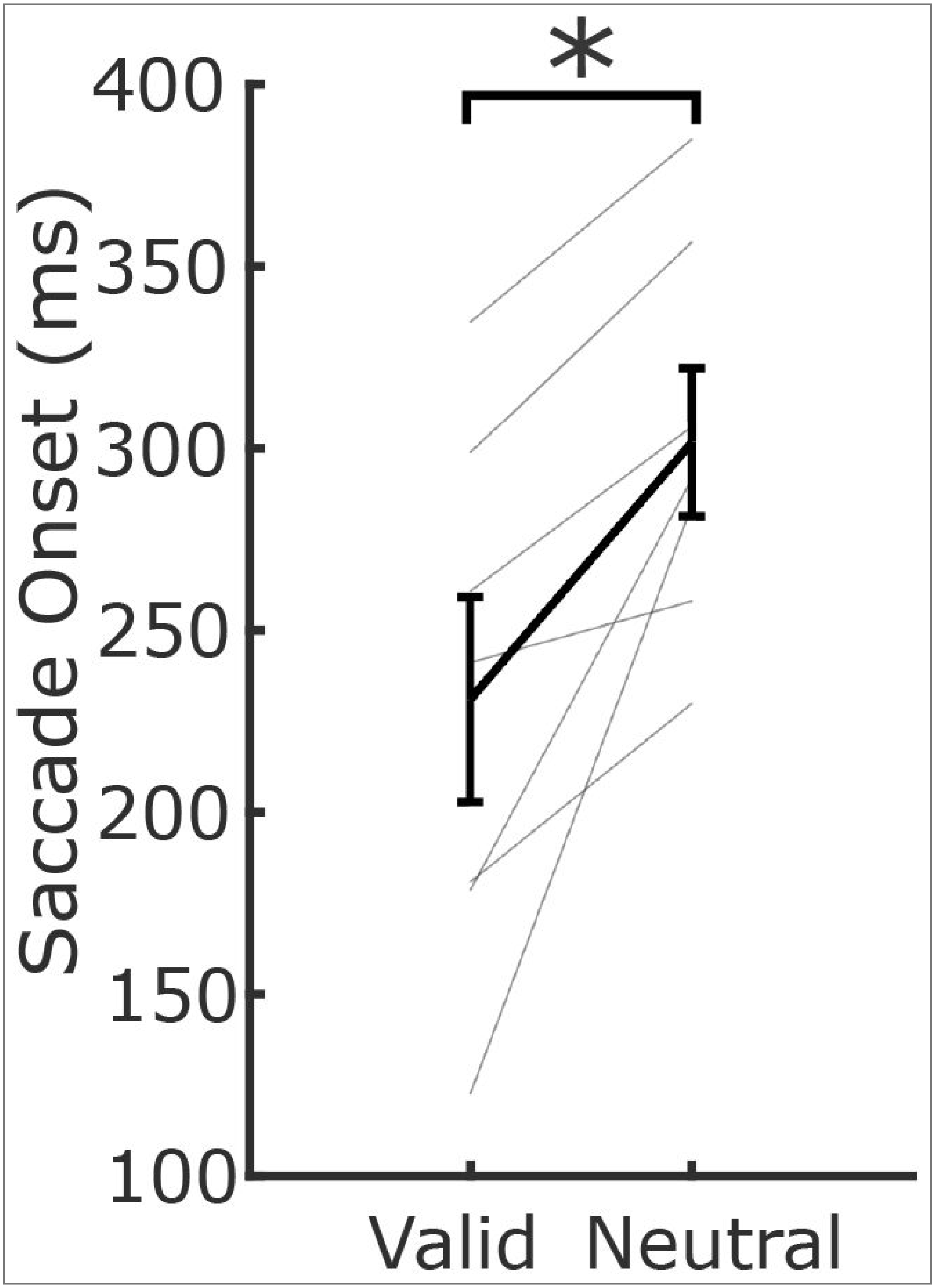


Figure 2—figure supplement 2. **Average saccades onset relative to the response cue onset in valid and neutral conditions (valid vs. neutral: $p < 0.01$).** Only saccades that occurred after fixation period were included in the analysis. The trials presented here were not included in main analyses examining the effects of attention. Lines represent individual observers. Error bars mark group SEM.

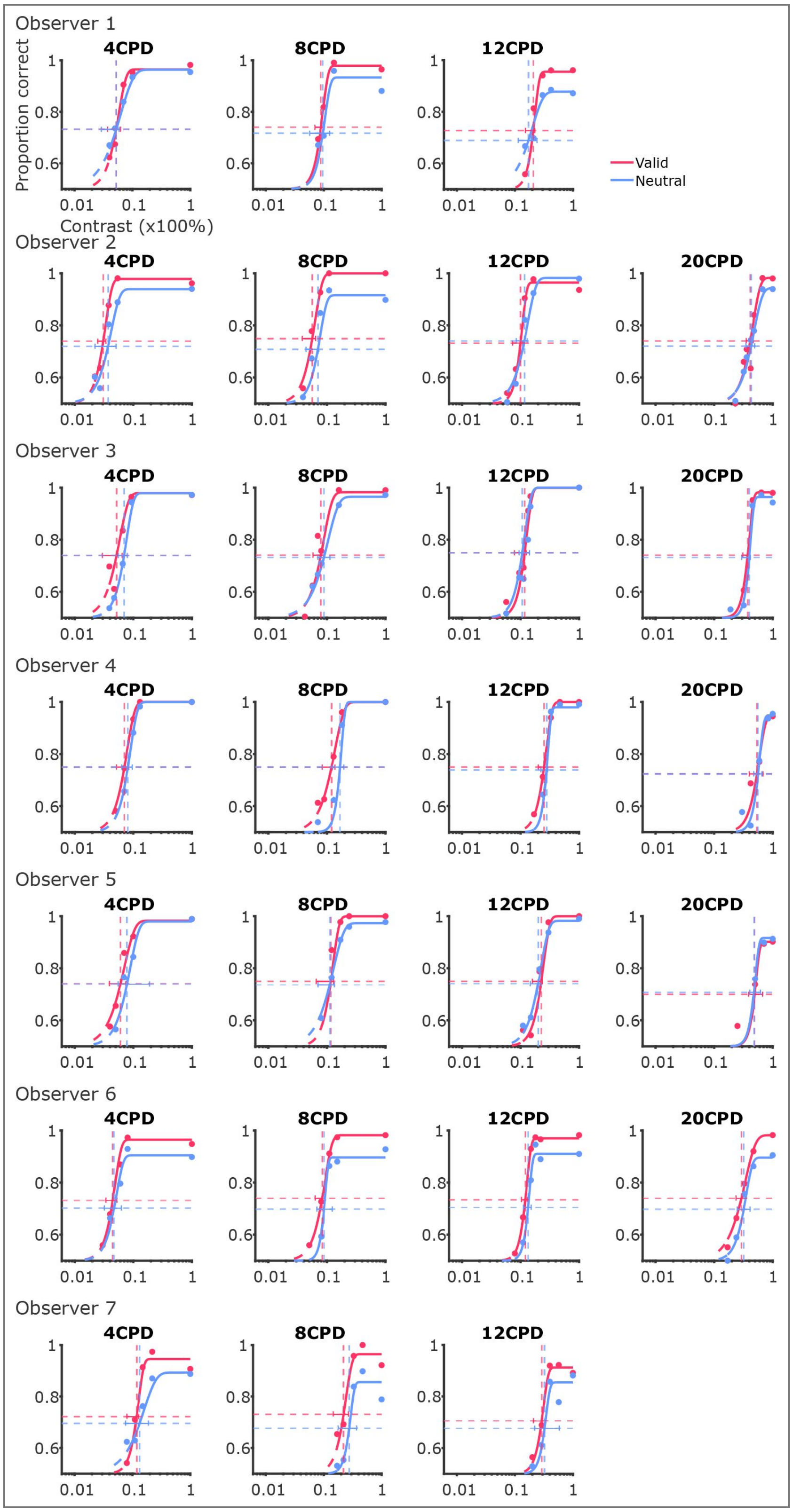


Figure 3—figure supplement 1. Psychometric Weibull function fits for all observers and conditions.

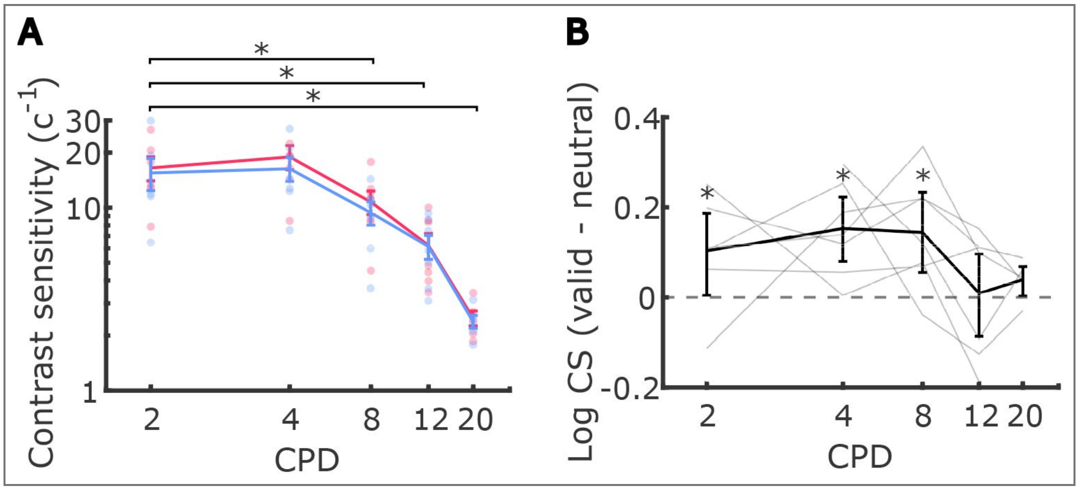


Figure 3—figure supplement 2. (**A**) Average contrast sensitivity, calculated as the inverse of the contrast threshold, across spatial frequencies, including 2 CPD in valid and neutral conditions. Each dot represents an individual observer. Error bars denote the standard error of the mean (SEM). Asterisks mark a significant difference in contrast sensitivity between 2 CPD and other spatial frequencies. (**B**) Average difference in log-scaled contrast sensitivity between valid and neutral conditions across different spatial frequencies. Each line corresponds to the log-scaled contrast sensitivities from each observer. Error bars represent the bootstrapped 95% confidence intervals. Asterisks mark post-hoc pairwise comparison results between valid and neutral conditions within each spatial frequency (p = 0.04 for valid vs. neutral at 2 CPD; ps > 0.17 for mean gain at 2 CPD vs. other SFs).

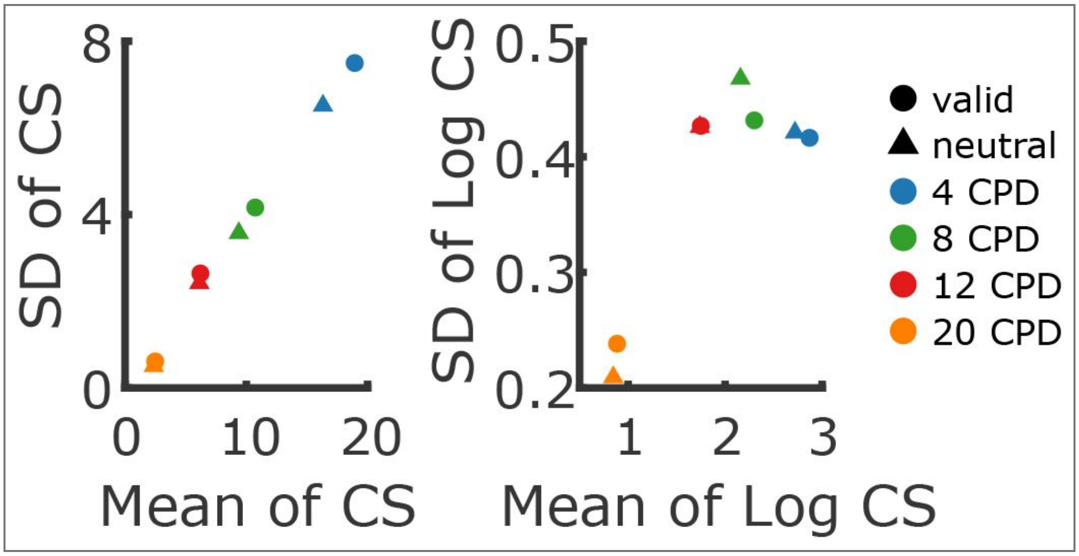


Figure 3—figure supplement 3. Relation between mean and variability of contrast sensitivity (CS), depending on whether CS is log-transformed (right panel) or not (left panel). Without a log-transform, the mean and standard deviation (SD) of CS are almost perfectly correlated, constituting a strong violation of the homoskedasticity assumption of linear models. For the present data, log-transforming CS *mostly* removes this correlation (except for the 20 CPD condition).

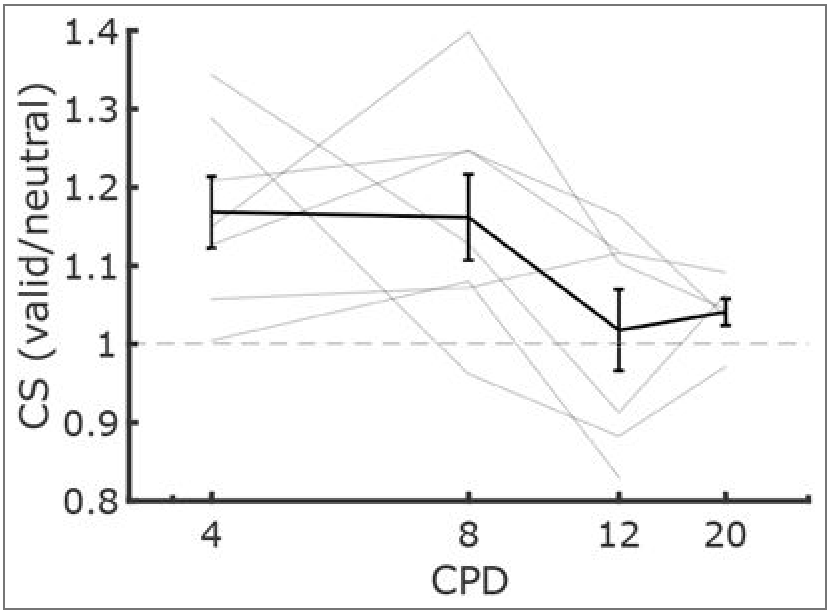


Figure 3—figure supplement 4. Average attentional benefit calculated as the ratio in contrast sensitivity between valid and neutral conditions.

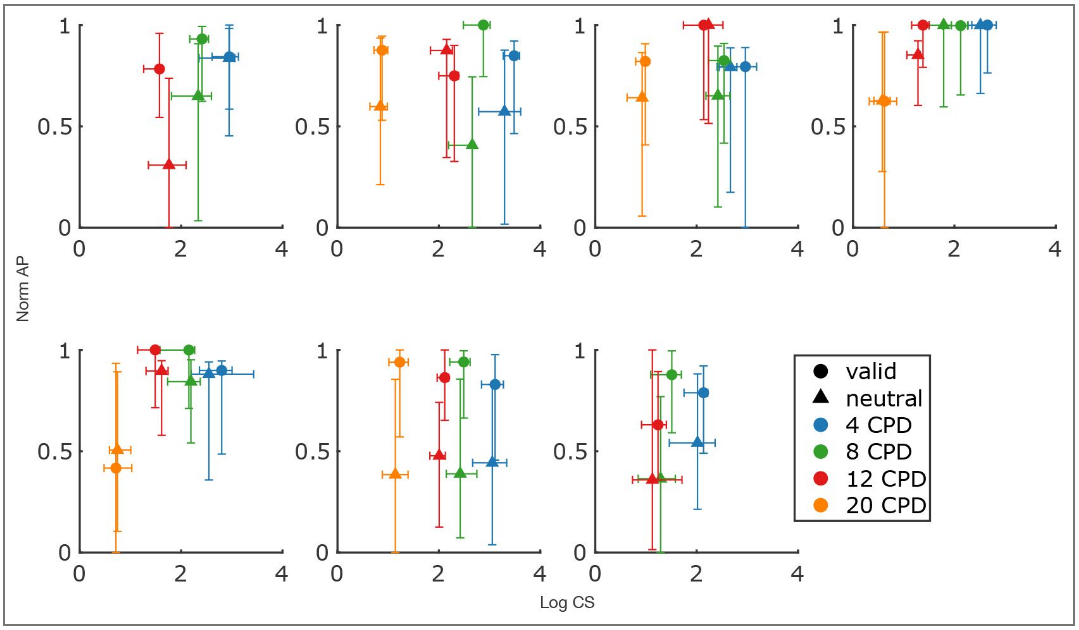


Figure 4—figure supplement 1. Maximum a posteriori (MAP) estimates (points) and 95% confidence intervals for contrast sensitivity (CS) and asymptotic performance (AP) for each experimental condition across seven observers. Both CS and AP were transformed in the same way as used in our mixed-effects analyses.

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Peer reviews

Reviewer #1 (Public review):

[Editors' note: this version has been assessed by the Reviewing Editor without further input from the original reviewers. The authors have addressed the weaknesses noted above, which were raised in the previous round of review.]

Summary:

The manuscript investigates how exogenous attention modulates spatial frequency sensitivity within the foveola. Using high-precision eye-tracking and gaze-contingent stimulus control, the authors show that exogenous attention selectively improves contrast sensitivity for low- to mid-range spatial frequencies (4-8 cycles/degree), but not for higher frequencies (12-20 CPD). In contrast, improvements in asymptotic performance at the highest contrast levels occur across all spatial frequencies. These results suggest that, even within the foveola, exogenous attention operates through a mechanism similar to that observed in peripheral vision, preferentially enhancing lower spatial frequencies.

Strengths:

The study shows strong methodological rigor. Eye position was carefully controlled, and the stimulus generation and calibration were highly precise. The authors also situate their work well within the existing literature, providing a clear rationale for examining the fine-grained effects of exogenous attention within the foveola. The combination of high spatial precision, gaze-contingent presentation, and detailed modeling makes this a valuable technical contribution.

Weaknesses:

The manipulation of attention raises some interpretive concerns. Clarifying this issue, together with additional detail about statistics, participant profiles, other methodological elements, and further discussion in relation to oculomotor control in general, could broaden the impact of the findings.

https://doi.org/10.7554/eLife.108788.2.sa3

Reviewer #2 (Public review):

Summary:

This study aims to test whether foveal and non-foveal vision share the same mechanisms for endogenous attention. Specifically, they aim to test whether they can replicate at the foveola previous results regarding the effects of exogenous attention for different spatial frequencies.

Strengths:

Monitoring the exact place where the gaze is located at this scale requires very precise eye-tracking methods and accurate and stable calibration. This study uses state-of-the-art methods to achieve this goal. The study builds on many other studies that show similarities between foveal vision and non-foveal vision, adding more data supporting this parallel.

Weaknesses:

The study lacks a discussion of the strength of the effect and how it relates to previous studies done away from the fovea. It would be valuable to know if not just the range of frequencies, but the size of the effect is also comparable.

https://doi.org/10.7554/eLife.108788.2.sa2

Reviewer #3 (Public review):

Summary:

This paper explores how spatial attention affects foveal information processing across different spatial frequencies. The results indicate that exogenously directed attention enhances contrast sensitivity for low- to mid-range spatial frequencies (4-8 CPD), with no significant benefits for higher spatial frequencies (12-20 CPD). However, asymptotic performance increased as a result of spatial attention independently of spatial frequency.

Strengths:

The strengths of this article lie in its methodological approach, which combines a psychophysical experiment with precise control over the information presented in the foveola.

Weaknesses:

The authors acknowledge that they used the standard approach of analyzing observer-averaged data, but recognize that this method has limitations: it ignores the uncertainty associated with parameter estimates and the relationships between different parameters of the psychometric model. This may affect the interpretation of attentional effects. In the future, mixed-effects models at the trial level could overcome these limitations.

https://doi.org/10.7554/eLife.108788.2.sa1

Author response:

The following is the authors' response to the original reviews.

> ***eLife Assessment***
>
> *This study explores how exogenous attention operates at the finest spatial scale of vision, within the foveola - a topic that has not been previously explored. The question is important for understanding how attention shapes perception, and how it differs between the periphery and the central regions of highest visual acuity. The evidence is compelling, as shown by carefully designed experiments with state-of-the-art eye tracking to monitor attended locations just a few tens of minutes of arc away from the fixation target, but additional clarification regarding analyses and implications for vision and oculomotor control would broaden the impact of the study.*

We thank the editors and reviewers for their thorough evaluation of our work. We have carefully revised the manuscript and substantially reworked the Discussion to address all of the points raised, eliminate redundancies, streamline the text, and clarify the implications of our findings for vision and oculomotor control. We have also expanded the documentation of our power analyses and conducted the additional analyses requested by the reviewers. Our point-by-point responses are provided.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***
>
> *Summary:*
>
> *The manuscript investigates how exogenous attention modulates spatial frequency sensitivity within the foveola. Using high-precision eye-tracking and gaze-contingent stimulus control, the authors show that exogenous attention selectively improves contrast sensitivity for low- to midrange spatial frequencies (4-8 cycles/degree), but not for higher frequencies (12-20 CPD). In contrast, improvements in asymptotic performance at the highest contrast levels occur across all spatial frequencies. These results suggest that, even within the foveola, exogenous attention operates through a mechanism similar to that observed in peripheral vision, preferentially enhancing lower spatial frequencies.*
>
> *Strengths:*
>
> *The study shows strong methodological rigor. Eye position was carefully controlled, and the stimulus generation and calibration were highly precise. The authors also situate their work well within the existing literature, providing a clear rationale for examining the fine-grained effects of exogenous attention within the foveola. The combination of high spatial precision, gazecontingent presentation, and detailed modeling makes this a valuable technical contribution.*
>
> *Weaknesses:*

> *The manipulation of attention raises some interpretive concerns. Clarifying this issue, together with additional detail about statistics, participant profiles, other methodological elements, and further discussion in relation to oculomotor control in general, could broaden the impact of the findings.*

We thank the reviewer for the helpful comments. In the Discussion, we have now considered additional factors that could have contributed to the observed attentional effects. First, the exogenous cue might have functioned as a temporal warning signal. However, the interval between cue and stimulus onset was fixed across trials, meaning that the cue did not provide temporal information beyond what participants could already anticipate. Furthermore, participants completed a large number of trials (≥ 4000), making it highly likely that the temporal relationship between trial onset and target onset was overlearned. These considerations indicate that the observed benefit in the valid condition was predominantly attributable to spatial reorienting induced by the cue, rather than to differences in the temporal predictability of the target across conditions.

Another possibility is that the 100% validity of the exogenous cue could potentially have promoted endogenous attentional engagement. Yet, several characteristics of our task strongly limited the extent to which such endogenous engagement could meaningfully influence performance. Endogenous attentional benefits typically emerge only after ~150-200 ms (Posner & Petersen, 1990; Carrasco, 2011), whereas our cue-target SOA was 100 ms, and the target remained visible for only 50 ms. Under these temporal constraints, any voluntary, slow endogenous enhancement would primarily occur after the stimulus offset. Thus, although endogenous maintenance is theoretically possible given the cue’s validity, it is unlikely to have substantially contributed to the observed attentional benefits in our task.

Regarding the points on statistical reporting and participant details, we followed the reviewer’s suggestions by adding post hoc power analyses and providing more comprehensive reporting of the linear model outputs (see Appendices 1 and 2). We also expanded the description of the training procedures conducted with participants prior to formal data collection in the Methods section.

We appreciate the reviewer for raising the important question of how our findings may relate to oculomotor control. To address this, we analyzed trials excluded from the manuscript due to saccades. This analysis revealed that saccade latencies were shorter in the valid condition than in the neutral condition (see Figure 2 — Supplementary Figure 2). This earlier saccade onset may reflect exogenously triggered preparatory activity in the oculomotor system in response to the salient cue. Future studies are needed to examine whether this preparatory mechanism serves to efficiently guide microsaccades or saccades toward behaviorally relevant stimuli in everyday vision. We have incorporated this point into the Discussion, highlighting a potential mechanistic link between exogenous attention and oculomotor behavior.

> ***Reviewer #2 (Public review):***
>
> *Summary:*
>
> *This study aims to test whether foveal and non-foveal vision share the same mechanisms for endogenous attention. Specifically, they aim to test whether they can replicate at the foveola previous results regarding the effects of exogenous attention for different spatial frequencies.*
>
> *Strengths:*
>
> *Monitoring the exact place where the gaze is located at this scale requires very precise eyetracking methods and accurate and stable calibration. This study uses state-of-the-art*

> *methods to achieve this goal. The study builds on many other studies that show similarities between foveal vision and non-foveal vision, adding more data supporting this parallel.*
>
> *Weaknesses:*
>
> *The study lacks a discussion of the strength of the effect and how it relates to previous studies done away from the fovea. It would be valuable to know if not just the range of frequencies, but the size of the effect is also comparable.*

We thank the reviewer for raising these important issues. In response, we have expanded the Discussion to link our findings to prior work. First, we included a direct comparison of our effect sizes with those reported in previous studies. This analysis revealed that our effect sizes are highly comparable to those earlier studies (see Figure 3 — Supplementary Figure 4). Second, we contextualized our findings within the popular framework of normalization model of attention in the Discussion. We detected a mixture of contrast and response gain effects, consistent with predictions from the normalization framework given our experimental design. Finally, we extended the Discussion to consider potential underlying neural mechanisms. Specifically, we suggested that differences in attentional modulation, particularly the manifestation in response gain vs. contrast gain between the fovea and extrafovea, may reflect distinct characteristics of foveal neurons relative to those in extrafoveal regions.

> ***Reviewer #3 (Public review):***
>
> *Summary:*
>
> *This paper explores how spatial attention affects foveal information processing across different spatial frequencies. The results indicate that exogenously directed attention enhances contrast sensitivity for low- to mid-range spatial frequencies (4-8 CPD), with no significant benefits for higher spatial frequencies (12-20 CPD). However, asymptotic performance increased as a result of spatial attention independently of spatial frequency.*
>
> *Strengths:*
>
> *The strengths of this article lie in its methodological approach, which combines a psychophysical experiment with precise control over the information presented in the foveola.*
>
> *Weaknesses:*
>
> *The authors acknowledge that they used the standard approach of analyzing observeraveraged data, but recognize that this method has limitations: it ignores the uncertainty associated with parameter estimates and the relationships between different parameters of the psychometric model. This may affect the interpretation of attentional effects. In the future, mixed-effects models at the trial level could overcome these limitations.*

We thank the reviewer for this comment. Our Methods section continues to transparently discuss these limitations, as well as the fact that these limitations are shared with most published studies in psychophysics. Additionally, we now include measures of uncertainty for all key effects (see Appendices 1 and 2), and we have reported effect sizes throughout the Results section. Finally, we have added post hoc power analyses to the Methods. Following previous approaches to power calculation for related experiments, we found that our study was sufficiently powered to detect the main effect of attention and had moderate power to detect the interaction between attention and spatial frequency.

> ***Recommendations for the authors:***
>
> ***Reviewer #1 (Recommendations for the authors):***
>
> *(1) The manipulation of attention raises some interpretive concerns. Since only valid and neutral cue conditions were included, the results might reflect differences in temporal predictability rather than true spatial reorienting of attention. In other words, the valid cue could act mainly as a temporal warning signal that reduces uncertainty about stimulus onset. Without invalid trials or a non-predictive control cue, it remains difficult to separate spatial and temporal contributions to exogenous attention.*

We thank the reviewer for raising this point. In this regard, we would like to clarify that there was no temporal uncertainty in stimulus onset: across all conditions and trial types, the stimulus was presented at the same time relative to the start of the trial, i.e., 600 ms after the start. Yet, we acknowledge that the shorter temporal proximity between the cue and stimulus in valid trials could serve as an additional temporal warning signal, potentially conferring an advantage relative to the neutral condition. While we cannot completely rule out a contribution of such temporal cueing within the constraints of the current experimental design, we believe its impact was limited. Specifically, the fixed cue-stimulus interval reduced the cue's ability to convey additional temporal information. Furthermore, observers completed a large number of trials (≥4000), and the temporal contingency between trial onset and target onset was likely overlearned. Taken together, these considerations indicate that the observed benefit in the valid condition was predominantly attributable to spatial reorienting induced by the cue, rather than to differences in the temporal predictability of the target across conditions. We now mention this in the revised Discussion (lines 309-318).

We recognized that the original Figure 2 illustrating the experimental paradigm may have caused confusion regarding the timing structure of the task. We have therefore updated the figure to more explicitly illustrate the trial timeline in both conditions.

> *(2) The reported effects seem small, and no power analysis is provided. With only seven participants, the study may not have enough statistical power to confirm that the observed differences are reliable or generalizable. Although the technical precision in gaze and stimulus control is impressive, it cannot offset the limitations of a small sample. The authors should include effect size estimates, confidence intervals, and ideally a post-hoc power analysis.*
>
> *The statistical results are reported only as χ^2 values from model comparisons, which do not show the direction or size of the effects. For clarity and transparency, these tests should be accompanied by fixed-effect estimates with their standard errors and confidence intervals, so readers can better assess both the reliability and perceptual relevance of the findings.*

The reviewer raised several important points regarding the study's statistical rigor.

In the revised manuscript, we now report effect size estimates (Cohen's d) in the Results section and Appendices. Effect sizes were in the medium-to-large range, including the effect of attention on contrast sensitivity at 4 and 8 CPD, and the difference in attentional benefit on contrast sensitivity between 4 and 12 CPD and between 8 and 12 CPD. We have also included the full model outputs, including standard errors and confidence intervals, in the Appendices.

The sample size for the current study was determined based on the magnitude of the attentional effects observed in our previous work (Guzhang et al., 2021). The experimental design and dependent measures were highly similar across the two studies, and the prior study revealed a robust effect, which accounted for a substantial proportion of within-observer variance in a tightly controlled repeated-measures design.

We have revised the manuscript, adding bootstrap-based power estimates, following the procedure described by Jigo and Carrasco (2020), using data from Guzhang et al. (2021). Assuming the effect size in our current study would be comparable to the prior one, 2 to 12 observers were randomly sampled with replacement, and a one-way repeated-measures ANOVA with attention as the main factor was used. This procedure was repeated 10,000 times, and power was estimated as the proportion of iterations yielding a significant main effect for each sample size. The results of this analysis indicate that a sample size of five observers would have been sufficient to achieve approximately 80% power to detect the main effect of attention in the prior study. Based on these estimates, the sample size used in the current study (seven observers) is adequately powered.

We also conducted a post hoc power analysis to evaluate the power of our design to detect the main effects and their interaction. It was performed using the R package *simr*, which estimates statistical power for mixed-effects models through model-based simulation. Specifically, *simr* generated datasets based on the fixed- and random-effect structure of the fitted model, preserving the observed effect sizes and variance components. For each simulated dataset, the model was refit, and the effect of interest was tested. By repeating this procedure 501 times across different sample sizes, power was estimated as the proportion of simulations in which the effect was statistically significant. Based on these post hoc simulations, we estimated that our study had high power (>95%) to detect the main effects and moderate power (>65%) to detect the interaction. Although the estimated power for the interaction was lower than for the main effects, the observed effect size was substantial (as indexed by Cohen's *d*), indicating that the interaction was not trivially small.

We now describe these analyses in lines 501-532 in the Methods section.

> *(3) The task seems quite demanding, requiring fine spatial discrimination, very small stimuli, and head stabilization with a bite bar. It is not clear whether participants were naïve or experienced observers. If they had prior psychophysical training, practice effects could have influenced the results, particularly given the lack of invalid trials. The manuscript would benefit from clarifying participants' experience level and describing any training or familiarization procedures.*

We appreciate the reviewer's concern regarding potential training effects. All observers had prior experience with similar tasks, but were naïve to the scope of this study. Each participant underwent an initial familiarization phase of approximately 50 trials with the experimental setup of this study. They then completed an additional ~50 trials to estimate their individual contrast thresholds per spatial frequency level before we proceeded with data collection at the five predefined contrast levels.

Based on our experience, we have found that, for experiments similar to the one described here, observers quickly adapt to the setup and are generally able to maintain reliable fixation and stable performance, even during the initial training phase. In addition, each participant completed approximately 400 trials before the data collection started. Even observers who began the session with no prior experience would have become practiced with the setup by the time the actual data-collection phase started, during which ~4000 trials were collected per observer. Therefore, whether an observer participated in previous experiments is unlikely to meaningfully affect the results, as the large number of trials ensures comparable levels of task familiarity across individuals.

Crucially, valid and neutral trials were interleaved throughout the session. Any general learning or practice would therefore influence both conditions equally. Despite this, we still observed clear performance improvements in the valid condition relative to the neutral condition, indicating that the observed benefits cannot be attributed solely to practice and reflect an attentional enhancement. We have added elaboration on the training procedures in Methods (lines 411-429).

Finally, we recognize that the lack of invalid trials may raise concerns given our 100% spatially predictive cue, as noted in Reviewer 3's first comment. We refer the reader to our response to that point for a more detailed discussion of cue validity and the distinction between exogenous and endogenous influences in our paradigm.

> *(4) The study would benefit from a clearer connection between the behavioral results and possible underlying neural mechanisms. How might the observed changes in contrast sensitivity relate to known physiological processes at the retinal, thalamic, or cortical level? The discussion could be strengthened by framing the findings within established models of attentional modulation or by referring to known effects of attention in the early visual cortex.*

This is an important point, and we agree that framing the findings within established models of attentional modulation can strengthen the discussion. We believe that the normalization model of attention (Reynolds and Heeger, 2009; Herrmann et al., 2010) offers a useful framework for interpreting our behavioral findings, especially the attention-related changes in contrast sensitivity and asymptotic performance observed at the foveal scale. We have now added a more detailed discussion linking our results to this model and considering, explicitly as speculation, how known physiological processes at different stages may contribute to the observed effects in Discussion (lines 264-307).

> *(5) The ecological relevance of the results is not fully developed. The authors propose that the observed effects may resemble natural attentional shifts triggered by salient events, yet the brief, highly localized flashes used here are somewhat artificial. A more likely interpretation is that these mechanisms relate to oculomotor control within the fovea, perhaps reflecting preparatory activity for microsaccades or fine fixation adjustments. Considering this view could broaden the impact of the findings and link them to current discussions on the relationship between attention and oculomotor control.*

We thank the reviewer for raising this important point regarding the ecological relevance of our findings, which we did not sufficiently address in the original manuscript. Although we briefly motivated scenarios that engage exogenous attention at high spatial resolution, such as detecting road signs or traffic lights at a distance while driving, we did not fully elaborate on how such attentional processes may link to downstream visual and oculomotor functions.

In our experiment, observers maintained fixation and avoided saccades throughout the trial. Nevertheless, in a subset of trials (on average 17% ± 3%), observers made saccades after stimuli disappeared and prior to providing a response. Typically, these movements were microsaccades with amplitudes smaller than 0.5°, directed toward the target location, in both valid and neutral trials. These saccades were discarded prior to the analyses performed in the manuscript. Inspired by the reviewer's feedback, we decided to examine the saccade latency in these trials relative to the onset of the response cue to assess whether exogenous cueing influenced oculomotor timing. Notably, we observed an earlier onset of microsaccades in valid compared to neutral trials (71 ms ± 50 ms faster, $P < 0.01$). We have now added this observation as Figure 2 — Supplementary Figure 2 in the manuscript. Because the presence of an exogenous pre-cue was the only difference between the two trial types, the earlier microsaccade onset likely reflects exogenously triggered preparatory activity in the oculomotor system in response to the salient pre-cue. Such fine-grained attention may prime potential eye movements toward behaviorally relevant stimuli for further examination. This interpretation is consistent with the reviewer's suggestion and supports a mechanistic link between exogenous attention and oculomotor behavior, extending the ecological relevance of our findings. This point has been added to the Discussion on lines 329 to 340.

We also conducted analysis to examine ocular drift behavior following the response cue. Although trials included in the manuscript analyses were constrained such that fixation during target presentation remained within a small window (10’ radius) around the fixation marker, we did not assess whether gaze subsequently drifted closer to the target location after the response cue. One possibility is that exogenous attention might bias ocular drift, shifting the preferred locus of fixation closer to the target. To address this, we computed the average Euclidean distance between gaze position and the target location following response cue onset for valid and neutral trials. However, we found no significant difference in gaze-target distance between valid and neutral trials (p = 0.57).

Although the spatial cueing approach has long been used to probe exogenous attention in a controlled manner in psychophysical experiments, we fully recognize the importance of understanding attention under more naturalistic viewing conditions that allow observers to freely move their eyes. Developing paradigms that incorporate more naturalistic, salient stimuli would be an important direction for future work, enabling investigation of exogenous attention in ecologically valid settings and its influence on sequential actions and processes, including oculomotor behavior.

> *(6) There is no statement about the availability of the data and code used for the experiment.*

We have now added the data and code for the analysis pipeline to the Open Science Framework (OSF).

> ***Reviewer #2 (Recommendations for the authors):***
>
> *(1) The study could discuss the strength of the effect and how it relates to previous studies.*

We thank the reviewer for raising this point. To facilitate direct comparison with the study by Jigo and Carrasco (2020), we computed attentional benefit as the ratio of contrast sensitivity between the valid and neutral conditions (now shown in Figure 3 — Supplementary Figure 4). In their data, the attentional benefit at 0° eccentricity peaked just below 4 CPD, with a ratio of approximately 1.2, corresponding to a ~20% increase in contrast sensitivity. This magnitude closely matches the benefit we observed for fine-grained attentional shifts within the foveola at spatial frequencies between 4 and 8 CPD (17% ± 12% and 16% ± 14% for 4 and 8 CPD, respectively). We have added this comparison to the Discussion (lines 246-262).

In addition, we acknowledge that prior studies have reported heterogeneous attentional effects, including pure contrast gain, pure response gain, or a mixture of the two. We now explicitly reference these findings in the Discussion and use the normalization model of attention (Reynolds and Heeger, 2009; Herrmann et al., 2010) to account for how differences in stimulus configuration, attention field size, and eccentricity may account for discrepancies between our findings and prior studies examining attention in the extrafovea or when broadly distributed across the fovea (lines 264-307).

> *(2) Minor details:*
>
> *(a) The abstract mentions gaze-contingent-display, but if I understand correctly, the stimulus was not presented in a gaze-contingent manner.*

That’s correct. Although stimuli were not presented gaze-contingently, we used a gaze-contingent calibration procedure (see Methods, lines 386-389) to achieve higher precision in localizing the line of sight. This increased accuracy was essential for selecting trials in which stimuli remained at the intended eccentricity relative to the preferred locus of fixation. To avoid potential confusion, however, we have removed this detail from the abstract.

> *(b) Line 361: What is the manual calibration the authors are referring to? It does not appear to be described.*

The text has been updated to explain more explicitly what auto and manual calibrations are.

> *(c) Line 402: There may be a typo towards the end of the line "t0" should be "to"?*

Text has been updated. Thank you.

> *(d) Line 405. What are the units of 30?*

It's in arcminutes. Text has been updated.

> ***Reviewer #3 (Recommendations for the authors):***
>
> *I found this paper very interesting, with a solid methodological approach and excellent data analyses. The authors present a well-designed psychophysical study that contributes valuable insights into the mechanisms of attention in the foveola. The methodology is rigorous, and the analyses are thoughtfully conducted and clearly presented.*
>
> *That said, I would like to offer a few comments and suggestions for clarification and further consideration:*
>
> *(1) Exogenous attention:*
>
> *If a 100% spatially predictive cue is compared to a neutral cue, the observed attentional effect should not be described as (purely) exogenous, since the cue fully predicts where the post-cue will request a response. This situation represents a case in which attention is exogenously driven but endogenously maintained (see e.g., Chica et al., 2013, Behavioural Brain Research). I recommend clarifying this distinction in the manuscript (and title) to avoid conceptual ambiguity.*

We thank the reviewer for raising this important conceptual point. We agree that because the pre-cue was 100% spatially predictive, the resulting attentional allocation cannot be considered purely exogenous. Although the abrupt, salient onset of the cue obligatorily triggers an exogenous shift of attention, its validity could also promote endogenous maintenance of attention at the cued location. Yet, several characteristics of our task strongly limit the extent to which such endogenous engagement could meaningfully influence performance. Endogenous attentional benefits typically emerge only after ~150-200 ms (Posner & Petersen, 1990; Carrasco, 2011), whereas our cue-target SOA was 100 ms, and the target remained visible for only 50 ms. Under these temporal constraints, any voluntary, slow endogenous enhancement would primarily occur after the stimulus offset. Thus, although endogenous maintenance is theoretically possible given the cue's validity, it is unlikely to have substantially contributed to perceptual encoding in our task.

We also considered the possibility that our response cue (a retro-cue indicating the target location) might recruit endogenous attention to the internal perceptual representation. Importantly, however, this retro-cue was equally informative in valid and neutral conditions. Any enhancement driven by the retro-cue should therefore benefit both trial types to the same extent. The fact that we still observe a robust advantage in valid trials supports the conclusion that the performance improvements predominantly reflect fast, spatially specific exogenous facilitation rather than slower endogenous processes.

We have revised the manuscript to clarify that although the cue obligatorily triggers an exogenous attentional shift, its 100% validity could allow for endogenous attention maintenance as shown by Chica et al. (2013). We also added an explanation detailing why such endogenous contributions are unlikely to drive our main results, given the rapid cue-target timing in our task in Discussion (lines 319-327). Finally, to further prevent ambiguity, we updated the manuscript title to refer to “exogenously triggered attention,” rather than simply “exogenous attention.”

> *(2) Interpretation of statistical effects:*
>
> *The statement "Therefore, asymptotic performance showed only independent, additive effects of frequency and attention, without a systematic influence of spatial frequency on the attentional benefit" seems not to be supported by the data, as the main effect of frequency was not significant.*

We thank the reviewer for this helpful observation. We agree that the original phrasing did not accurately reflect the results, as the main effect of spatial frequency was not significant (p = .0545). We have revised the sentence to “Therefore, asymptotic performance reflected an effect of attention alone, with no detectable contribution of spatial frequency or of the interaction between spatial frequency and attention” to avoid implying such an effect (lines 210-211).

> *If data from two participants were missing in one condition, the authors should consider replacing this data with new participants.*

We agree with the reviewer that having two observers with missing data in one condition is not ideal. However, the 20 cpd condition was deliberately positioned near the resolution limit at the tested eccentricity and was therefore extremely demanding. Observers also had to monitor two stimulus locations simultaneously, further increasing task difficulty. This condition was challenging for all observers and, despite testing up to the highest contrast, two of seven observers were unable to perform above chance, indicating that for a non-trivial fraction of observers, this condition was effectively unmeasurable with our paradigm. As noted in the manuscript, the 20 cpd condition also has a statistical limitation: thresholds clustered near the upper bound (approaching 100% contrast), compressing the dynamic range and markedly reducing variance relative to lower spatial frequencies, which violates the homoscedasticity assumption of linear models. For these reasons, we did not pursue additional data collection in this condition. Nevertheless, we report the data that were successfully obtained, as they remain informative about performance near the resolution limit.

We finally note that even when setting aside the 20 CPD condition, our data support this conclusion: comparisons between 4 and 12 CPD, as well as between 8 and 12 CPD, revealed large differences in the magnitude of the attentional benefit (d = 0.65, 95% CI [0.11, 1.18] and d = 0.62, 95% CI [0.08, 1.14], respectively). To further quantify these effects, we have added Cohen’s d to report the effect sizes for these spatial-frequency comparisons across texts in Results as well as in tables in Appendices.

> *(3) Sample size:*
>
> *As this is a psychophysical experiment with many trials and few participants, I am curious about how the authors determined the appropriate sample size and the number of trials required to detect the expected effects. Given that many effects were found to be significant, it seems that statistical power was adequate; however, it would be helpful if the authors could explain how this issue was addressed a priori during experimental planning.*

We appreciate that the reviewer raised this point. Please see the reply to the second point from Reviewer 1, who raised a related question about statistical power.

> *(4) Figure 2 clarification:*

> *In Figure 2B, I do not fully understand the "Valid" and "Neutral" representation. Both conditions include a post-cue indicating the right position; however, in the neutral condition, there is a central fixation square, whereas in the valid condition, there is not. Please clarify this aspect of the figure. I think I understood the paradigm, but this part of the figure is misleading.*

Precue only exists in valid condition. But there is a mistake where fixation marker is missing in valid condition in panel B.

We thank the reviewer for pointing this out. We have updated Figure 2 to explicitly show the sequence of valid vs. neutral trials. The fixation mark remained on the screen throughout the trial in both the valid and neutral conditions. After a 500 ms fixation period, an exogenous cue was presented for 30 ms in valid trials, followed by a 70 ms interval before stimulus onset. In neutral trials, no cue was presented, and the screen remained blank for 100 ms before the stimuli appeared. In conditions, a response cue would appear 50 ms after stimulus offset.

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