Differential effects of endogenous and exogenous attention on sensory tuning

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Abstract

Covert spatial attention benefits performance in many visual tasks (e.g. orientation discrimination, visual search). However, in texture segmentation tasks in which increasing spatial resolution can be detrimental, endogenous and exogenous attention have differential effects on performance. Here we tested whether these differences manifest in sensory representations. We used reverse correlation to assess, in a within-subjects design, whether and how endogenous and exogenous attention differentially alter the representation of orientations and spatial frequencies. The same observers detected a vertical grating embedded in noise following central (endogenous attention; Experiment 1) or peripheral (exogenous attention; Experiment 2) pre-cues. We found that both endogenous and exogenous attention similarly improved performance at the attended location by enhancing the gain of all orientations without changing tuning width. Additionally, endogenous attention enhanced the gain of spatial frequencies above and below the target spatial frequency, whereas exogenous attention preferentially enhanced the gain of spatial frequencies higher than the target spatial frequency. We conclude that these changes in sensory tuning may underlie differential effects of endogenous and exogenous attention on performance.

Orienting covert spatial attention to a target location benefits performance in many visual tasks in human and non-human primates. These improvements often manifest via an increase in contrast sensitivity—the ability to distinguish an object from its surroundings—and spatial resolution—the ability to see fine detail—at the attended location (reviews, Carrasco 2011, 2014; Anton-Erxleben & Carrasco, 2013; Carrasco & Yeshurun, 2009; Carrasco & Barbot, 2014).

Covert spatial attention can be deployed either endogenously or exogenously. Endogenous attention is goal driven or voluntary, and takes about 300-500ms to be deployed to a given spatial location. Conversely exogenous attention is involuntary and driven automatically by the sudden onset of a stimulus (e.g. flash of light). As a result, exogenous attention is quick to deploy—100-120ms—and transient—peaking and decaying quickly (reviews, Carrasco 2011, 2014). Similar differences in the temporal dynamics of endogenous and exogenous attention have been reported from single cell recordings in macaque area MT (Busse, Katzner & Treue, 2008).

Endogenous attention is prompted by central or symbolic cues and the strength of the attentional benefit and its corresponding cost at unattended locations increases with the cue validity (e.g., Sperling & Melcher, 1978; Mangun & Hillyard, 1990; Giordano, McElree & Carrasco 2009). Exogenous attention is manipulated via peripheral cues and is invariant to the cue validity—its benefits and costs are present to the same extent regardless of cue validity (e.g., Pestilli & Carrasco 2005; Giordano et al., 2009; Yeshurun & Rashal, 2010; Fernández & Carrasco 2020). Despite these differences, both types of covert attention typically alter performance in a similar fashion; they both improve visual processing at the attended location at the expense of processing at

unattended locations (Desimone & Duncan 1995; Shiu & Pashler 1995; Luck, Hillyard, Mouloua & Hawkins, 1996; Reynolds, Chelazzi & Desimone 1999; Vanduffel, Tootell & Orban, 2000; Pestilli & Carrasco 2005; Pestilli, Viera & Carrasco 2007; Montagna, Pestilli & Carrasco, 2009; Giordano et al., 2009; Maunsell 2015).

One way in which attention improves performance is by increasing contrast sensitivity. However, there are differences in how endogenous and exogenous attentional systems modulate contrast response functions. Endogenous attention typically increases contrast sensitivity via a contrast gain change, whereas exogenous attention increases maximal contrast responses via a response gain change (Ling & Carrasco, 2006; Pestilli, Ling & Carrasco 2009). The normalization model of attention postulates that these differences are due to changes in the size of the attention field relative to the stimulus size (Reynolds & Heeger, 2009). A small attention field leads to response gain and a large attention field leads to contrast gain (Reynolds & Heeger, 2009; Herrmann, Montaser-Kouhsari, Carrasco & Heeger, 2010). Additionally, both types of attention increase contrast sensitivity under high levels of external noise (Lu & Dosher 1998), but exogenous attention only does so when external noise levels are low (Dosher & Lu, 2000).

Attention also improves sensitivity by enhancing spatial resolution. How covert attention modulates the intrinsic resolution limits of our visual system has been studied using texture segmentation tasks as a model system. In these tasks, baseline performance follows an inverted-U shape across eccentricity (Gurnsey, Pearson & Day, 1996; Kehrer, 1997; Morikawa, 2000). Performance peaks at the mid-periphery (where resolution is optimal) and drops off at peripheral locations (where resolution is too low) and at the fovea (where resolution is too high), i.e. there is a central performance drop. In this task, endogenous attention optimizes resolution to improve performance at central and peripheral locations (Yeshurun, Montagna, & Carrasco, 2008; Barbot & Carrasco, 2017; Jigo & Carrasco, 2018). However, exogenous attention inflexibly increases resolution resulting in a central attentional impairment; performance benefits occur at at peripheral locations but performance costs occur at foveal locations (Yeshurun & Carrasco, 1998, 2000; Talgar & Carrasco, 2002; Yeshurun et al., 2008).

Selective adaptation has been used to investigate how endogenous and exogenous attention modulates performance. Adapting observers to high spatial frequencies removes the central performance drop and the attentional impairment seen in exogenous attention. These findings suggest that exogenous attention inflexibly increases resolution by enhancing sensitivity to high spatial frequencies (Carrasco, Loula & Ho, 2006). However, endogenous attention improves performance at all eccentricities by flexibly increasing or decreasing resolution. It does so by adjusting the contribution of high-frequency information according to task demands (Barbot & Carrasco, 2017).

The proposal that attention modulates resolution by adjusting sensitivity to high spatial frequencies extends to rodents. Neurons in mouse primary visual cortex that are tuned for high spatial frequencies have increased gain relative to neurons that are tuned for

low spatial frequencies during locomotion and heightened attention (Mineault, Tring, Trachtenberg & Ringach, 2016). This increase in high spatial frequency sensitivity translates to improved spatial resolution in the mouse and parallels known benefits of attention in humans.

Given that there is a tradeoff between spatial and temporal resolution, similar differential effects in performance exist in temporal processing. In temporal segregation tasks, exogenous attention enhances spatial resolution but degrades temporal resolution. For instance, a peripheral cue diminishes observers' ability to indicate whether a target is continuous or flickering at the attended location (Yeshurun 2004; Yeshurun & Levy 2003; Rolke, Dinkelbach, Hein & Ulrich 2008). Similarly, automatic orienting of attention impairs discrimination of the temporal order of two dots (Hein, Rolke & Ulrich 2006), degrades perceived apparent motion (Yeshurun and Hein 2011) and leads to longer temporal integration (Megna, Rocchi & Baldassi 2012). Conversely, endogenous attention improves both spatial and temporal resolution (Hein, Rolke & Ulrich, 2006; Sharp, Melcher & Hickey, 2018).

Here, we investigate whether the differential impact of endogenous and exogenous attention on visual performance arise due to changes in sensory representations. We focus on two building blocks of vision–orientation and spatial frequency–that are coded in primary visual cortex (Hubel & Wiesel, 1959; Maffei & Florentini, 1977; Sirovich & Uglesich, 2004). Sensory representations were assessed using psychophysical reverse correlation, a technique that has been widely used to probe the mechanisms underlying behavioral responses to noisy stimuli (Ahumada 1996; Eckstein & Ahumada 2002; Wyart, Nobre & Summerfield, 2012; Li, Barbot & Carrasco, 2016) and can approximate sensory tuning properties reported in electrophysiological studies (Neri & Levi, 2006). Reverse correlation, which provides a measure of how changes in external noise influence performance, complements conventional methods such as signal detection theory that cannot distinguish between external and internal performance limiting noise. Here we use signal detection theory to assess performance benefits and costs with endogenous and exogenous attention and reverse correlation to uncover the computational mechanism underlying them.

Covert attention can alter neural tuning via two computations, gain and width change (reviews, Reynolds & Chelazzi, 2004; Reynolds & Heeger 2009; Maunsell 2015). Attention can scale the amplitude of responses by some factor, a gain change (Hillyard, Vogel & Luck,1998; McAdams & Maunsell, 1999; Treue & Martinez-Trujillo, 1999; Rabinowitz, Goris, Cohen & Simoncelli, 2015) and/or increase selectivity by narrowing the width of the response profile, a width change (Spitzer, Desimone & Moran, 1988; Martinez-Trujillo & Treue, 2004).

Regarding orientation and motion, endogenous attention modulates sensory responses by strictly boosting the gain of all feature detectors without changing selectivity, in both humans (*psychophysical*: Lu & Dosher, 2004; Ling, Liu & Carrasco, 2009; Paltoglou & Neri, 2012; Wyart, Nobre & Summerfield, 2012; Barbot, Wyart & Carrasco, 2014; *EEG:* Foster, Thyer, Wennberg & Awh, 2021) and non-human primates (n*europhysiology*:

Cook & Maunsell, 2004; McAdams & Maunsell, 1999; Treue, 2001). For exogenous attention, there are no neurophysiological studies and psychophysical results are unclear. Previous work has shown that exogenous attention affects sensory responses by boosting the gain across all orientations without changing tuning width (Baldassi & Verghese, 2005; Fernández, Li & Carrasco, 2019). However, studies examining position tuning have found contradictory results with reports of only gain (Eckstein, Shimozacki, & Abbey, 2002) or a mix of only tuning or gain and tuning depending on target eccentricity (Megna, Rocchi, & Baldassi, 2012).

Regarding spatial frequency representations, the only study that has tested endogenous attention found no change in the tuning profile (Lu & Dosher, 2004). Results with exogenous attention are inconclusive, maybe due to different behavioral manipulations, tasks, and analysis methods. Two studies reported no change in the spatial frequency profile in a letter identification (Talgar, Pelli & Carrasco, 2004) or a detection (Fernández et al., 2019) task, but a study found increased power over high spatial frequencies in a spatio-temporal task (Megna, et al., 2012).

Here, the same observers completed two different experiments with identical stimuli and task. In the first experiment we maximized the deployment of endogenous attention via a central cue and longer ISI, whereas in the second experiment we maximized exogenous attention via peripheral cues and a shorter ISI. We tested valid, neutral, and invalid cues to assess attentional tradeoffs; i.e., benefits at the attended and costs at the unattended locations. This is an important addition, as previous studies either did not include a neutral condition and could not assess benefits (Lu & Dosher, 2004; Eckstein et al., 2002; Wyart et al., 2012; Barbot et al., 2014) or did not include an invalid condition and could not assess costs (Talgar et al., 2004; Ling et al., 2009; Megna et al., 2012; Paltoglou & Neri 2012).

We found that both endogenous and exogenous attention alter orientation tuning via a multiplicative gain enhancement without changing tuning width. Critically, in the spatial frequency dimension, differential effects emerged: endogenous attention enhanced sensitivity to spatial frequencies above and below the target spatial frequency, whereas exogenous attention preferentially enhanced spatial frequencies above the target spatial frequency.

Experiment 1 — Endogenous Attention

Methods

Observers

Six observers (aged 19-26; 4 females), including authors A.F. and S.O., participated in 15 experimental sessions. All observers had normal or corrected-to-normal vision and provided informed consent. All experimental procedures were in agreement with the

Helsinki declaration and approved by the university committee on activities involving human subjects at New York University.

Apparatus

Stimuli were generated using MATLAB (MathWorks, Natick, MA) and the Psychophysics toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Observers sat in a dimly lit room with their head positioned on a chinrest 57 cm away from a 22-inch Iiyama Vision Master Pro 514- CRT monitor (1280 x 960 resolution; 100 Hz). A ColorCAL MKII Colorimeter was used for gamma correction (Cambridge Research Systems, Rochester, Kent, UK). Observers viewed the monitor display binocularly and fixation was monitored using an EyeLink 1000 eye tracker (SR Research, Ottawa, Ontario, Canada) at a sampling rate of 1000 Hz.

Stimuli

Stimuli were presented on a gray background at four spatial locations denoted by placeholders composed of four black dots forming a square (3° wide; **Figure 1A**). The placeholders remained on the screen for the entire experimental session and were presented at each intercardinal location at 7° of eccentricity. The target was a random phase vertical Gabor generated by modulating a 2 cpd sine wave with a Gaussian envelope (0.8° SD). Four white noise patches were independently and randomly generated on each trial and presented inside each placeholder. The noise was bandpass-filtered to contain spatial frequencies between 1 and 4 cpd and scaled to have 0.12 root-mean-square contrast. On any given trial the test stimulus could be a noise patch or a target embedded in noise (**Figure 1A,B**).

Procedure

Observers performed a visual detection task. A test stimulus, defined as the patch probed by the response cue, was presented at one of four possible spatial locations denoted by placeholders. In half of the trials, the test stimulus contained only noise; in the other half, the target was embedded in the noise. To diminish temporal expectation and ensure our attention effects were driven by the cues, each trial began with one of three equally likely fixation periods (300, 400, or 500 ms). After the fixation period, a pre-cue was presented for 150 ms, followed by a brief inter stimulus interval of 350 ms. Next, four patches (three irrelevant stimuli and one test stimulus), one inside each placeholder, were simultaneously presented for 100 ms. Each placeholder could encompass a patch composed of a target embedded in the noise or just noise with 50% probability. Thus on any given trial, whether a target was presented was independently determined for all four locations.

The test stimulus was indicated by a central response cue, which was presented 100 ms after the offset of the patches and remained on the screen until response. The cue validity was manipulated such that 60% of the trials were valid, 20% were neutral, and the remaining 20% were invalid; from the cued trials indicating one location, 75% were

valid trials (**Figure 1C**). Therefore, observers were incentivized to deploy their voluntary spatial attention to the location probed by the pre-cue as the majority of the trials were valid. In the valid and invalid trials, the pre-cue was presented as a central line pointing to one of the placeholders. In valid trials, the pre-cue matched the response cue; in invalid trials the pre-cue and response cue did not match. In neutral trials, all locations were pre-cued (4 lines, one pointing to each placeholder) to distribute attention to all placeholders. The observers task was to detect whether the test stimulus contained a target by pressing the "z" key for yes or "?" for no on an apple keyboard. On incorrect trials observers received auditory feedback in the form of a tone. At the end of each block observers also received feedback in the form of percent correct.

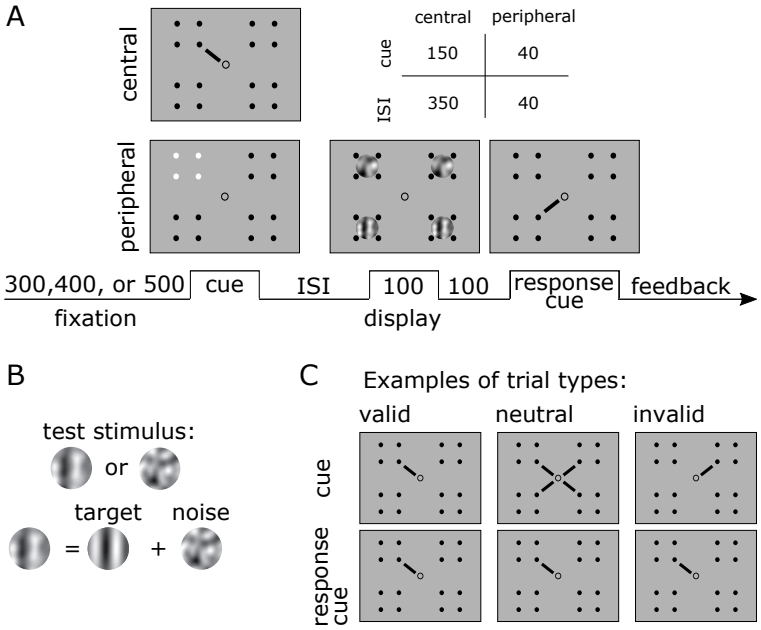

Figure 1. (**A**) *Trial Timeline in ms.* Observers performed two yes/no detection tasks. For endogenous attention (experiment 1), the cue was a line extending from the center indicating one spatial location (central cue). For exogenous attention (experiment 2), the placeholder at one spatial location briefly changed in polarity (peripheral cue). The timings (cue and ISI) differed for both experiments (central and peripheral cue) to optimize the effectiveness of the cues. (**B**) *Stimuli.* In half of the trials the test stimulus consisted of a Gabor embedded in noise, in the other half the stimulus was just noise. (**C**) *Trial types.* The example demonstrates valid, neutral, and invalid trial in Experiment 1. In Experiment 2, the cue and response cue mappings were the same but the cue was peripheral instead of central.

All attention conditions (valid, invalid, and neutral) were interleaved within each block. Observers completed 7 blocks for a total of 1008 trials per session. Each observer completed a training session (1008 trials) to familiarize themselves with the task. This was followed by 15 experimental sessions (15,120. During training, a contrast threshold —defined as the level of contrast needed to achieve 75% accuracy on neutral trials— was determined for the target using an adaptive titration method (Best PEST; Petland, 1980). If an observer was under/over-performing by ≥5% on neutral trials on any given session, their contrast threshold was updated in the following session.

Stimulus presentation was contingent upon central fixation. Fixation was monitored from the start of the trial until response cue presentation. Trials with fixation breaks—defined as a deviation in eye-position by ≥1.5° from fixation—were repeated at the end of the block.

Data analysis

Performance was evaluated by $d'(Z[H]-Z[FA])$, criterion$(-0.5[Z(H)+Z(FA)])$, where H stands for hit rate, FA for false alarm rate, and Z for z-score. Reaction time was assessed as a secondary dependent variable.

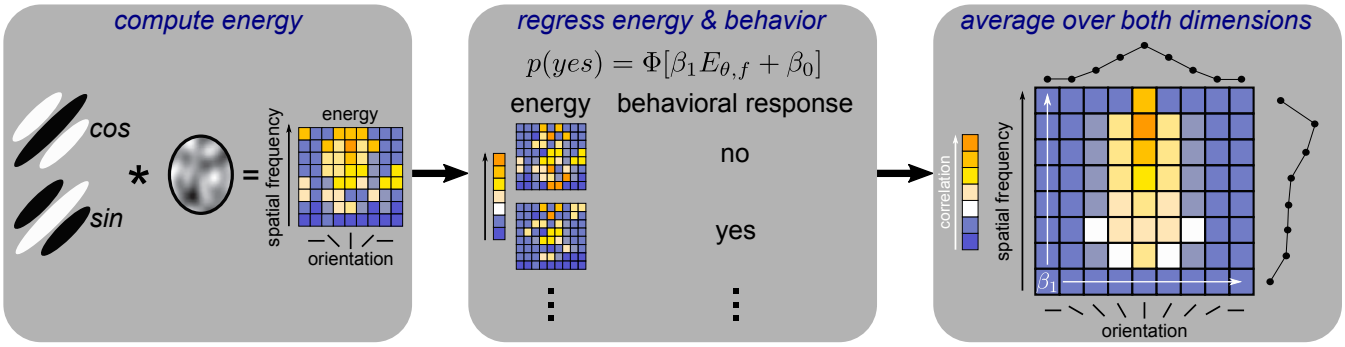

Figure 2. *Reverse Correlation:* (1) Compute energy by convolving a bank of Gabor filters in quadrature phase with the noise patches; (2) Regress the trial-wise energy fluctuations with behavioral responses; (3) The slope of the regression indexes sensitivity; take the mean (marginals) of the slope across the orientation and spatial frequency dimension to compute tuning functions.

Reverse correlation

Reverse correlation, assuming a general linear model approach (**Figure 2**; Wyart et al., 2012; Li, et al., 2016; Fernández et al., 2019), was used to assess the computations underlying attention's modulatory effect on performance. The noise image of the test stimulus was transformed from a space defined by pixel luminance intensities to a space defined by the contrast energy across orientation (-80 to 80 with 19 points equally spaced on a linear scale) and spatial frequency (from 1 cpd to 4 cpd with 15 points evenly spaced on a log scale) components in the noise. We took the noise images S across trials and convolved them with two Gabor filters g (same size as the target) in quadrature phase with the corresponding orientation θ and spatial frequency f to compute energy $E_{\theta,f}$ for all components, which is given by the following expression:

$$E_{\theta,f} = \sqrt{(S * g_{\theta,f,sin})^2 + (S * g_{\theta,f,cos})^2}$$

We regressed the energy of each component with behavioral responses using probit binomial regression. The regression model was expressed as such:

$$p(yes) = \Phi[\beta_1 E_{\theta,f} + \beta_0]$$

Where β_1 is the slope of the regression and indicates the level of correlation between the energy and behavioral reports, β_0 is an intercept term, $\Phi[\,.\,]$ indicates a probit link—inverse of the normal cumulative distribution function. We used the slope to index

perceptual sensitivity. A slope of zero indicates that the energy of that component did not influence the observer's responses. Prior to regressing, the energy of each component was sorted into a present or absent group and the mean of the energy for each group was subtracted and normalized to have a standard deviation of one, which allowed us to use only the energy fluctuations produced by the noise. The estimated sensitivity kernel K was a 2D matrix in which each element was a β_1 value. This process was completed independently for each of the three attention conditions.

Spatial frequency and orientation tuning functions were computed by taking the marginals of the 2D sensitivity kernels. Marginals for orientation θ_m were computed by taking the mean across the orientation dimension and were fit with a Gaussian of the form:

$$\theta_m = \alpha G(\mu, \sigma) + b$$

Where α controls the amplitude, μ the center, σ the width, and b the baseline or y-intercept. Conversely, marginals for spatial frequency f_m were computed by taking the mean across the spatial frequency dimension and were fit with a truncated log parabola of the form (Watson & Ahumada, 2005):

$$f_m(f_1) = \begin{cases} \alpha[10^{-(\frac{log_{10}(f_1/f_0)}{\sigma})^2}] + b \\ 1 - \lambda, \end{cases} \quad \text{if} \quad f_1 < f_0 \quad \text{and} \quad f_m < 1 - \lambda$$

Where f_1 are the tested spatial frequencies, f_0 controls the peak frequency, σ controls the width, λ is a truncation parameter that flattens the curve, α scales the function, and b the baseline or y-intercept. The amplitude of the functions was computed by taking the difference between α and $|b|$. Endogenous attention was fit with a log parabola without truncation.

We conducted marginal reconstruction to determine whether we could treat orientation and spatial frequency as separate dimensions. We took the outer product of the marginal orientation and the marginal of the absolute value of the spatial frequency tuning functions to reconstruct the sensitivity kernels for all attention conditions. We then correlated the reconstructed sensitivity kernels with the original kernels. The higher the correlation the higher the separability.

Statistical analysis

A bootstrapping procedure was used to test for statistical significance across all fitted parameters (Li, Pan, Carrasco 2019). We first resampled, with replacement, each observers' data to generate new 2D sensitivity kernels per the exogenous and endogenous attention conditions. We then averaged across observers to arrive at a new mean sensitivity kernel. This was followed by taking the marginals for orientation and spatial frequency and fitting them with a Gaussian and truncated log parabola, respectively. We then took the difference in fitted parameters between valid and invalid, valid and neutral, and neutral and invalid to generate difference scores. This process

was repeated 1000 times to arrive at distributions of difference scores. Significance was defined as the proportion of the difference scores that fell above or below zero. When appropriate, e.g. when looking at the differences in the bootstrapped marginals, adjustments for multiple comparisons were conducted via Bonferroni correction (Holm 1979).

Parameters estimated from the bootstrapped data were also used to compare the attentional effects generated by endogenous and exogenous attention. First, parameter estimates across each bootstrapping iteration for the valid and invalid functions were subtracted to generate attentional effects. Second, we took the difference in attentional effects between endogenous and exogenous attention to generate difference-difference scores. Significance was defined as the proportion of the difference-difference scores that fell above or below zero.

Significance for detection sensitivity (d'), criterion (c), and reaction time was computed using within subjects ANOVAs and when necessary two-tailed *t*-tests. Effect sizes are reported as generalized eta squared (η_G^2; Bakeman, 2005) or Cohen's d (Cohen, 1992). For all reported null effects we provide a complementary Bayesian approach (Masson, 2011). The ANOVA sum of squared errors were transformed to estimate Bayes Factors (B) as well as Bayesian information criterion probabilities ($pBIC$) for the null(H_0) and alternative(H_1) hypothesis given the data (D). We report Bayes Factors as odds in favor of the null hypothesis (e.g. $B[4:1]$ indicates 4 to 1 odds in favor of the null hypothesis).

Model Comparisons

To assess which model best fit the orientation and spatial frequency tuning functions we conducted model comparisons using the Akaike information criterion corrected for small sample sizes (AICc). Assuming normally distributed error and constant variance, AICc can be computed from the estimated residuals (Burnham & Anderson, 2002):

$$AIC = n\log(\hat{\sigma}^2) + 2k$$

$$\hat{\sigma}^2 = \frac{\sum \hat{E}_i^2}{n}$$

$$AICc = AIC + \frac{2k(k+1)}{n-k-1}$$

Here n is the number of data points, k is the number of parameters in the candidate model, and $\hat{E}_i$ is the estimated residuals. We report differences in AICc scores ($\Delta AICc$):

$$\Delta AICc_i = AICc_i - AICc_{min}$$

The best model is one where $\Delta AICc_i \equiv \Delta_{min} \equiv 0$. The level of support for model i is substantial if $\Delta AICc_i$ falls within 0-2, considerably less if it falls within 4-7, and no support if >10 (Burnham & Anderson, 2002). We discarded all models with a $\Delta AICc$ > 10. In all cases the chosen model had a $\Delta AICc \leqslant 2$.

Model comparisons were computed on the non-bootstrapped individual data. In the orientation dimension, eight models with different combinations of shared parameters for the valid, neutral, and invalid functions were tested (e.g. if only σ is shared then only one σ parameter was used to capture the width of all three cues, while three separate parameters for the gain (α) and baseline (b) were used for a total of seven [$k = 7$] free parameters). In the spatial frequency dimension, sixteen models were tested. For exogenous attention, the truncation term was always left free to vary across attentional cues. For endogenous attention, the truncation term was removed. Once the best model was determined, it was then fit to the bootstrapped data for statistical analysis.

Results

We first examined the effect of endogenous attention on performance (**Figure 3**). Endogenous attention improved sensitivity (indexed by d'; F(2,10) = 42.88, p < 0.001, η_G^2 = 0.42) at the target location. Sensitivity for valid cue trials was higher than for the neutral (t(5) = 6.246, p = 0.002, d = 1.041), which in turn was higher than for invalid cues (t(5)=5.716, p = 0.002, d= 0.827). We also analyzed RTs as a secondary variable, to assess if there were any speed-accuracy tradeoffs. Attention sped responses (F(2,10) = 35.32, p < 0.001, η_G^2 = 0.24). Observers were faster to respond when presented with a valid than a neutral cue (t(5)= -6.532, p = 0.001, d = -0.816), which in turn was faster than for an invalid cue (t(5)= -4.61, p = 0.005, d = 0.44). These results rule out any speed-accuracy tradeoffs. Furthermore, there were no significant differences in decision criterion across all attention conditions (F(2,10)= 2.006, p = 0.185; $B[2.18:1]$; $pBIC(H_1|D) = 0.314$; $pBIC(H_0|D) = 0.686$). In sum, sensitivity was improved at the attended location and impaired at the unattended location.

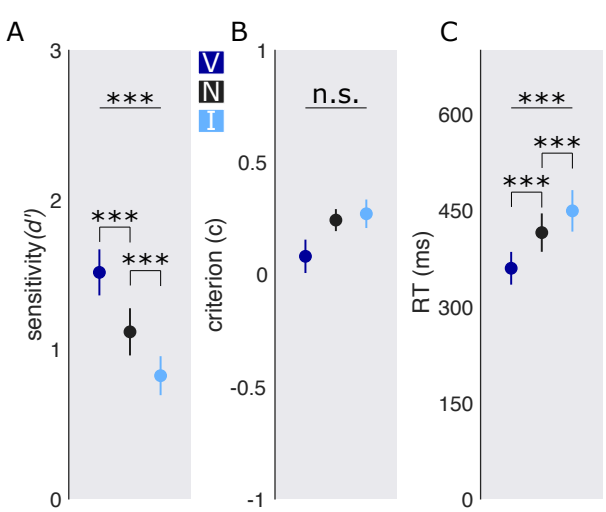

Figure 3. *Performance, Experiment 1: Endogenous attention*. (**A**) *Detection sensitivity indexed by d' with central cues.* (**B**) *criterion*. (**C**) *Reaction time (RT) in milliseconds*. All dots represent the group average. Error bars are ± 1 SEM. *** p < 0.001.

Having established that the cues successfully manipulated endogenous attention and affected performance, we next regressed the energy across trials with each observer's responses using binomial regression. This provided a 2D sensitivity kernel where each component consisted of a β_1 weight representing the level of correlation between reporting the target as present in the test stimulus and the energy in the noise. High weights indicate a high correlation, suggesting that this component in the noise positively influenced the observers responses, whereas weights close to zero or below indicate no correlation or a negative relation. As expected, the highest weights were observed at the components corresponding to the orientation and spatial frequency of the target.

To ensure that we could treat orientation and spatial frequency as separable dimensions in our data, we conducted a separability test via marginal reconstruction. We observed high levels of separability; the mean across subjects and conditions was 0.87±0.05.

Having established that the feature dimensions are separable, we focused our analysis on the marginals of the 2D sensitivity kernels. We fit the orientation marginals with Gaussians and the spatial frequency marginals with truncated log parabolas.

Model comparisons revealed that all orientation tuning functions were best fit with a shared width parameter (σ) across attentional conditions; indicating that the width of the functions did not differ (**Figure 4A**). The valid central cue and the neutral cue increased the gain on orientations more than the invalid cue (*valid vs invalid*: p = 0.002; *neutral vs invalid*: p = 0.044; **Figure 4B-D**). Endogenous attention enhanced the gain across all orientations without changing tuning width.

The best fit model in the spatial frequency dimension was also one with only a shared width parameter (σ) across all cues (**Figure 5A**). The valid central cue increased sensitivity—via an amplitude enhancement—more than the invalid cue (p<0.001). A followup bootstrapping analysis on the functions revealed that this enhancement spanned spatial frequencies below and above the target spatial frequency (1.43-2.32 cpd). Additionally, the valid cue shifted peak sensitivity to lower spatial frequencies than the neutral cue, p=0.018 (**Figure 5B-D**). Endogenous attention enhanced spatial frequencies at, above and below the target spatial frequency.

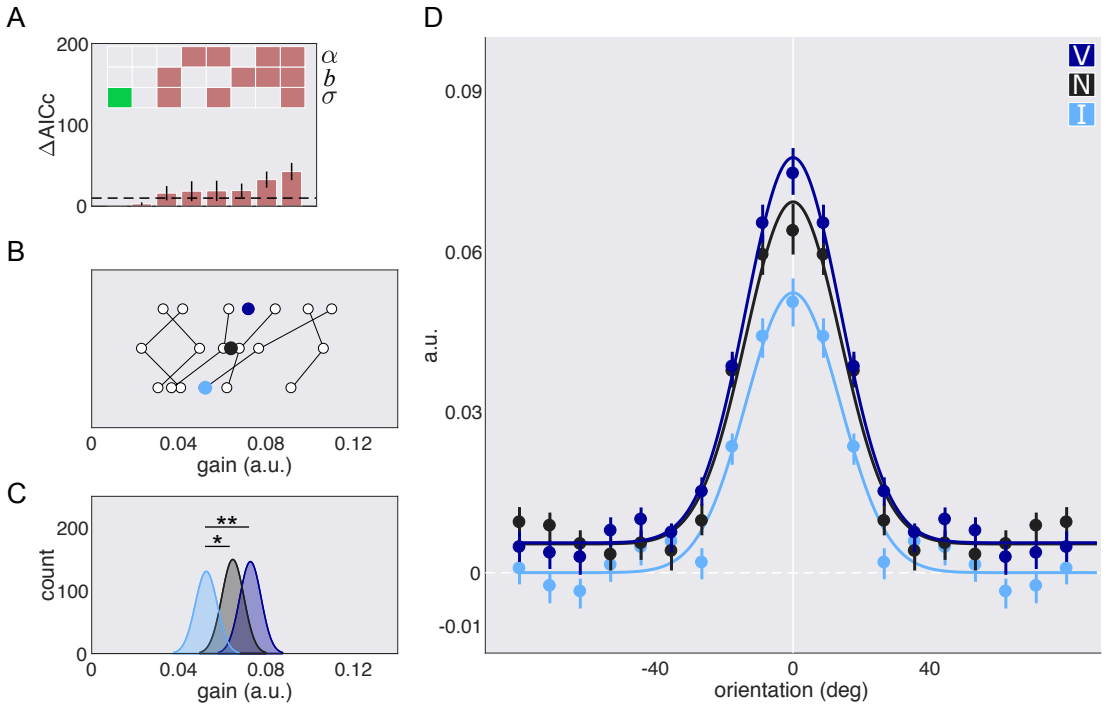

Figure 4: *Orientation tuning functions with central cues, Experiment 1: Endogenous attention.* (A) model comparison results: gain α, width σ, and baseline b; empty squares = not shared; filled in squares = shared; green square = chosen model. Dashed line = cutoff for significance (10). (B) Parameter estimates for the gain of the fit to the *individual* data of the chosen model. (C) Parameter estimates for the gain of the fit to the *bootstrapped* data of the chosen model. (D) Best fit tuning functions (using the chosen model) to the group averaged data; the units are arbitrary (a.u.). Error bars are 68% C.I. * $p < 0.05$; ** $p < 0.01$.

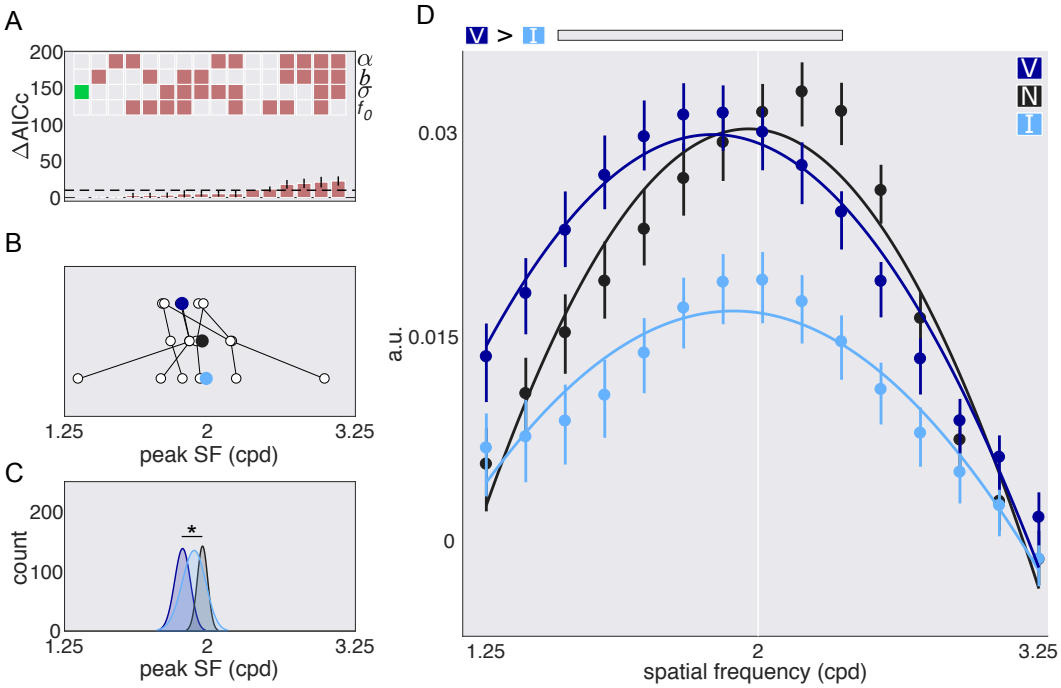

Figure 5: *Spatial frequency tuning functions with central cues, Experiment 1: Endogenous attention.* (A) model comparison results: gain α, width σ, baseline b, and peak f_0; empty squares = not shared; filled in squares = shared; green square = chosen model. Dashed line = cutoff (10). (B) Parameter estimates for the peak of the fit to the *individual* data of the chosen model. (C) Parameter estimates for the peak of the fit to the *bootstrapped* data of the chosen model. (D) Best fit tuning functions (using the chosen model) to the group averaged data. Gray horizontal bars = significance; the units are arbitrary (a.u.). Error bars are 68% C.I. * $p < 0.05$.

Experiment 2 — Exogenous Attention

Methods

Observers, Stimuli and Procedure

The same six observers that participated in the endogenous attention task, Experiment 1, also participated in the exogenous attention task, Experiment 2, and completed the same total amount of sessions (15) and trials (15,120 trials). The task was very similar to experiment 1 with slight differences to to facilitate the effects of exogenous attention on performance. The attentional cues changed from central to peripheral (**Figure 1**) and the duration of the cue and ISI was decreased to 40ms each (**Figure 1)**. Cue validity was equated across valid, invalid and neutral trials (33% for each condition), making the cues uninformative. The stimuli remained the same.

Results

Exogenous attention also improved performance (**Figure 6**). Peripheral cues enhanced detection sensitivity at the target location (F(2,10)=17.06, p < 0.001, η_G^2 = 0.216); sensitivity was higher for the valid than the neutral cue (t(5)=4.159, p < 0.001, d= 0.649), which in turn was higher than invalid cues (t(5)=3.8, p < 0.012, d = 0.533). The type of cue also modulated reaction time (F(2,10)=7.299, p = 0.011, η_G^2 = 0.143). Responses were faster for valid than neutral (t(5)=-2.918, p = 0.033, d= -0.610) and invalid (t(5)=-2.707, p = 0.042, d= -0.875), and marginally faster for neutral than invalid cues(t(5)=-2.175, p = 0.082). There were no speed-accuracy tradeoffs. Decision criteria did not differ across attention conditions (F(2,10)<1; $B[4.55:1]$; $pBIC(H_1|D) = 0.179$; $pBIC(H_0|D) = 0.821$). In sum, sensitivity was improved at the attended location and impaired at the unattended location.

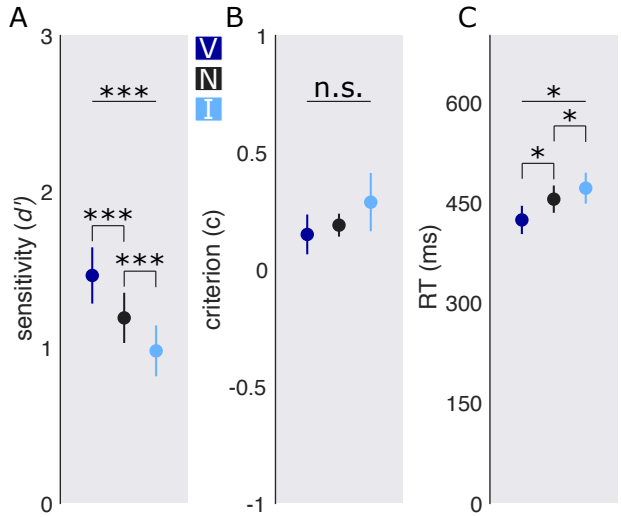

Figure 6. *Performance, Experiment 2: Exogenous attention.* (A) *Detection sensitivity indexed by d' with peripheral cues.* (B) *criterion*. (C) *Reaction time (RT) in milliseconds*. All dots represent the group average. Error bars are ± 1 SEM. * p < 0.05; *** p < 0.001.

When examining the 2D sensitivity kernels, much like in Experiment 1, the highest weights also corresponded to the components representing the orientation and spatial frequency of the target and there was a high level of separability between both feature dimensions (mean: 0.81±0.05).

To facilitate comparisons with endogenous attention we fit the orientation data with only a common width (σ) parameter (*2nd best model:* $\Delta AICc = 2$; **Figure 7A**). The difference between the two best models was negligible as the level of support for $\Delta AICc$ differences of 0-2 is the same (Burnham & Anderson 2002). The valid peripheral cue enhanced the gain (α) across all orientations more so than the neutral, $p < 0.001$, or invalid cue, $p < 0.001$ (**Figure 7B-D**). Exogenous attention altered orientation representations by boosting the gain without changing tuning width.

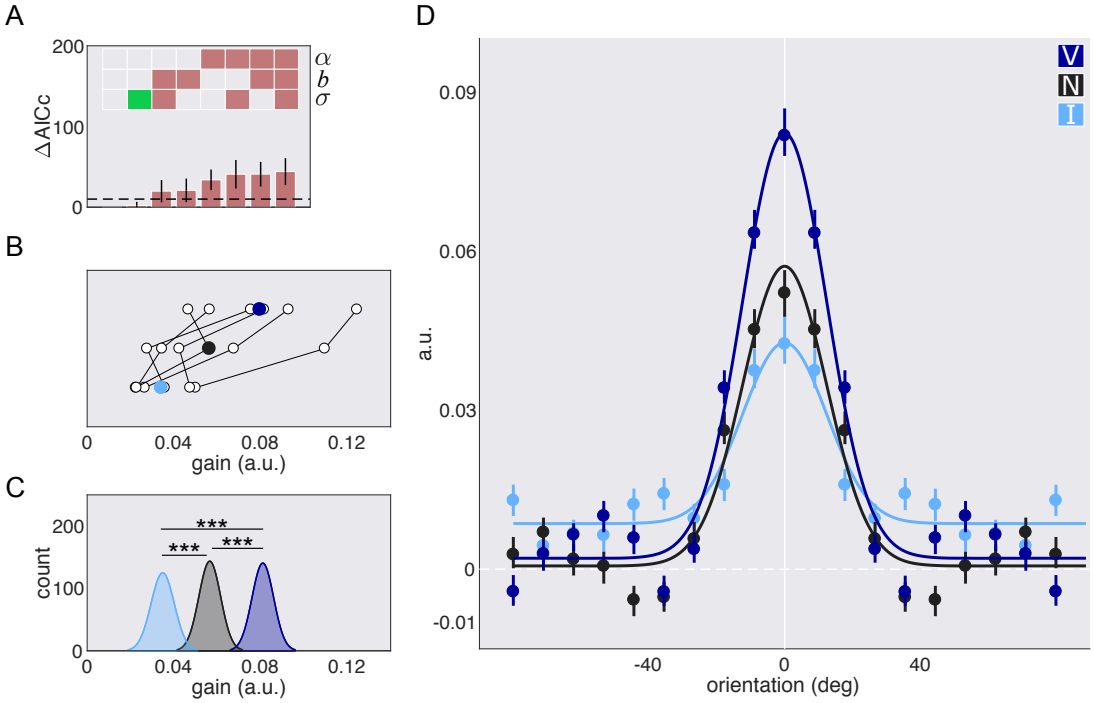

Figure 7: *Orientation tuning functions with peripheral cues, Experiment 2: Exogenous attention.* (A) model comparison results: gain α, width σ, and baseline b; empty squares = not shared; filled in squares = shared; green square = chosen model. Dashed line = cutoff for significance. (B) Parameter estimates for the gain of the fit to the *individual* data of the chosen model. (C) Parameter estimates for the gain of the fit to the *bootstrapped* data of the chosen model. (D) Best fit tuning functions (using the chosen model) to the group averaged data; the units are arbitrary (a.u). Error bars are 68% C.I. *** $p < 0.001$.

In the spatial frequency domain, the best fit model also contained only a shared parameter for the width (**Figure 8A**). The valid cue shifted peak sensitivity (f_0) to higher spatial frequencies when compared to the neutral (p = 0.011) and invalid cues (p = 0.003). Additionally, the valid function had greater amplitude than the neutral (p=0.003)

and invalid functions (*p*=0.04). Further examination of the bootstrapped marginals revealed that this difference was driven by spatial frequencies above the target spatial frequency (valid vs neutral: 2.16-2.84 cpd; valid vs invalid: 2.31-2.64 cpd; **Figure 8B-D**). No differences in the amplitude of the valid, neutral, and invalid functions for spatial frequencies below the target spatial frequency survived corrections for multiple comparisons. Exogenous attention preferentially enhanced sensitivity to spatial frequencies higher than the target spatial frequency.

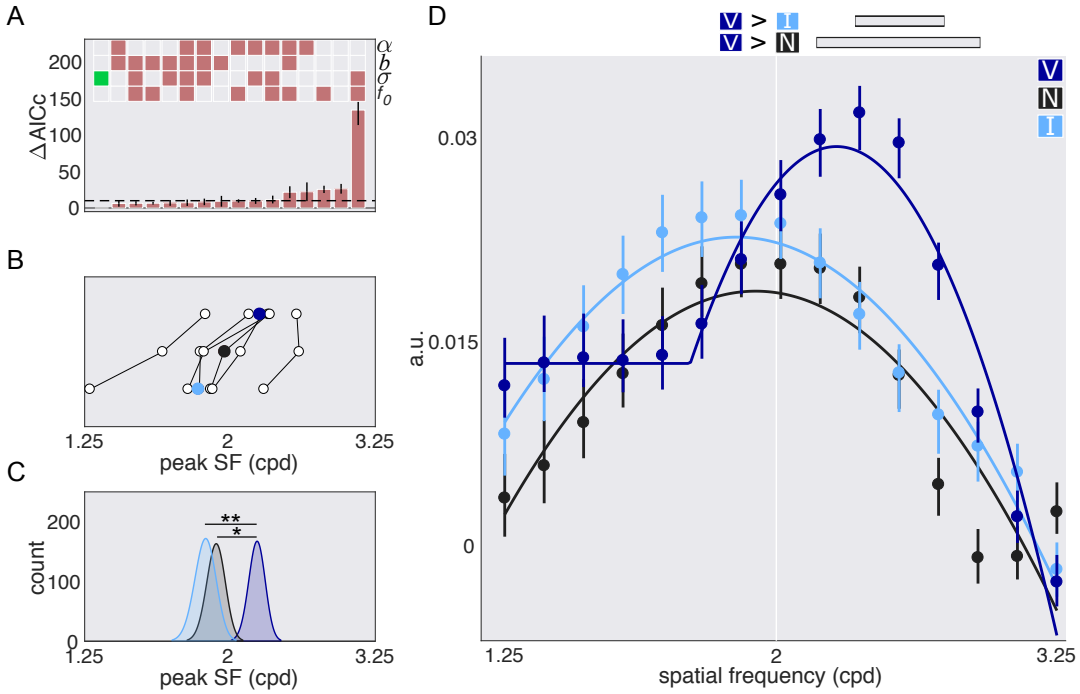

Figure 8: *Spatial frequency tuning functions with peripheral cues, Experiment 2: Exogenous attention.* (A) model comparison results: gain α, width σ, baseline b, and peak f_0; empty squares = not shared; filled in squares = shared; green square = chosen model. Dashed line = cutoff (10). (B) Parameter estimates for the peak of the fit to the *individual* data of the chosen model. (C) Parameter estimates for the peak of the fit to the *bootstrapped* data of the chosen model. (D) Best fit tuning functions (using the chosen model) to the group averaged data. Gray horizontal bars = significance; the units are arbitrary (a.u.). Error bars are 68% C.I. * *p* < 0.05; ** p < 0.01

Comparisons—endogenous vs. exogenous attention

Effects on detection sensitivity

To ensure that differences between endogenous and exogenous attention in sensory tuning are not driven by changes in detection sensitivity; we assessed whether both endogenous and exogenous attention affected task performance in a similar fashion. Both types of covert attention similarly affected detection sensitivity (d'; F(1,5)<1; $B[3.94:1]; pBIC(H_1|D) = 0.202; pBIC(H_0|D) = 0.798$) and the effect of the cues did not

depend on the type of attention being deployed (F(2,10)=2.77; p=0.109; $B[1.58:1]$; $pBIC(H_1|D) = 0.387; pBIC(H_0|D) = 0.613$).

Sensory tuning

To compare whether and how endogenous and exogenous attention differentially alter sensory representations we examined the difference in attentional effects indexed by valid minus invalid parameter estimates (**Figure 9**). In the orientation dimension, the gain enhancement provided by exogenous was greater than endogenous attention (p<0.001; **Figure 9A,** data fall above the reference line). In the spatial frequency dimension, exogenous attention shifted peak sensitivity to higher spatial frequencies than endogenous attention (p<0.001; **Figure 9B,** data fall below the reference line), and this shift was accompanied by a greater amplitude enhancement for endogenous than exogenous attention (p<0.001; **Figure 9C,** data fall above the reference line).

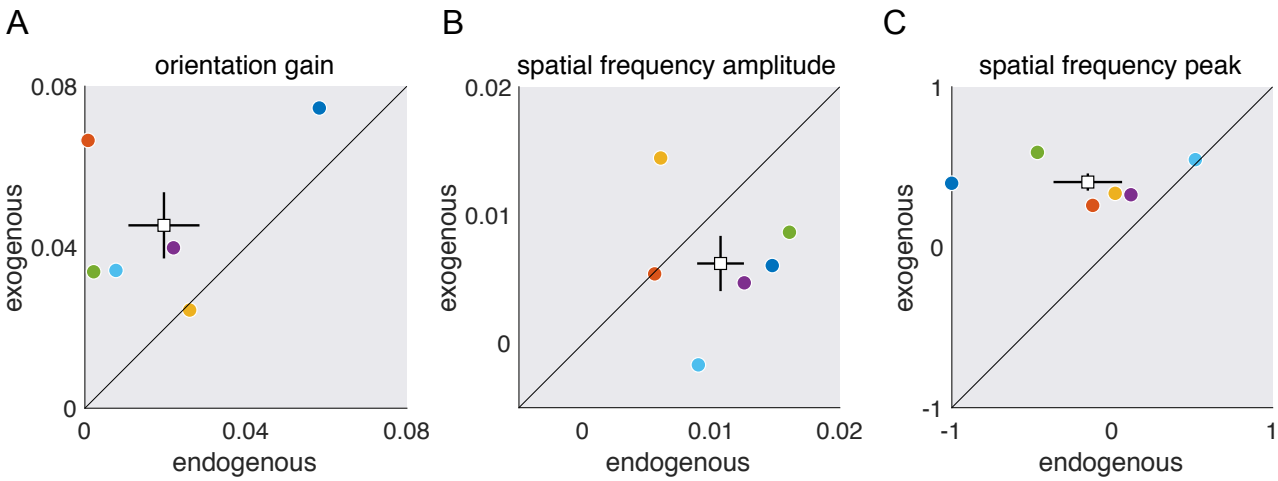

Figure 9: *Comparison of attentional effects (valid-invalid).* Scatter plots of attentional effects for endogenous vs exogenous attention computed from fits to the individual data for parameter estimates for the (A) orientation gain, (B) spatial frequency amplitude, and (C) spatial frequency peak. The colored circles represent individual subjects. The white squares represent the group means. Error bars are ±1 SEM.

Discussion

Here, for the first time, we have assessed and compared the effects of endogenous and exogenous attention on orientation and spatial frequency tuning, with the same observers, task and stimuli. Both endogenous and exogenous attention yielded benefits in detection sensitivity at the attended location and costs at unattended locations. The magnitude of these behavioral effects were similar between both endogenous and exogenous attention, ruling out performance differences as a possible explanation for the differences found in sensory tuning. Reaction times were fastest for valid cues and slowest for invalid cues in both experiments, ruling out speed-accuracy trade-offs.

Moreover, there were no differences in decision criterion amongst the valid, neutral, and invalid cues for either type of attention.

Orientation tuning

Tuning functions were derived using reverse correlation. In the endogenous attention manipulation, the winning model fit to the orientation data had a shared parameter for the width of the valid, neutral, and invalid functions. This suggests that endogenous attention does not alter tuning width. Indeed we found only gain changes, and this is consistent with previous studies (Wyart et al., 2012; Barbot et al., 2014; Paltoglou & Neri 2012). The same model was fit to the orientation data when exogenous attention was manipulated. Exogenous attention also influenced orientation tuning by boosting the gain across all orientation detectors without changing tuning width; this result is also consistent with previous studies (Baldassi & Verghese, 2005; Fernández et al., 2019).

When comparing attentional effects (indexed by valid minus invalid parameter estimates) between endogenous and exogenous attention, we found that gain enhancements by exogenous attention were greater than those of endogenous attention. We can only speculate why. A possible explanation could be due to the involuntary vs. voluntary nature of the effect; exogenous attention exerts its effects automatically to the same degree regardless of cue validity whereas the effect of endogenous attention increases with cue validity (Giordano, McElree & Carrasco, 2009). Although cue validity for endogenous was high (75%), it is possible that the effects would have been more pronounced had the cue been valid 100% of the time. This finding could also be related to the fact that attentional modulations of neural activity by exogenous attention are approximately constant from early (V1,V2,V3: Müller & Kleinschmidt, 2007; Müller & Ebeling, 2008; Dugué, Merriam, Heeger & Carrasco, 2020) to intermediate (V3A, hV4, LO1: Dugué et al., 2020) visual areas, whereas modulations of neural activity by endogenous attention increase from early to intermediate visual areas (Dugué et al., 2020; MT, VIP: Maunsell & Cook, 2002) and persists in parietal and frontal areas (Kastner et al., 1999). Consistent with the idea that endogenous attention is a top-down modulation from frontal and parietal areas feeding back to visual cortex, with diminishing effects in earlier visual areas (reviews: Chica, Bartolomeo & Lupiáñez, 2013; Beck & Kastner, 2009).The present task is likely to depend on the computations of early visual cortex, which plays a causal role in attentional modulations by exogenous attention (Fernández & Carrasco 2020) but not by endogenous attention (Fernández & Carrasco, in prep). In any case, more research is necessary to assess whether this result is due to a mechanistic effect of attention or to the experimental parameters used.

Spatial frequency tuning

The spatial frequency data for both experiments was fit with the same model—shared parameter for the width. When manipulating endogenous attention, we found that the valid cue enhanced the amplitude of spatial frequencies above and below the target spatial frequency when compared to the invalid cue without changing peak sensitivity.

This is consistent with previous reports of endogenous attention excluding external noise without changing spatial frequency tuning (Lu & Dosher, 2004). However, endogenous attention shifted peak sensitivity to lower spatial frequencies than the neutral curve. This shift may have had no effect on task performance as the amplitude of the neutral and valid functions did not differ. Another possibility is that low spatial frequencies in the noise were suppressed or masked by the target spatial frequency (Meese & Hess, 2004). Had this been the case, endogenous attention could have flexibly shifted sensitivity to lower spatial frequencies to counteract any effect of masking.

When manipulating exogenous attention, we found shifts in peak sensitivity to spatial frequencies greater than that of the peak frequency for the neutral and invalid functions. This shift was accompanied by a preferential gain enhancement at spatial frequencies above the target spatial frequency. When assessing the difference in attentional effects between endogenous and exogenous attention, we found that exogenous attention shifted peak sensitivity to higher frequencies than endogenous attention. Perhaps as a consequence of this shift, the differences in gain between valid and invalid cues was greater for endogenous than exogenous attention.

Previous psychophysical studies using both reverse correlation and critical-band-masking have found no change in spatial frequency tuning with exogenous attention (Talgar et al., 2004; Fernández et al., 2019). Here, we capitalized on our previous work with exogenous attention as well as recent psychophysical results to improve our task design. We hypothesize that the biggest contributors for the observed shift in peak sensitivity to high spatial frequencies with exogenous attention was: (1) bringing the stimuli closer to the fovea and (2) increasing the target spatial frequency. In our previous study (Fernández et al., 2019), the stimuli were placed at 10 deg of eccentricity, and the target spatial frequency was 1.5 cpd, which is outside the optimal range of cueing benefits with exogenous attention (Jigo & Carrasco, 2020). By decreasing the eccentricity and increasing the target spatial frequency, we brought the stimulus parameters within the optimal range for exogenous attention, and could observe shifts in sensory tuning induced by involuntary attention.

A recent study has revealed differential effects of exogenous and endogenous attention on contrast sensitivity (indexed by d'; Jigo & Carrasco, 2020). Exogenous attention preferentially enhances spatial frequencies higher than the intrinsic peak frequency in a neutral baseline condition, whereas endogenous attention provides similar benefits at a broad range of spatial frequencies above and below the peak at baseline. Conventional signal detection theory is agnostic as to the underlying computational mechanism. Here, using reverse correlation, we show the computation (gain changes) that may underlie the differential effects of endogenous and exogenous attention and compare differences in gain modulation between both types of attention. These differential gain effects on spatial frequency tuning are necessary to successfully model the effects of endogenous and exogenous attention on contrast sensitivity, spatial resolution and texture segmentation (Jigo, Heeger & Carrasco, 2021).

Given that observers were always looking for a vertical grating, is it possible that the measured tuning functions were influenced by feature based attention (FBA)—attention to a stimulus feature (e.g. orientation or spatial frequency) regardless of spatial location? Although FBA can modulate sensory responses (e.g., Maunsell & Treue, 2006; Yoo, Martinez-Trujillo, Treue, Tsotsos & Fallah, 2021), this possibility is highly unlikely for the following reasons: (1) Endogenous FBA spreads across locations (Serences & Boynton 2007; White, Rolfs & Carrasco 2015), even for irrelevant tasks (White & Carrasco, 2011), thus, it would have had the same effects at spatial valid and invalid locations; (2) Endogenous FBA affects sensory responses by both boosting the gain and decreasing the width of the function (Barbot et al., 2014; Ling, Liu & Carrasco 2009; Fang & Liu, 2019), had FBA influenced responses a change in tuning width would have been observed; (3) Empirical evidence for exogenous FBA is still under debate (Lin, Hubert-Wallander, Murray & Boynton, 2011; Qian & Liu, 2015; Donovan, Zhou & Carrasco, 2019) and elusive at best (Donovan et al., 2019).

What is the functional significance of the observed differences in spatial frequency tuning between endogenous and exogenous attention? For circumstances in which increasing resolution is not beneficial (e.g. when driving through a foggy road) the flexible, voluntarily controlled endogenous attention would be necessary. In fight or flight situations, an exogenous attentional system that is quick, reactive, and inflexibly increases resolution would be beneficial. Mice exhibit primate-like behavioral signatures of both endogenous and exogenous attention (You & Mysore, 2020) despite having poorer contrast sensitivity (Histed, Carvalho & Maunsell, 2012), and lacking a fovea. Additionally, mice show increased gain in neurons tuned for high spatial frequencies while under a state of heightened attention, thereby increasing their spatial acuity (Mineault et al., 2016). This evidence suggests that despite pronounced differences in the visual system of mice and primates, a similar mechanism (e.g. attention) may underly the tuning properties of mammals, perhaps because it is phylogenetically beneficial. Therefore, how attention reshapes the tuning of basic visual dimensions is of critical importance.

In summary, this study has uncovered the differential effects of endogenous and exogenous attention on sensory tuning. Both types of covert attention modulate orientation at the attended location by boosting the gain of all orientation channels without changing tuning width. This boost was greater with exogenous than endogenous attention. In the spatial frequency domain, endogenous attention enhanced the gain of spatial frequencies above and below the target spatial frequency whereas exogenous attention only enhanced those above. We propose these changes in sensory tuning may underlie the differential effects of endogenous and exogenous attention on performance in texture segmentation, contrast sensitivity, and temporal resolution tasks.

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