

On spatial attention and its field size on the repulsion effect

Elizabeth K. Cutrone

Department of Psychology, New York University,
New York, NY, USA

David J. Heeger

Department of Psychology,
New York University, New York, NY, USA
Center for Neural Science, New York University,
New York, NY, USA

Marisa Carrasco

Department of Psychology, New York University,
New York, NY, USA
Center for Neural Science, New York University,
New York, NY, USA



We investigated the attentional repulsion effect—stimuli appear displaced further away from attended locations—in three experiments: one with exogenous (involuntary) attention, and two with endogenous (voluntary) attention with different attention-field sizes. It has been proposed that differences in attention-field size can account for qualitative differences in neural responses elicited by attended stimuli. We used psychophysical comparative judgments and manipulated either exogenous attention via peripheral cues or endogenous attention via central cues and a demanding rapid serial visual presentation task. We manipulated the attention field size of endogenous attention by presenting streams of letters at two specific locations or at two of many possible locations during each block. We found a robust attentional repulsion effect in all three experiments: with endogenous and exogenous attention and with both attention-field sizes. These findings advance our understanding of the influence of spatial attention on the perception of visual space and help relate this repulsion effect to possible neurophysiological correlates.

covert attention also modulates the activity, size, and location of receptive fields (for reviews, see Anton-Erxleben & Carrasco, 2013; Reynolds & Chelazzi, 2004; Reynolds & Heeger, 2009).

In addition to affecting performance in many visual perception tasks, covert attention also affects spatial aspects of stimulus appearance. For example, perceived contrast (e.g., Barbot & Carrasco, 2018; Carrasco, Ling, & Read 2004; Cutrone, Heeger, & Carrasco, 2014; Liu, Abrams, & Carrasco, 2009; Störmer, McDonald, & Hillyard, 2009) and spatial frequency and gap size (Abrams, Barbot, & Carrasco, 2010; Gobell & Carrasco, 2005) as well as objects' perceived size (Anton-Erxleben, Henrich, & Treue, 2007) and shape (Fortenbaugh, Prinzmetal, & Robertson, 2011).

The spatial effects of attention are not constrained to spatial patterns of the stimulus; attention also alters perceptual organization (Barbot, Liu, Kimchi, & Carrasco, 2017) and warps the fabric of our perception of visual space (Liverence & Scholl, 2011), making stimuli appear displaced farther away from attended locations. This is known as the attentional repulsion effect (DiGiacomo & Pratt, 2012; Kosovicheva, Fortenbaugh, & Robertson, 2010; Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997). It has been shown that this effect is not due to figural aftereffects or apparent motion (Suzuki & Cavanagh, 1997). This repulsion effect has been measured and characterized using the double-cue protocol (e.g., DiGiacomo & Pratt, 2012; Gozli & Pratt, 2012; Kosovicheva et al., 2010; Pratt & Arnott, 2008; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997) in conjunction with two-alternative forced-choice protocols (DiGiacomo & Pratt, 2012; Kosovicheva et

Introduction

Covert attention, the ability to selectively and preferentially process information at a given location in the absence of accompanying gaze movements, affects spatial aspects of visual perception, e.g., spatial resolution and contrast sensitivity (for reviews, see Carrasco, 2011; Carrasco, 2014; Carrasco & Barbot, 2014; Carrasco & Yeshurun, 2009). Neurophysiological studies with nonhuman primates have shown that

Citation: Cutrone, E. K., Heeger, D. J., & Carrasco, M. (2018). On spatial attention and its field size on the repulsion effect. *Journal of Vision*, 18(6):8, 1–15, <https://doi.org/10.1167/18.6.8>.

<https://doi.org/10.1167/18.6.8>

Received November 7, 2017; published June 21, 2018

ISSN 1534-7362 Copyright 2018 The Authors



al., 2010; Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997) and by collecting reports of stimulus locations using mouse clicks or physical pointing (Pratt & Turk-Browne, 2003). All these protocols have shown consistent findings.

Neurophysiological studies have revealed that attention affects the size and shape of neural receptive fields, which underlie the representation of visual space in the brain (e.g., Anton-Erxleben, Stephan, & Treue, 2009; Moran & Desimone, 1985; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Receptive field (RF) shifts concentrate processing resources at the focus of attention and lead to an enhanced representation of the attended stimulus. Thus, RF shifts can explain improved performance in various psychophysical tasks, such as acuity and hyperacuity (e.g., Carrasco, Williams, & Yeshurun, 2002; Golla, Ignashchenkova, Haarmeier, & Thier, 2004; Yeshurun & Carrasco, 1999), visual search (e.g., Cameron, Tai, Eckstein, & Carrasco, 2004; Carrasco & Yeshurun, 1998; Giordano, McElree, & Carrasco, 2009), and texture segmentation (e.g., Carrasco, Loula, & Ho, 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998). RF shifts can also distort perception of space. Many authors have suggested that these warped receptive fields are the cause of the attentional repulsion effect (DiGiacomo & Pratt, 2012; Kosovicheva et al., 2010; Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997) although the nature of that link is still undetermined.

Suzuki and Cavanagh (1997) proposed three possible mechanisms: (a) surround suppression, with which the cell activity surrounding the focus of attention could be suppressed by lateral inhibition, resulting in greater spatial selectivity at the attended location due to inhibition of interference from neighboring cells; (b) RF shrinking, with which RF position tunings shrink around the attention focus, thus decreasing response to stimuli surrounding the focus of attention and skewing the population response away from the attended location; and (c) RF recruitment, whereby RF's near the attended location shift toward it, thus decreasing response to stimuli in the area bordering the focus of attention.

The visual system can extract position information from the activity of spatially selective RFs in retinotopic maps (Eurich & Schwegler, 1997). Using a labeled-line code, the visual system could construct a map of objects in the visual field by evaluating the relative response strength of different neurons that represent different spatial locations. The shift of RFs toward the focus of attention changes the location at which a stimulus elicits the strongest response from a given neuron. When attention is directed to a location nearby the stimulus, RFs originally centered beyond

the stimulus shift toward the attentional focus so that they are activated by the stimulus. But, because the RFs still code for their original position, the perceived position of the stimulus is repulsed away from the attentional focus (Anton-Erxleben & Carrasco, 2013).

The attentional repulsion effect has been well characterized with regard to exogenous (involuntary) attention (e.g., DiGiacomo & Pratt, 2012; Gozli & Pratt, 2012; Kosovicheva et al., 2010; Pratt & Arnott, 2008; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997), but only one study has explored the effects of endogenous (voluntary) attention on the repulsion effect (Suzuki & Cavanagh, 1997, experiment 4). This situation leaves a disconnect between behavioral and physiological experiments, which have measured receptive fields under endogenous attention conditions (e.g., Anton-Erxleben et al., 2009; Womelsdorf et al., 2006). Whereas endogenous attention and exogenous attention often cause similar perceptual changes (e.g., Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Montagna, Pestilli, & Carrasco, 2009), there are some pronounced differences on their perceptual consequences, and particularly relevant for the present study are those regarding their effects on spatial resolution. Endogenous attention always improves performance by flexibly adjusting spatial resolution (Barbot & Carrasco, 2017; Yeshurun, Montagna, & Carrasco, 2008) whereas exogenous attention always increases resolution even when detrimental for the task at hand (Carrasco et al., 2006; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2000; Yeshurun & Carrasco, 2008). Moreover, their temporal dynamics differ; exogenous attention peaks at about 100–120 ms whereas endogenous attention becomes effective at about 300 ms and can be sustained for many seconds (Carrasco et al., 2004; Ling & Carrasco, 2006; Liu, Stevens, & Carrasco, 2007; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989). Furthermore, the effect of endogenous attention scales with cue validity (Giordano et al., 2009; Kinchla, 1980; Sperling & Melchner, 1978), and that of exogenous attention does not vary with cue validity (Giordano et al., 2009). Last, neuroimaging studies have revealed that these two types of attention recruit partially overlapping sets of neural resources (e.g., Beck & Kastner, 2009; Chica, Bartolomeo, & Lupiáñez, 2013; Corbetta & Shulman, 2002; Dugué, Merriam, Heeger, & Carrasco, 2017; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). Given these differences, it is important to characterize the repulsion effect in terms of both exogenous and endogenous attention.

Another potentially important dimension to link the repulsion effect to possible neurophysiological correlates is the size of the attention field, the region of space over which observers spread their attention. The

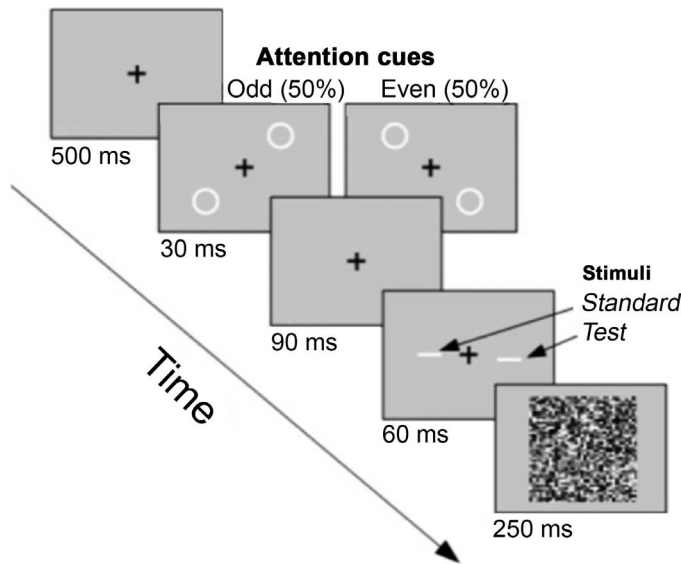


Figure 1. Trial sequence, exogenous attention. The two exogenous cue types are named according to the relation between the test location and its associated attention cue: odd (upper right and lower left) or even (upper left and lower right).

normalization model of attention (Reynolds & Heeger, 2009) posits that differences in attention-field size can account for qualitative differences in neural responses elicited by attended stimuli. Psychophysical studies have confirmed some of these predictions for covert spatial attention by manipulating the attention-field size via spatial uncertainty of stimulus locations (Herrmann et al., 2010) and for feature-based attention by manipulating the uncertainty range of the relevant features (Herrmann, Heeger, & Carrasco, 2012). Indeed, a recent study has confirmed that spatial uncertainty of the target location is an effective manipulation of attention-field size (Huang, Xue, Wang, & Chen, 2016).

The effects of covert spatial attention depend on the relation of the attention-field size and the stimulus size. When the attention field is large relative to the stimulus, changes arise in contrast gain (horizontal shift of the psychometric function), and when it is small, changes arise in response gain (vertical shift of the upper asymptote; Herrmann et al., 2010; Reynolds & Heeger, 2009). It is often presumed that exogenous cues induce smaller attention fields than endogenous attention; in the former, the cues are adjacent to the stimuli and spatial uncertainty is lower whereas, in the latter, the cues are distant from the stimuli and spatial uncertainty is higher (Herrmann et al., 2010). So we might expect that the size of the spatial attention field would differentially affect spatial receptive fields. Were this the case, models for the attention repulsion effect could be constrained.

Here we investigate the attentional repulsion effect in three experiments: one with exogenous attention and

two with endogenous attention in which we manipulate, for the first time, the attention-field size. We used a comparative judgment as it has been shown to be an effective method to evaluate the effects of subjective appearance (Anton-Erxleben, Abrams, & Carrasco, 2010; Anton-Erxleben et al., 2011).

Methods

Observers

Six observers (four females; average age: 27 years old) each participated in two 1-hr psychophysical sessions. All were experienced psychophysical observers, and all but one (a coauthor) were naïve to the purpose of the experiment. None of the naïve participants had any prior expectation of the differences between the different attention types or attention-field sizes. All observers had normal or corrected-to-normal vision and all provided informed consent. The University Committee on Activities Involving Human Subjects at New York University approved the experimental procedures.

Apparatus and stimuli

Observers sat in a silent and dimly lit room with their head positioned on a chin rest. Stimuli were generated and presented using MATLAB (MathWorks) and the MGL toolbox (<http://gru.standord.edu/doku.php/mgl/overview>) on a Macintosh computer. They were displayed on a gamma-corrected CRT monitor (resolution: $1,152 \times 870$ pixels; refresh rate: 75 Hz) with a background luminance of 25 cd/m^2 , positioned 57 cm from the observers. An EyeLink 1000 Desktop Mount (SR Research, Ottawa, Canada) monitored and recorded observers' gaze position.

The stimuli were two bright horizontal line segments (43 cd/m^2 , $1.3^\circ \times 0.04^\circ$) presented on a dark background (25 cd/m^2) at 4.9° of eccentricity to the left and right of fixation (Figure 1). On each trial, one line was centered on the horizontal meridian, and the other was displaced slightly above or below the meridian. A central black fixation cross ($0.5^\circ \times 0.5^\circ$) remained on the screen throughout the experiment.

Attention manipulations

There were two different types of attention manipulations: exogenous and endogenous cues. In both exogenous and endogenous conditions, the main task was a vernier line judgment on the two horizontal line

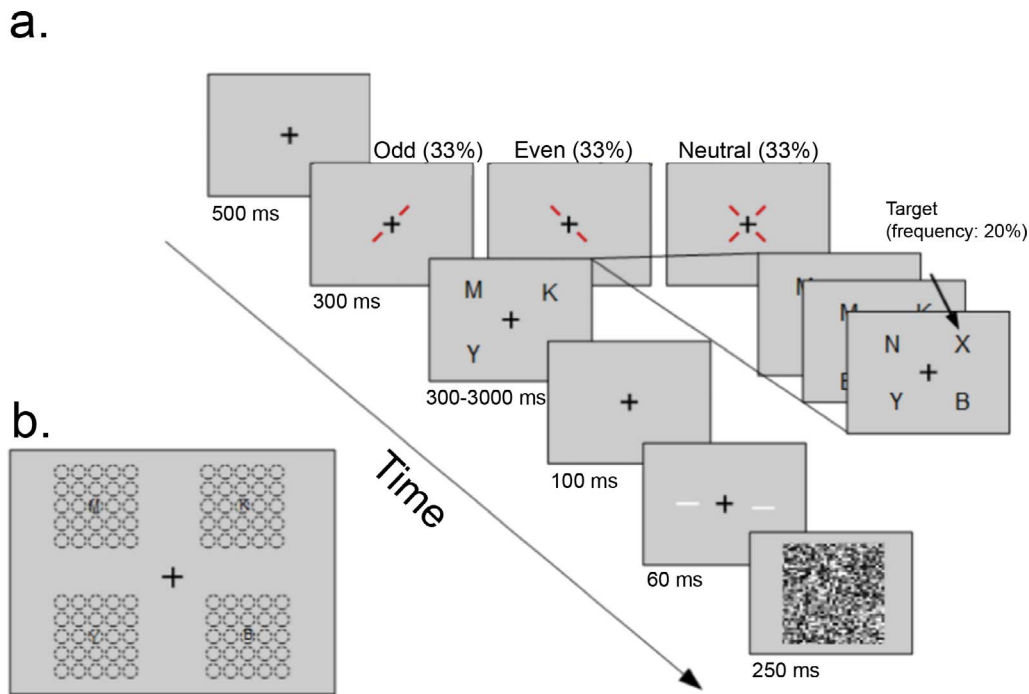


Figure 2. Trial sequence, endogenous attention. (a) Trial sequence. The two central cue types are named according to the relation between the test location and its associated attention cue: odd (upper right and lower left) or even (upper left and lower right). In the neutral condition, all four streams of letters are cued. (b) Attention-field manipulation. Letters indicate RSVP locations for small attention field; dotted circles show possible locations for large attention field. Dotted circles were not displayed to observers. In each quadrant, only one letter was present in one location in each frame; locations were randomly shuffled. Note that letter size is not to scale; it was the same in conditions with both small and large attention fields.

stimuli: observers indicated the direction of the misalignment, whether the left line or the right line appeared higher (e.g., Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997). As in most studies of the repulsion effect, we used the double cueing protocol with one cue being relevant for each of the horizontal lines (e.g., DiGiacomo & Pratt, 2012; Gozli & Pratt, 2012; Kosovicheva et al., 2010; Pratt & Arnott, 2008; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997). Two cues have also been successfully used to investigate other perceptual consequences of endogenous and exogenous attention (e.g., Bay & Wyble, 2014; Montagna et al., 2009; Szpiro & Carrasco, 2015). To maximize the respective effects of both cues on this comparative judgment, as in previous studies (e.g., Barbot, Landy, & Carrasco, 2012; Dugué, Merriam et al., 2017, Herrmann et al., 2010; Montagna et al., 2009; Yeshurun et al., 2008), the cue-to-stimulus interval was shorter for exogenous than endogenous attention, and the endogenous cue was 100% valid as its effects scale with cue validity (e.g., Giordano et al., 2009; Kinchla, 1980; Sperling & Melchner, 1978).

On each exogenous trial, only two cues were presented, either in the upper-left and lower-right quadrants (even cues) or the lower-left and upper-right (odd cues; Figure 1). These cues were referred to as “odd” or “even” because they were presented in the

first and third or second and fourth quadrants of the screen, respectively. Exogenous cues were circles, subtending $1.3^\circ \times 1.3^\circ$, outlined in gray (43 cd/m^2 ; Figure 1). Exogenous cues were centered on locations $\pm 4.9^\circ$ horizontal and $\pm 4.9^\circ$ vertical from fixation— 4.9° directly above or below the stimulus locations.

On each endogenous trial, observers saw four rapid serial visual presentations (RSVP), streams of a subset of capital letters; each stream appeared in a different quadrant, centered on locations $\pm 4.9^\circ$ horizontal and $\pm 4.9^\circ$ vertical from fixation— 4.9° directly above or below the vernier stimulus locations—streams of a subset of capital letters; each stream appeared in a different quadrant (Figure 2). The letters had the same luminance as the exogenous cues and subtended about $0.8^\circ \times 0.7^\circ$. Endogenous attention cues were small red lines ($0.5^\circ \times 0.04^\circ$) presented just adjacent to the fixation cross and pointing at either two (for focused-attention trials) or four (neutral trials) of the RSVP locations. This task yields behavioral benefits at the location of the attended RSVP stream (Abrams et al., 2010; Barbot et al., 2017; Liu et al., 2009). All four RSVP streams were presented on every trial; focused-attention trials and neutral trials occurred with equal frequency. As with exogenous cues, we refer to trials with lower-left/upper-right cues as odd trials and trials with upper-left/lower-right cues as even trials.

There were two versions of the endogenous experiment: small attention field and large attention field. In both conditions, the task was the same, and the letters subtended $0.8^\circ \times 0.7^\circ$. On trials with small attention fields, each successive letter was presented in the same location. On trials with large attention fields, each letter was assigned to one location on a five-by-five grid (Barbot et al., 2017) with the locations randomly shuffled within each of the four RSVP streams (Figure 2b). Each grid was centered on the same location as the corresponding letters on the small attention field and subtended a total of $4^\circ \times 4^\circ$ (such that none of the letter positions would overlap with each other or with the vernier stimuli).

Because the RSVP streams lasted up to 3 s, eye tracking was used to monitor observers' fixation during all trials; trials did not begin until the observer had fixated for 500 ms, and if the observer broke fixation (if the eyes deviated by $\geq 2^\circ$ from the fixation point) during the presentation of the attention cues or RSVP stream, the trial was skipped. This ensured that observers did not move their eyes toward any of the attention locations or toward the stimuli. Because parameters were selected pseudo-randomly on each trial, trials skipped due to fixation breaks did not affect the proportion of trials in each condition. One observer was removed from the analysis due to a high rate of fixation breaks ($>30\%$ overall; no difference between attention-field conditions).

Task

In both exogenous and endogenous conditions, the main task was a two-alternative forced-choice task, vernier line judgment on the horizontal line stimuli. Observers used a key press to indicate the direction of the misalignment, i.e., whether the left line appeared higher on the screen than the right line or vice versa. On each trial, one of the stimuli, which we refer to as the *standard*, was displayed on the horizontal meridian; the vertical position of the other line, which we refer to as the *test* stimulus, varied from trial to trial based on four interleaved one-up, one-down staircases (60 trials per staircase with two high and two low starting points and one step size). The location of the standard and test stimuli were to the left and right of fixation, respectively, on half the trials and vice versa in the other half. Stimulus location was randomly interleaved within blocks. In the exogenous task, observers were explicitly told that the attention cues provided no task-relevant information.

On endogenous blocks, observers were instructed to detect the target letter, "X," in the RSVP stream. This target letter was equally likely to appear in one of the two or four locations for the attention and neutral cues, respectively, and its probability of occurrence was

equally likely during the RSVP interval, which lasted 300–3,000 ms so that observers had to deploy their attention continuously to the cued locations. Observers used the space bar to indicate that the target letter was present, and when they did not see the target letter, they used the same left and right keys from the exogenous experiment to report their judgment of the vernier stimuli. We did not ask observers to perform the vernier task on trials in which they reported the "X" was present because it was likely that they would stop attending upon detection of the target letter.

Observers were explicitly told that the target letter was present on 20% of all trials and that the attention cues were 100% valid; i.e., if the target letter was present, it was always in one of the two cued locations. Auditory feedback was given based on the RSVP detection task. Feedback was not provided for the vernier task as in previous tasks of interest for appearance studies (e.g., Abrams et al., 2010; Anton-Erxleben et al., 2007; Barbot et al., 2017; Carrasco et al., 2004; Liu et al., 2009) to prevent biasing subjective appearance judgments.

Procedure

Each session began with one block of 180 exogenous trials. This was followed by an endogenous experiment with either the small or large attention field; attention-field size was blocked by session and counterbalanced across observers. Even though the timing of exogenous attention is too short for endogenous attention to be deployed (e.g., Liu et al., 2007; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989), we decided not to counterbalance the order between exogenous and endogenous attention conditions in order to prevent any possible contamination from the endogenous to the exogenous condition.

Each endogenous experiment began with a practice block of 60 trials, all with neutral cues, during which a psychophysical staircase (one-up, two-down staircase) dynamically adjusted the speed of the RSVP stream to determine the observer's speed threshold. This ensured that each observer's overall accuracy in the RSVP task was about 80%. Observers then completed three 12-minute blocks of 180 endogenous trials, between which the experimenter adjusted the RSVP rate to ensure that accuracy remained at about the desired level. RSVP rate was constant for each observer within blocks (on average, each letter in the RSVP sequence was presented for 100 ms). In an attempt to keep performance constant, if performance was higher than 85% or lower than 75%, the RSVP rate was slightly increased or decreased to make the task harder or easier, respectively.

Each trial began with a 500-ms gaze-contingent fixation screen, during which only the fixation cross

was displayed. From there, the timing of each trial type was chosen specifically to align with the known time course of exogenous or endogenous attention. In the exogenous blocks (Figure 1), the fixation screen was followed by a brief presentation of the attention cues (30 ms), a short interstimulus interval (ISI; 90 ms), and the line stimuli (60 ms), such that the cue-to-target stimulus-onset asynchrony totaled 120 ms, which is when exogenous attention has been shown to peak (Liu, Fuller, & Carrasco, 2006; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989).

In the endogenous blocks (Figure 2), the fixation screen was followed by the red attention cues presented for 300 ms, followed by 300–3,000 ms of RSVP stimuli, a short ISI (100 ms), and then the line stimuli (60 ms). This ensured that the stimuli appeared after at least the 300 ms required for endogenous attention to peak (Ling & Carrasco, 2006; Liu et al., 2007; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989). The randomized length of the RSVP streams provided temporal uncertainty, ensuring that observers attended continuously until either the target letter or the line stimuli appeared. Research on attentional dwell time has shown that it takes about 250 ms to disengage voluntary attention (Horowitz, Wolfe, Alvarez, Cohen, & Kuzmova, 2009; Theeuwes, Godijn, & Pratt, 2004). Therefore, we predicted that, if attention would alter the vernier task, it would do so within a short interval after the RSVP as it does for perceived contrast (Liu et al., 2009), spatial frequency (Abrams et al., 2010), and perceptual organization (Barbot et al., 2017); longer times between the RSVP and the appearance of comparative judgment obliterate the effect (Abrams et al., 2010; Barbot et al., 2017).

For both conditions, each trial ended with a $10^\circ \times 10^\circ$ square mask presented for 250 ms immediately after the stimuli. Following Suzuki and Cavanagh (1997), the mask was composed of one-pixel gray squares, each with luminance drawn from a uniform distribution.

Data analysis and statistics

Attentional repulsion effect

We measured the difference in the perceived location of the test stimulus between the two focused-attention conditions (odd and even). Our measure of perceived location was the point of subjective colinearity (PSC), defined as the position at which observers chose the test stimulus with a frequency of 50%. For each of the eight conditions (exogenous odd and even cues and endogenous large and small attention fields crossed with odd, even, and neutral cues) and for each test location, we computed the proportion of trials in which the observer reported the test stimulus as being higher than the standard (we refer to these as test-choice trials). We fitted modified cumulative-normal functions to these

data for each condition, using maximum-likelihood fitting to optimize the parameter values. The modified cumulative-normal functions utilize guess rate and lapse rate parameters to improve slope and threshold estimations from psychophysical data (Wichmann & Hill, 2001). PSCs were then interpolated from the functions fit to each condition. We took the difference in PSC between the two focused-attention conditions (odd and even cues) as a measure of the attentional repulsion effect for each experiment.

We used bootstrapping to obtain confidence intervals on the PSCs. For each of the eight conditions, a new data set was simulated for each observer by resampling (with replacement). At each test location, the simulated observer's response on a single trial was determined by randomly selecting one from the set of recorded responses. We simulated the same number of trials that were acquired in the experiment, which was different for each location due to the adaptive staircase procedure implemented in the experiment, and calculated the proportion of trials in which the simulated observer chose the test stimulus. We, thus, simulated the entire experiment, refit each psychometric function, and interpolated the PSCs. This was repeated 2,000 times to generate a distribution of PSCs for each condition, from which we defined the 95% confidence intervals.

Attention effects on accuracy

To ensure the efficacy of attention in the endogenous experiments, we compared observers' accuracy in the RSVP task for the focused-attention versus neutral cueing conditions. Observers who attended as directed would have performed better in the focused-attention conditions, in which they had to attend to only two out of four RSVP streams (vs. all four in the neutral conditions).

Endogenous versus exogenous attention

To test whether the type of attention (exogenous vs. endogenous) influenced the magnitude of the mislocalization effect, we used a randomization test for each observer. This statistical test was based on obtaining null distributions for the relevant PSCs. To generate null distributions, we took the data from the relevant experimental conditions (i.e., all the exogenous trials and the equivalent endogenous trials with small attention fields and focused-attention cues) and shuffled the labels for attention type (exogenous or endogenous). We then refit the psychometric functions and interpolated the PSCs. This was repeated 2,000 times, generating a null distribution for each of the PSCs. The true PSCs, determined with the correct attention labels, were then compared with the null distributions. If the endogenous

PSCs fell outside the 95% confidence intervals of the null distributions, it indicated a significant difference between the attention types.

Attention-field size

To test whether attention-field size modulated the attentional repulsion effect, we used a cross-validation analysis on the data from the endogenous conditions for each observer. These data were partitioned into two sets by randomly permuting a list of all trials and dividing it in half. To one half of the data, the training set, we fit the psychometric functions (described above) to each condition, according to two models. One model, the null hypothesis, yoked the PSC parameters for the corresponding conditions with small and large attention fields, such that there were only three model parameters (for the odd, neutral, and even cue conditions). In the alternative model, there were six model parameters, one for each combination of cue type and attention field. To allow for the possibility that the two tasks were not equally difficult, both models included six slope parameters, one for each condition. Because the blocks with small and large attention fields were performed on different days, both models also included separate parameters for lapse rates and guess rates.

We evaluated each model by taking the best-fitting parameters from the training data and using the other half of the data set, the test data, to compute a measure of error associated with the model. Specifically, we used the negative log-likelihood value associated with the model to quantify error. The data were repartitioned, and this procedure was repeated 2,000 times, generating a distribution of error values for each model, ϵ_{null} for the null model and ϵ_{alt} for the alternative model. The difference in model fits was then given by $\epsilon_{\text{null}} - \epsilon_{\text{alt}}$. We computed a p value for determining statistical significance of this difference by taking the proportion of values that were less than zero. A $p < 0.05$ indicated that the alternative model was a better fit, rejecting the null hypothesis that there was no difference in attentional repulsion for large and small attention-field sizes. This cross-validation analysis accounts for differences in the number of free parameters in different models. For each repartitioning of the data, the models with more free parameters will tend to over-fit the first half of the raw data, reflecting noise in that half of the data set and resulting in more error with respect to the second half (Arlot & Celisse, 2010).

Predicted results

If attention repelled apparent stimulus location, the PSCs would be greater than zero for odd-cue condi-

tions and less than zero for even-cue conditions. This is because repulsion in an odd trial from a cue on the upper right would cause the test stimuli at positive y coordinates to appear closer to the horizontal meridian, such that observers would report them, on average, to be collinear with the standard. Conversely, attentional repulsion on an even trial from a cue on the lower right would cause the test stimuli below the horizontal to appear higher. If endogenous attention yielded a different amount of repulsion than exogenous attention, the randomization analysis would show that the PSCs for relevant endogenous conditions fell significantly outside of their respective null distributions generated by the randomization test. If attention field size influenced attentional repulsion, the cross-validation analysis would show that a model with different PSCs for each attention-field size fits the data significantly better than one without that distinction.

Results

Attentional repulsion effect

The PSCs were positive for odd-cue conditions and negative for even-cue conditions in all three experiments ($p < 0.05$ based on bootstrapping tests; Figure 3). In the endogenous attention experiments, for neutral-cue conditions, PSCs were not significantly different from zero (Figure 3, blue bars). This was true for each individual observer (Figure 3b, circles).

Endogenous versus exogenous attention

Endogenous attention resulted in a stronger attentional repulsion effect than exogenous attention (Figure 3b). Although there were individual differences in the extent of the effect of the cues, PSCs for odd-cue trials were significantly greater ($p < 0.0005$ for all observers, randomization test), and PSCs for even-cue trials were significantly lower ($p < 0.0005$ for all observers) with endogenous than exogenous attention. We note that this comparison should be interpreted carefully as we used optimal parameters for the cues to manipulate each attention type, but that does not guarantee that the cues affect performance with equal magnitude.

Attention improved accuracy

In conditions with both small and large attention fields, all but one observer performed the RSVP task (detecting the letter “X”) with higher accuracy in the focused-attention cue than in the neutral cue conditions (Figure 4a), suggesting that observers were using the attention cues as directed. For both attention-field

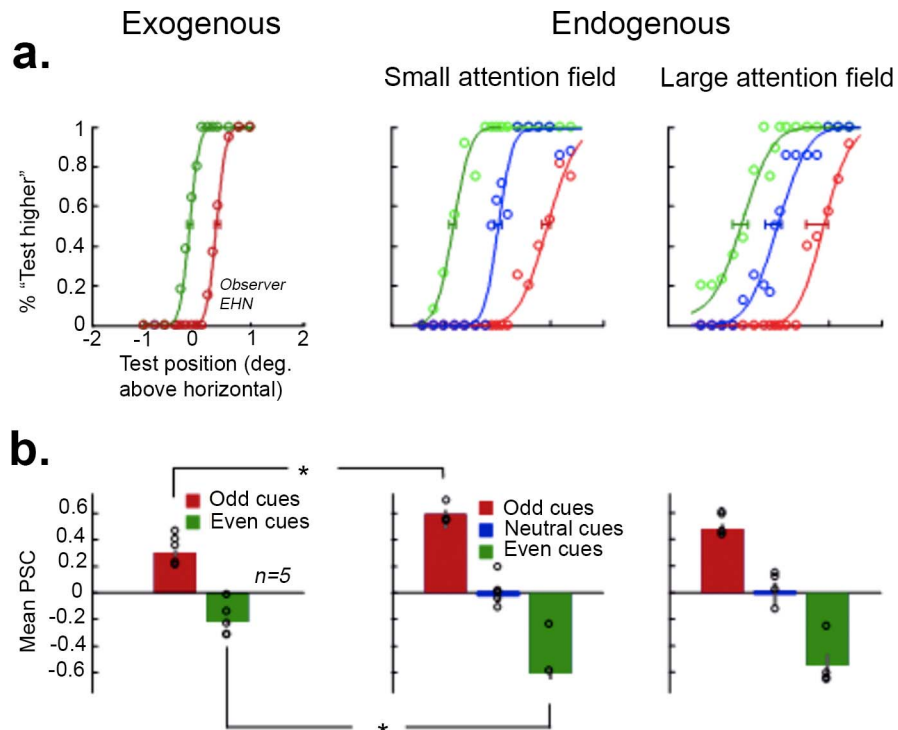


Figure 3. Attentional repulsion effect. (a) Data from a representative observer. Left, exogenous attention. Green, even cue; red, odd cue. Horizontal error bars show PSC 95% confidence intervals. Middle and right panels show endogenous experiments with small and large attention fields, respectively. Blue, neutral cue; red and green as in exogenous plot. (b) Mean PSC across observers. Error bars show 95% confidence intervals (based on bootstrapping, see Statistics); open circles show five individual observers. (Note that many points overlap).

sizes, RSVP accuracy was improved in the focused-attention conditions compared with the neutral condition (Figure 4a; $p < 0.001$, paired-samples t test). Observers also performed this task significantly better with a large than a small attention field (Figure 4a; $p < 0.001$, paired-samples t test). We speculate that this may be due to a reduction in masking and/or adaptation in the condition with the large attention field, in which the positions of the letters in each RSVP stream were shuffled and nonoverlapping.

There was a significant correlation between the effects of attention on accuracy (focused-attention vs. neutral) and appearance (Figure 4b; one-tailed Pearson's $r = 0.575$, $p < 0.05$, $n = 10$). This indicates that observers whose performance in the RSVP task was most improved in the focused-attention condition compared with their neutral condition also experienced the largest perceived repulsion in the vernier task. This finding provides converging evidence of a positive correlation between attention-modulated performance and appearance (e.g., perceived contrast, Barbot & Carrasco, 2018). Moreover, this finding supports the idea that attention, rather than some other visual process, was the cause of the repulsion effect.

Attention field size

To test whether attention-field size modulated the attentional repulsion effect, we used a cross-validation analysis on the data from the endogenous conditions for each observer. We found that attention-field size did not influence the attentional repulsion effect (Figure 5; $p > 0.10$ for all observers, cross-validation).

Discussion

Here we investigated the attentional repulsion effect with respect to exogenous and endogenous attention as well as attention-field size manipulations. It is often assumed that there is a link between attentional repulsion and attention-induced shifts in neural receptive fields (e.g., Anton-Erxleben & Carrasco, 2013; DiGiacomo & Pratt, 2012; Kosovicheva et al., 2010; Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997). However, there are notable gaps between physiological and psychophysical studies. Here we took a step toward bridging them by probing the attentional repulsion effect under different attentional conditions. Namely, we manipulated both the

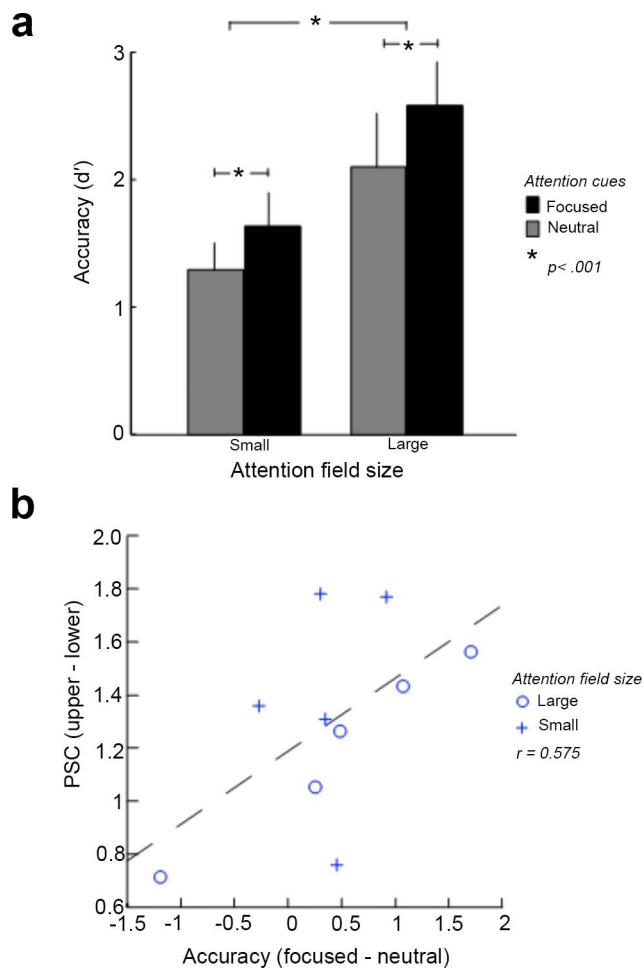


Figure 4. RSVP accuracy. (a) Accuracy in focused-attention versus neutral cue conditions. Error bars show standard error of the mean. Asterisks indicate significant differences (paired t test, $p < 0.05$). (b) Accuracy correlated with appearance. Blue symbols show individual observers' appearance effect (PSC difference between odd and even trials) and accuracy effect (focused-attention vs. neutral cues) in conditions with small (cross symbols) and large (circle symbols) attention fields. Black dotted line shows best linear fit (slope = 0.28; intercept = 1.19; Pearson's $r = 0.575$, $p < 0.05$).

type of attention—exogenous versus endogenous—and the attention-field size.

We compared exogenous with endogenous attention because most physiological studies of receptive fields have employed endogenous attention, and most psychophysical studies of perceived location have used exogenous attention. Additionally, attentional repulsion may be related to attention-field size, which is presumed to be smaller for exogenous attention because the cue must be displayed adjacent to the stimulus and the spatial uncertainty is low. Attention-field size has been hypothesized (Reynolds & Heeger, 2009) and shown (Herrmann et al., 2010) to change the

Model comparison: attention field size

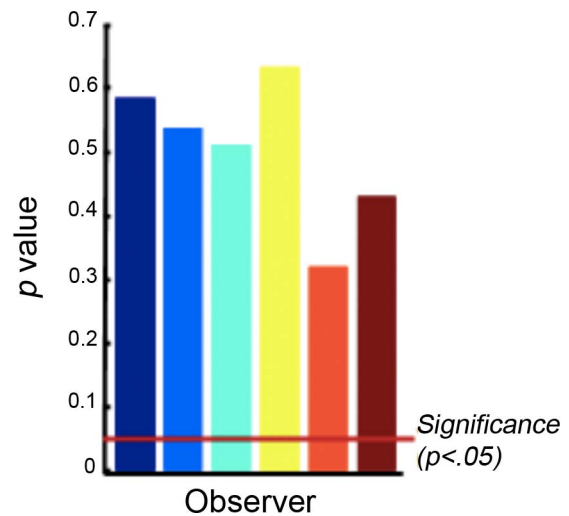


Figure 5. Effect of attention-field size. Bars show p values for each observer of the model comparison from cross-validation. Red line shows significance cutoff (0.05).

influence of attention on neural tuning and contrast-response functions.

We manipulated attention by presenting cues near the locations of both stimuli on every trial, randomizing whether attention was above the left stimulus and below the right stimulus (even cues) or below the left and above the right (odd cues). Previous research has established that observers are able to attend to two locations simultaneously (Awh & Pashler, 2000; Bay & Wyble, 2014; Carmel & Carrasco, 2009; Kawahara & Yamada, 2006; Montagna et al., 2009; Szpiro & Carrasco, 2015) and that the attention field needed to be neither circular nor contiguous in space (e.g., Gobell, Tseng, & Sperling, 2004; Shih & Sperling, 2002). Attending to two locations instead of one may (Carmel & Carrasco, 2009) or may not (Bay & Wyble, 2014) attenuate the effect on each individual location, but in any case, the effects remain. Additionally, although there is no consensus on whether endogenous attention to multiple locations is allocated to all locations in parallel or to each location in quick succession (e.g., Buetti, Cronin, Madison, Wang, & Lleras, 2016; Dugué, McLelland, Lajous, & VanRullen, 2015; Dugué, Xue, & Carrasco, 2017; McElree & Carrasco, 1999), we note that this deployment would not affect our results. Given that attention is oriented and reoriented sequentially in a periodic fashion (Dugué, Roberts, & Carrasco, 2016), the location that is attended once the relevant stimuli are displayed should be random and not affected by the experimental manipulations.

By using optimal cue parameters to manipulate each attention type, we compared the magnitude of the

perceptual effects brought about by endogenous and exogenous attention. However, this does not guarantee that these two types of attention have the same strength. With the cue parameters used in this study, there was a stronger repulsion effect for endogenous than exogenous attention. In contrast, the only other study that had explored the effects of endogenous attention on the repulsion effect (Suzuki & Cavanagh, 1997) reported a slightly smaller repulsion effect in their endogenous (see their experiment 4) than exogenous attention tasks. However, their manipulation of voluntary attention, without tracking eye position and with a cue validity of 50%, was suboptimal as the effect of endogenous attention scales with cue validity (Giordano et al., 2009; Kinchla, 1980; Sperling & Melchner, 1978). Here, we maximized the effect of endogenous attention via a 100% valid cue. Regardless of whether the strength of endogenous attention is greater than that of exogenous attention, which may or may not be the case with different parameter manipulations, here we document that endogenous attention strongly modulates the repulsion effect.

Some of the notable differences between the perceptual consequences of endogenous versus exogenous attention are related to spatial resolution; specifically, exogenous attention always increases spatial resolution even when it hinders task performance (e.g., Carrasco et al., 2006; Yeshurun & Carrasco, 1998) whereas endogenous attention is flexible and can increase or decrease the spatial resolution depending on the task demands (Barbot & Carrasco, 2017; Yeshurun et al., 2008). That endogenous attention is more flexible suggests that it might also be graded depending on task difficulty; we speculate that the stronger repulsion effect in the endogenous experiment is partially due to the difficulty of the RSVP task used to control attention, which taxed spatial attention to a greater degree than the automatic exogenous cue. Another possible contributing factor is the different neural mechanisms underlying endogenous and exogenous attention. For example, endogenous attention, but not exogenous, relies on feedback from the frontal and parietal regions (e.g., Beck & Kastner, 2009; Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Buffalo, Fries, Landman, Liang, & Desimone, 2009; Corbetta & Shulman, 2002; Hamker & Zirnsak, 2006; Lauritzen, D'Esposito, Heeger, & Silver, 2009). So it may be that location perception relies more on the regions involved in endogenous attention. In any case, the difference in attentional repulsion between the endogenous and exogenous attention conditions suggests that we should be cautious when relating the behavioral repulsion effect to receptive field changes measured physiologically. Whereas the evidence for the former has been mostly obtained with exogenous attention, the latter has been obtained with endogenous attention. Not-

withstanding this caveat, the qualitative similarity in the two conditions may mean that the same type of computational mechanism supports both.

We manipulated attention field size in the endogenous experiment by increasing the spatial uncertainty of the target letters in the RSVP task. Spatial uncertainty has been used in previous studies of attention field size. Herrmann et al. (2010) confirmed such manipulation; using fMRI, they showed a larger spatial extent of increased neural activity in V1 when observers performed the task with than without spatial uncertainty. Attention-field size is also affected by cue size (e.g., Yeshurun & Carrasco, 2008), but that manipulation may not be as effective as spatial uncertainty (Huang et al., 2016).

We found no significant difference in the amount of attentional repulsion between the two attention-field sizes. The normalization model of attention (Reynolds & Heeger, 2009) predicts that feature tuning curves can be either scaled, when the task demands spatial attention but not necessarily a narrow attention field in the feature space, or sharpened, when feature-based attention is narrowly focused on a feature value. These predictions are born out in psychophysical studies (e.g., Baldassi & Verghese, 2005; Ling, Liu, & Carrasco, 2009; Paltoglou & Neri, 2012). So we might expect that the size of the spatial attention field would differentially affect spatial receptive fields. But to probe this difference, the proper ratio of attention-field size to tuning bandwidth (i.e., RF size) is necessary. For example, attending to a wider range of orientations did not affect contrast-response functions differently than attending to a narrower range because tuning bandwidth for orientation is broad (Herrmann et al., 2012). To induce an attention field broader than this tuning range would have been experimentally intractable. Analogously, in our experiment, it is possible that the larger attention field was not broad enough given the receptive field sizes at 4°–6° eccentricity.

However, the fact that the responses of individual neurons vary with different attention-field sizes may not carry as much weight in predicting stimulus appearance, which likely results from the combined influence of many visual neurons. The relation between single neurons' responses and population readout is often indirect; for example, the effect of attention on contrast-response functions is different for a population mean than for the single neurons it contains (Hara, Pestilli, & Gardner, 2014). This difference can account for the fact that electrophysiological studies, which concern the activity of individual neurons, typically find multiplicative effects of attention whereas fMRI, which captures a measure of gross cortical activity at the millimeter level, often shows additive effects (Hara et al., 2014; Pestilli, Carrasco, Heeger, & Gardner, 2011). In fact, in our previous study on contrast

appearance (Cutrone et al., 2014), we found through a controlled psychophysical task that the effect of attention on perceived contrast, hypothesized to arise from a population response, could best be explained by a model with an additive baseline shift, similar to that shown in Hara et al.'s (2014) population model.

In the sensory adaptation literature, models of sensory aftereffects in both orientation and motion direction have shown that although adaptation causes individual neurons' tuning curves to shift with respect to the adapted direction, the population readout is also influenced by gain changes across the population (Gilbert & Wiesel, 1990; Jin, Dragoi, Sur, & Seung, 2005; Kohn & Movshon, 2004). For example, in orientation adaptation, orientation tuning curves shift away from the adapted orientation. A labeled-line model, in which a given neuron's activity is always interpreted as indicating a stimulus in its classical receptive field, would predict an attractive aftereffect, but in fact, the tilt aftereffect is repulsive due to the decrease in gain at the adapted orientation (Gilbert & Wiesel, 1990; Jin et al., 2005). This literature indicates that a population model is often necessary to accurately predict perceptual effects and that looking only at tuning changes—in the case of spatial attention, receptive field shifts—may not be sufficient.

Another factor that could have contributed to the similar attentional repulsion effect for conditions with both large and small attention fields is the reduction in masking in the large compared with the small attention-field condition. In the former, the positions of the letters in each RSVP stream were shuffled and nonoverlapping; in the latter, the position of the letters in the RSVP streams was constant.

That the repulsion effect resulted from all our experimental attentional manipulations further substantiates the dissociation between covert attention and eye movements. Whereas we, and others (e.g., DiGirolamo & Pratt, 2012; Kosovicheva et al., 2010; Ono & Watanabe, 2011; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997) find that attention repels perceived locations, stimuli presented just before a saccade are perceptually attracted to the target (Hamker, Zirnsak, Calow, & Lappe, 2008; Ross, Morrone, & Burr, 1997). This behavioral difference is consistent with other behavioral differences between endogenous covert attention and saccade preparation (Li, Barbot, & Carrasco, 2016; Rolfs & Carrasco, 2012). A distinction in neural mechanisms is also clear: Saccade preparation recruits some of the same brain areas as spatial covert attention (e.g., Kustov & Robinson, 1996; Moore, Armstrong, & Fallah, 2003), but distinct neural populations within those areas support either covert attention or eye movements (Gregoriou, Gotts, & Desimone, 2012; Ignashchenkova, Dicke, Haarmeier,

& Thier, 2004; Juan, Shorter-Jacobi, & Schall, 2004; Thompson, Biscoe, & Sato, 2005).

In conclusion, we have shown the repulsion effect to be robust to manipulations of attention type—exogenous or endogenous—and attention-field size. This finding adds to the growing literature on attention and appearance and calls for further study of the neural substrates of attentional warping of visual space.

Keywords: endogenous attention, exogenous attention, attention-field size, repulsion effect

Acknowledgments

This work was supported by National Institutes of Health grants R01-EY019693 (to MC and DJH) and R01-EY016200 (to MC). We thank members of the Carrasco Lab and Mike Landy for helpful comments.

Commercial relationships: none.

Corresponding author: Marisa Carrasco.

Email: marisa.carrasco@nyu.edu.

Address: Department of Psychology and Center for Neural Sciences, New York University, New York, NY, USA.

References

- Abrams, J., Barbot, A., & Carrasco, M. (2010). Voluntary attention increases perceived spatial frequency. *Attention, Perception, & Psychophysics*, *72*, 1510–1521.
- Anton-Erxleben, K., Abrams, J., & Carrasco, M. (2010). Evaluating comparative and equality judgments in contrast perception: Attention alters appearance. *Journal of Vision*, *10*(11):6, 1–22, <https://doi.org/10.1167/10.11.6>. [PubMed] [Article]
- Anton-Erxleben, K., Abrams, J., & Carrasco, M. (2011). Equality judgments cannot distinguish between attention effects on appearance and criterion: A reply to Schneider (2011). *Journal of Vision*, *11*(13):8, 1–8, <https://doi.org/10.1167/11.13.8>. [PubMed] [Article]
- Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioral and neurophysiological evidence. *Nature Reviews Neuroscience*, *14*, 188–200.
- Anton-Erxleben, K., Henrich, X., & Treue, S. (2007). Attention changes perceived size of moving visual patterns. *Journal of Vision*, *7*(11):5, 1–9, <https://doi.org/10.1167/7.11.5>. [PubMed] [Article]

- Anton-Erxleben, K., Stephan, V. M., & Treue, S. (2009). Attention reshapes center-surround receptive-field structure in macaque cortical area MT. *Cerebral Cortex*, *19*, 2466–2478.
- Arlot, S., & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys*, *4*, 40–79.
- Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 834–846.
- Baldassi, S., & Verghese, P. (2005). Attention to locations and features: Different top-down modulation of detector weights. *Journal of Vision*, *5*(6):7, 556–570, <https://doi.org/10.1167/5.6.7>. [PubMed] [Article]
- Barbot, A., & Carrasco, M. (2017). Attention modifies spatial resolution according to task demands. *Psychological Science*, *28*(3), 285–296.
- Barbot, A., & Carrasco, M. (2018). Emotion and anxiety potentiate the way attention alters visual appearance. *Scientific Reports*, *8*(1):5938.
- Barbot, A., Landy, M. S., & Carrasco, M. (2012). Differential effects of exogenous and endogenous attention on 2nd-order texture contrast sensitivity. *Journal of Vision*, *12*(8):6, 1–15, <https://doi.org/10.1167/12.8.6>. [PubMed] [Article]
- Barbot, A., Liu, S., Kimchi, R., & Carrasco, M. (2017). Attention enhances apparent perceptual organization. *Psychonomic Bulletin & Review*. Advance online publication. <https://doi.org/10.3758/s13423-017-1365-x>.
- Bay, M., & Wyble, B. (2014). The benefit of attention is not diminished when distributed over two simultaneous cues. *Attention, Perception, & Psychophysics*, *76*, 1287–1297.
- Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Research*, *49*(10), 1154–1165.
- Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *Journal of Neuroscience*, *28*(40), 10056–10061.
- Buetti, S., Cronin, D. A., Madison, A. M., Wang, Z., & Lleras, A. (2016). Towards a better understanding of parallel visual processing in human vision: Evidence for exhaustive analysis of visual information. *Journal of Experimental Psychology: General*, *145*(6), 672–707.
- Buffalo, E. A., Fries, P., Landman, R., Liang, H., & Desimone, R. (2009). A backward progression of attentional effects in the ventral stream. *Proceedings of the National Academy of Sciences, USA*, *107*(1), 361–365.
- Cameron, E. L., Tai, J. C., Eckstein, M. P., & Carrasco, M. (2004). Signal detection theory applied to three visual search tasks: Identification, yes/no detection and localization. *Spatial Vision*, *17*, 295–325.
- Carmel, D., & Carrasco, M. (2009). Bright and dark attention: Distinct effect of divided attention at attended and unattended locations. *Journal of Vision*, *9*(8): 123, <https://doi.org/10.1167/9.8.123>. [Abstract]
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484–1525.
- Carrasco, M. (2014). Spatial attention: Perceptual modulation. In S. Kastner & A. C. Nobre (Eds.), *The Oxford Handbook of Attention* (pp. 183–230). Oxford, UK: Oxford University Press.
- Carrasco, M., & Barbot, A. (2014). How attention affects spatial resolution. *Cold Spring Harbor Symposia on Quantitative Biology*, *79*, 149–160, doi: <http://doi.org/10.1101/sqb.2014.79.024687>.
- Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*, 308–313.
- Carrasco, M., Loula, F., & Ho, Y.-X. (2006). How attention enhances spatial resolution: Evidence from selective adaptation to spatial frequency. *Perception & Psychophysics*, *68*, 1004–1012.
- Carrasco, M., Williams, P. E., & Yeshurun, Y. (2002). Covert attention increases spatial resolution with or without masks: Support for signal enhancement. *Journal of Vision*, *2*(6):4, 467–479, <https://doi.org/10.1167/2.6.4>. [PubMed] [Article]
- Carrasco, M., & Yeshurun, Y. (1998). The contribution of covert attention to the set-size and eccentricity effects in visual search. *Journal of Experimental Psychology: Human Perception & Performance*, *24*(2), 673–692.
- Carrasco, M., & Yeshurun, Y. (2009). Covert attention effects on spatial resolution. In N. Srinivasan (Ed.), *Progress in Brain Research*, vol. 176 Attention (pp. 65–86). Amsterdam, The Netherlands: Elsevier.
- Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. *Behavioural Brain Research*, *237*, 107–123.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215.
- Cutrone, E. K., Heeger, D. J., & Carrasco, M. (2014).

- Attention enhances contrast appearance via increased input baseline of neural responses. *Journal of Vision*, 14(14):16, 1–14, <https://doi.org/10.1167/14.14.16>. [PubMed] [Article]
- DiGiacomo, A., & Pratt, J. (2012). Misperceiving space following shifts of attention: Determining the locus of the attentional repulsion effect. *Vision Research*, 64, 35–41.
- Dugué, L., McLelland, D., Lajous, M., & VanRullen, R. (2015). Attention searches nonuniformly in space and time. *Proceedings of the National Academy of Sciences, USA*, 112(49), 15214–15219.
- Dugué, L., Merriam, E., Heeger, D. J., & Carrasco, M. (2017). Specific visual sub-regions of TPJ mediate reorienting of spatial attention. Advance online publication. <https://doi.org/10.1093/cercor/bhx140>.
- Dugué, L., Roberts, M., & Carrasco, M. (2016). Attention reorients periodically. *Current Biology*, 26, 1595–1601.
- Dugué, L., Xue, A. M., & Carrasco, M. (2017). Distinct perceptual rhythms for feature and conjunction searches. *Journal of Vision*, 17(3):22, 1–15, <https://doi.org/10.1167/17.3.22>. [PubMed] [Article]
- Eurich, C. W., & Schwegler, H. (1997). Coarse coding: Calculation of the resolution achieved by a population of large receptive field neurons. *Biological Cybernetics*, 76, 357–363.
- Fortenbaugh, F. C., Prinzmetal, W., & Robertson, L. C. (2011). Rapid changes in visual–spatial attention distort object shape. *Psychological Bulletin Review*, 18, 287–294.
- Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings of the National Academy of Sciences, USA*, 103(26), 10046–10051.
- Gilbert, C. D., & Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vision Research*, 30, 1689–1701.
- Giordano, A. M., McElree, B., & Carrasco, M. (2009). On the automaticity and flexibility of covert attention: A speed-accuracy trade-off analysis. *Journal of Vision*, 9(3):30, 10–31, <https://doi.org/10.1167/9.3.30>. [PubMed] [Article]
- Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science*, 16, 644–651.
- Gobell, J. L., Tseng, C. H., & Sperling, G. (2004). The spatial distribution of visual attention. *Vision Research*, 44(12), 1273–1296.
- Golla, H., Ignashchenkova, A., Haarmeier, T., & Thier, P. (2004). Improvement of visual acuity by spatial cueing: A comparative study in human and non-human primates. *Vision Research*, 44, 1589–1600.
- Gozli, D. G., & Pratt, J. (2012). Attentional repulsion effect despite a colour-based control set. *Visual Cognition*, 20(6), 696–716.
- Gregoriou, G. G., Gotts, S. J., & Desimone, R. (2012). Cell-type-specific synchronization of neural activity in FEF with V4 during attention. *Neuron*, 73, 581–594.
- Hamker, F. H., & Zirnsak, M. (2006). V4 receptive field dynamics as predicted by a systems-level model of visual attention using feedback from the frontal eye field. *Neural Networks*, 19, 1371–1382.
- Hamker, F. H., Zirnsak, M., Calow, D., & Lappe, M. (2008). The Peri-saccadic perception of objects and space. *PLoS Computational Biology*, 4(2): e31.
- Hara, Y., Pestilli, F., & Gardner, J. L. (2014). Differing effects of attention in single-units and populations are well predicted by heterogeneous tuning and the normalization model of attention. *Frontiers in Computational Neuroscience*, 8: 12.
- Herrmann, K., Heeger, D. J., & Carrasco, M. (2012). Feature-based attention enhances performance by increasing response gain. *Vision Research*, 74, 10–20.
- Herrmann, K., Montaser-Kouhsari, L., Carrasco, M., & Heeger, D. J. (2010). When size matters: Attention affects performance by contrast or response gain. *Nature Neuroscience*, 13(12), 1554–1559. PMC3058765.
- Horowitz, T. S., Wolfe, J. M., Alvarez, G. A., Cohen, M. A., & Kuzmova, Y. I. (2009). The speed of free will. *The Quarterly Journal of Experimental Psychology*, 62(11), 2262–2288.
- Huang, D., Xue, L., Wang, X., & Chen, Y. (2016). Using spatial uncertainty to manipulate the size of the attention focus. *Scientific Reports*, 6: 32364.
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, 7, 56–64.
- Jin, D. Z., Dragoi, V., Sur, M., & Seung, H. S. (2005). The tilt aftereffect and adaptation-induced changes in orientation tuning in visual cortex. *Journal of Neurophysiology*, 94, 4038–4050.
- Juan, C. H., Shorter-Jacobi, S. M., & Schall, J. D. (2004). Dissociation of spatial attention and saccade preparation. *Proceedings of the National Academy of Sciences, USA*, 101, 15541–15544.
- Kawahara, J., & Yamada, Y. (2006). Two noncontig-

- uous locations can be attended concurrently: Evidence from the attentional blink. *Psychonomic Bulletin & Review*, *13*, 594–599.
- Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related fMRI study of voluntary and stimulus-driven orienting of attention. *Journal of Neuroscience*, *25*, 4593–4604.
- Kinchla, R. (1980). The measurement of attention. In R. Nickerson (Ed.), *Attention and Performance, Vol. VIII* (pp. 213–238). Princeton, NJ: Psychology Press.
- Kohn, A., & Movshon, J. A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience*, *7*, 764–772.
- Kosovicheva, A., Fortenbaugh, F. C., & Robertson, L. C. (2010). Where does attention go when it moves? Spatial properties and locus of the attentional repulsion effect. *Journal of Vision*, *10*(12):33, 1–13, <https://doi.org/10.1167/10.12.33>. [PubMed] [Article]
- Kustov, A. A., & Robinson, D. L. (1996, November 7). Shared neural control of attentional shifts and eye movements. *Nature*, *384*, 74–77.
- Lauritzen, T. Z., D’Esposito, M., Heeger, D. J., & Silver, M. A. (2009). Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision*, *9*(13):18, 1–14, <https://doi.org/10.1167/9.13.18>. [PubMed] [Article]
- Li, H. H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26*(12), 1564–1570.
- Ling, S., & Carrasco, M. (2006). When sustained attention impairs perception. *Nature Neuroscience*, *9*, 1243–1245.
- Ling, S., Liu, T., & Carrasco, M. (2009). How spatial and feature-based attention affect the gain and tuning of population responses. *Vision Research*, *49*, 1194–1204.
- Liu, T., Abrams, J., & Carrasco, M. (2009). Voluntary attention enhances contrast appearance. *Psychological Science*, *20*(3), 354–362.
- Liu, T., Fuller, S., & Carrasco, M. (2006). Attention alters the appearance of motion coherence. *Psychological Bulletin Review*, *13*(6), 1091–1096.
- Liu, T., Stevens, S. T., & Carrasco, M. (2007). Comparing the time course and efficacy of spatial and feature-based attention. *Vision Research*, *47*, 108–113.
- Liverence, B. M., & Scholl, B. J. (2011). Selective attention warps spatial representation: Parallel but opposing effects on attended versus inhibited objects. *Psychological Science*, *22*(12), 1600–1608.
- McElree, B., & Carrasco, M. (1999). Temporal dynamics of visual search: A speed-accuracy analysis of feature and conjunction searches. *Journal of Experimental Psychology: Human Perception & Performance*, *25*(6), 1517–1539.
- Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, *40*, 671–683.
- Montagna, B., Pestilli, F., & Carrasco, M. (2009). Attention trades off spatial acuity. *Vision Research*, *49*, 735–745.
- Moran, J., & Desimone, R. (1985, August 23). Selective attention gates visual processing in the extrastriate cortex. *Science*, *229*(4715), 782–784.
- Muller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perceptual Performance*, *15*, 315–330.
- Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*, 1631–1647.
- Ono, F., & Watanabe, K. (2011). Attention can retrospectively distort visual space. *Psychological Science*, *22*, 472–477.
- Paltoglou, A. E., & Neri, P. (2012). Attentional control of sensory tuning in human visual perception. *Journal of Neurophysiology*, *107*(5), 1260–1274.
- Pestilli, F., Carrasco, M., Heeger, D. J., & Gardner, J. L. (2011). Attentional enhancement via selection and pooling of early sensory responses in visual cortex. *Neuron*, *72*, 832–846.
- Pratt, J., & Arnott, S. R. (2008). Modulating the attentional repulsion effect. *Acta Psychologica*, *127*, 137–145.
- Pratt, J., & Turk-Browne, N. B. (2003). The attentional repulsion effect in perception and action. *Experimental Brain Research*, *152*, 376–382.
- Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. *Annual Review of Neuroscience*, *27*, 611–647.
- Reynolds, J. H., & Heeger, D. J. (2009). The normalization model of attention. *Neuron*, *61*(2), 168–185.
- Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *34*(40), 13744–13752.
- Ross, J., Morrone, M. C., & Burr, D. C. (1997, April

- 10). Compression of visual space before saccades. *Nature*, 386(6625), 598–601.
- Shih, S., & Sperling, G. (2002). Measuring and modeling the trajectory of visual spatial attention. *Psychological Review*, 109(2), 260–305.
- Sperling, G., & Melchner, M. J. (1978, October 20). The attention operating characteristic: Examples from visual search. *Science*, 202, 315–318.
- Störmer, V. S., McDonald, J. J., & Hillyard, S. A. (2009). Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli. *Proceedings of the National Academy of Sciences, USA*, 106(52), 22456–22461.
- Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: An attentional repulsion effect. *Journal of Experimental Psychology: Human Perceptual Performance*, 23(2), 443–463.
- Szpiro, S. F. A., & Carrasco, M. (2015). Exogenous attention enables perceptual learning. *Psychological Science*, 26(12), 1854–1862.
- Talgar, C. P., & Carrasco, M. (2002). Vertical meridian asymmetry in spatial resolution: Visual and attentional factors. *Psychonomic Bulletin & Review*, 9(4), 714–722.
- Theeuwes, J., Godijn, R., & Pratt, J. (2004). A new estimation of the duration of attentional dwell time. *Psychonomic Bulletin Review*, 11(1), 60–64.
- Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *Journal of Neuroscience*, 25, 9479–9487.
- Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics*, 63, 1314–1329.
- Womelsdorf, T., Anton-Erxleben, K., Pieper, F., & Treue, S. (2006). Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nature Neuroscience*, 9, 1156–1160.
- Yeshurun, Y., & Carrasco, M. (1998, November 5). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, 396, 72–75.
- Yeshurun, Y., & Carrasco, M. (1999). Spatial attention improves performance in spatial resolution tasks. *Vision Research*, 39(2), 293–306.
- Yeshurun, Y., & Carrasco, M. (2000). The locus of attentional effects in texture segmentation. *Nature Neuroscience*, 3(6), 622–627.
- Yeshurun, Y., & Carrasco, M. (2008). The effects of transient attention on spatial resolution and the size of the attentional cue. *Perception & Psychophysics*, 70(1), 104–113.
- Yeshurun, Y., Montagna, B., & Carrasco, M. (2008). On the flexibility of sustained attention and its effects on a texture segmentation task. *Vision Research*, 48(1), 80–95.