

Effects of involuntary and voluntary attention on critical spacing of visual crowding

Joel D. Bowen

Vision Science Graduate Group, University of California
Berkeley, Berkeley, CA, USA



Carissa V. Alforque

Herbert Wertheim School of Optometry & Vision Science,
University of California Berkeley, Berkeley, CA, USA



Michael A. Silver

Vision Science Graduate Group, University of California
Berkeley, Berkeley, CA, USA
Herbert Wertheim School of Optometry & Vision Science,
University of California Berkeley, Berkeley, CA, USA
Helen Wills Neuroscience Institute, University of
California Berkeley, Berkeley, CA, USA



Visual spatial attention can be allocated in two distinct ways: one that is voluntarily directed to behaviorally relevant locations in the world, and one that is involuntarily captured by salient external stimuli. Precueing spatial attention has been shown to improve perceptual performance on a number of visual tasks. However, the effects of spatial attention on visual crowding, defined as the reduction in the ability to identify target objects in clutter, are far less clear. In this study, we used an anticueing paradigm to separately measure the effects of involuntary and voluntary spatial attention on a crowding task. Each trial began with a brief peripheral cue that predicted that the crowded target would appear on the opposite side of the screen 80% of the time and on the same side of the screen 20% of the time. Subjects performed an orientation discrimination task on a target Gabor patch that was flanked by other similar Gabor patches with independent random orientations. For trials with a short stimulus onset asynchrony between cue and target, involuntary capture of attention led to faster response times and smaller critical spacing when the target appeared on the cue side. For trials with a long stimulus onset asynchrony, voluntary allocation of attention led to faster reaction times but no significant effect on critical spacing when the target appeared on the opposite side to the cue. We additionally found that the magnitudes of these cueing effects of involuntary and voluntary attention were not strongly correlated across subjects for either reaction time or critical spacing.

Introduction

Processing visual images, reading text, and navigating through the world all require a visual system that continuously parses cluttered scenes. Spatial attention is one mechanism for selecting regions of the visual scene for preferential processing (Carrasco, 2011; Anton-Erxleben & Carrasco, 2013). Covert spatial attention (i.e., directing attention to a location without accompanying eye movements) can either be voluntarily allocated (endogenous) or involuntarily captured by an external stimulus (exogenous) (Posner, Cohen, & Rafal, 1982; Yantis & Jonides, 1990). The effects of involuntary attention occur rapidly after stimulus onset but dissipate quickly (Posner, Cohen, & Rafal, 1982). In contrast, the onset of voluntary attention effects is slower (Posner, Cohen, & Rafal, 1982), but voluntary attention can be sustained for much longer (Silver, Ress, & Heeger, 2007). These two types of attention also have different effects on perceptual factors such as contrast sensitivity (Barbot, Landy, & Carrasco, 2012; Jigo & Carrasco, 2020), sensory tuning (Fernández, Okun, & Carrasco, 2021), and texture discrimination (Yeshurun & Carrasco, 1998; Yeshurun, Montagna, & Carrasco, 2008; Barbot & Carrasco, 2017; Jigo, Heeger, & Carrasco, 2021).

The effect of spatial attention on perceptual performance is perhaps most evident in peripheral vision, where perception is limited by a number of factors. Visual crowding, the decrease in the ability to identify target objects in the periphery in the presence of similar flanking objects, is one of the strongest

Citation: Bowen, J. D., Alforque, C. V., & Silver, M. A. (2023). Effects of involuntary and voluntary attention on critical spacing of visual crowding. *Journal of Vision*, 23(3):2, 1–14, <https://doi.org/10.1167/jov.23.3.2>.

<https://doi.org/10.1167/jov.23.3.2>

Received April 23, 2022; published March 2, 2023

ISSN 1534-7362 Copyright 2023 The Authors



of these limitations (Levi, 2008; Whitney & Levi, 2011). Previous research has shown that capture of involuntary attention with a peripheral cue improves performance (Felisberti, Solomon, & Morgan, 2005; Scolari, Kohlen, Barton, & Awh, 2007) and decreases critical spacing (i.e., the minimum target/flanker spacing at which the target is correctly identified at a specified level of performance) on crowding tasks (Yeshurun & Rashal, 2010; Rashal & Yeshurun, 2014; Kewan-Khalayly, Migó, & Yashar, 2022). Although these studies have characterized effects of involuntary attention on critical spacing in visual crowding, less is known about the effects of voluntary attention and how the effects of these two types of attention might be related.

In studies of visual crowding, peripheral targets are typically easy to identify in the absence of flanking stimuli, and this differentiates perceptual limitations due to crowding from those based on visual acuity. Crowding has been modeled as arising from inherent limits in the size and density of cortical receptive fields (RFs) in the visual periphery, especially when compared with central vision (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001; Balas, Nakano, & Rosenholtz, 2009; Dakin, Cass, Greenwood, & Bex, 2010; Greenwood, Bex, & Dakin, 2010; Freeman & Simoncelli, 2011; Rosenholtz, 2016). One mechanism by which visual spatial attention might relieve crowding is by locally increasing the density of RFs that sample the target location (Baruch & Yeshurun, 2014; Theiss, Bowen, & Silver, 2021). Neurophysiologically, it has been shown that sustained visual spatial attention causes RFs to shift toward the locus of attention and to shrink in size (Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006; Klein, Harvey, & Dumoulin, 2014).

At the behavioral level, spatial attention can influence the spatial resolution of texture discrimination for both involuntary (Yeshurun & Carrasco, 1998) and voluntary (Yeshurun, Montagna, & Carrasco, 2008) attention. In these studies, in the absence of spatial attention cues, texture discrimination performance varies as an inverted U-shaped function of eccentricity, with maximal performance at midperipheral eccentricities. Involuntary attention cues caused peak texture discrimination performance to shift toward more peripheral eccentricities across all cue locations, thereby decreasing performance at more central locations compared with a cue that did not specify a particular location in the stimulus array (Yeshurun & Carrasco, 1998, 2008). However, voluntary attention was found to enhance performance at all eccentricities, including both peripheral and central locations (Yeshurun, Montagna, & Carrasco, 2008). It is currently unknown whether the control of perceptual spatial resolution that has previously been attributed to voluntary attention could also account for attentional effects on critical spacing in visual crowding.

In most studies of spatial attention, involuntary attention is captured by a peripheral cue at the stimulus location, with a very short duration between cue and stimulus onsets (approximately 40–100 ms) (Posner, 1980). Voluntary attention, in contrast, is typically directed using a cue that is not at the location to be attended, but instead specifies this location through symbolic or abstract information. For example, a central cue that points toward a location at which an upcoming target is likely to appear will enhance target processing at that location. Studies of voluntary attention typically employ a relatively long duration between cue and stimulus onsets (>300 ms) (Posner, Cohen, & Rafal, 1982).

In this study, we used an anticueing paradigm (Posner, Cohen, & Rafal, 1982; Rokem, Landau, Garg, Prinzmetal, & Silver, 2010) and a crowding task to measure the effects of both involuntary and voluntary attention on critical spacing while controlling for a number of experimental factors. Specifically, varying only the duration of the stimulus onset asynchrony (SOA) between the presentation of a peripheral cue and a target stimulus allowed us to select whether involuntary or voluntary attention was primarily engaged for orientation discrimination of a Gabor target. We measured the effects of involuntary and voluntary attention over a range of target/flanker spacings to determine the effects of both types of attention on critical spacing in visual crowding. We show that, when involuntary attention was directed to the target location, the critical spacing of crowding decreased compared with when involuntary attention was directed elsewhere. However, when voluntary attention was directed to the target location, there was no significant effect on critical spacing. Additionally, we found that the effects of involuntary and voluntary attention were not strongly correlated across subjects for either response time (RT) or critical spacing.

Methods

Subjects

The University of California Berkeley Committee for Protection of Human Subjects approved all experimental procedures. Twenty-four subjects (16 females; 8 males; aged 20–52 years) with normal or corrected-to-normal vision participated in this study. Of these subjects, 17 were naive to the experimental design, and 7 (including all 3 authors) had at least some knowledge of the design. The number of subjects was chosen to be larger than those in similar previous studies of crowding and attention (e.g., Yeshurun & Rashal, 2010; Albonico, Martelli, Bricolo, Frasson, & Daini, 2018). Subjects were compensated for their time.

Stimuli and apparatus

We presented stimuli using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007) on a 53 cm Dell UltraSharp LCD monitor with a 1680 × 1050 resolution, 60-Hz refresh rate, and 300 cd/m² peak brightness. We recorded eye position with the Eyelink 1000 (SR Research Ltd., Ottawa, Canada). Subjects sat at a distance of 50 cm from the screen with their heads on a chinrest in a dark room. Stimuli consisted of five equally sized circular Gabor patches (100% contrast, four cycles; spatial frequency varied for each participant [as described later in this section]; random spatial phase) arranged in a vertical configuration: one target in the middle and two flankers both above and below the target. The target was tilted either 45° or 135° away from horizontal, and the flanker orientations were randomly chosen to be between 0° and 180°. To avoid target pop-out and other forms of saliency based on differences in orientation between the target and flankers, flanker orientations could not be within ±10° of horizontal (0°), vertical (90°), or either of the two possible target orientations (45° or 135°). The target was presented at an eccentricity of 14° of visual angle either to the left or right of fixation.

Procedure

All subjects completed 4 experimental sessions, with an interval of 24 hours or more between sessions. During the first session, subjects completed two baseline experiments. The first of these experiments was used to derive a threshold size for the target in the absence of flankers for each participant. To do this, we presented a single Gabor target (100% contrast, 4 cycles; random spatial phase; eccentricity of 14° of visual angle) on either the left or right side of the screen (balanced across subjects) and used a three-down/one-up staircase procedure to adjust the diameter of the target in units of degrees of visual angle (133 ms stimulus presentation; 100 trials; 1.8° initial diameter; 0.1° staircase step size). Subjects performed a two-alternative forced choice task on the orientation of the target (45° or 135°) using a key press. We then fit a Weibull cumulative distribution function (Equation 1; for $s = 1$) to the data using a squared error cost function weighted by the proportion of trials per target size in the staircase (Equation 2), and the size of the target and flankers for all subsequent crowding experiments for a given subject was then set at 1.5× the diameter at 80% performance on the unflanked orientation discrimination task, based on the fitted psychometric curve. We chose this value for the diameter of the target so that task performance in the subsequent experiments would be limited by

target/flanker interactions in crowding and not by target visibility. Note that this procedure for selecting the size of the Gabor patches resulted in differences across participants in the spatial frequency of the target and flanker Gabor patches. The range of spatial frequencies was 2.27 to 4.59 cycles/degree.

The second baseline experiment was used to specify a range of target/flanker spacings for each subject. To do this, we presented a Gabor target with flankers on the same side of the screen as in the first baseline experiment described before in this section. The size and spatial frequency of the target and flanker stimuli were based on the results of the first baseline experiment for each participant. We used a three-down/one-up staircase procedure to adjust the center-to-center target/flanker spacing, measured in degrees of visual angle (133 ms stimulus presentation; 150 trials; 5° initial spacing; 0.2° staircase step size). We then fit another Weibull function (as described later in this section) to the spacing data, and the set of target/flanker spacings for all subsequent crowding experiments for each participant was defined as seven evenly-spaced values, ranging from a lower limit (the spacing at 55% performance) to an upper limit (1.5× the spacing at 80% performance), based on the fitted psychometric curve. We selected this range of target/flanker spacings for each subject to avoid floor and ceiling effects that could have limited our ability to measure the effects of attention on critical spacing.

For the remainder of the first session and all subsequent sessions, we used an anticueing task (Posner, Cohen, & Rafal, 1982; Rokem, Landau, Garg, Prinzmetal, & Silver, 2010) to separately measure the effects of precueing involuntary and voluntary attention on RT and on critical spacing of visual crowding. After a 1,200-ms fixation period at the start of each trial (Figure 1, left), one set of vertical bars (presented at 14 degrees of visual angle from fixation on either the left or right side of the screen) became thicker (changing from 0.05° to 0.15° visual angle) and brighter (changing from 25% to 75% maximal luminance) for 40 ms (Figure 1, middle). Next, the crowded array of Gabor patches was presented for 133 ms, 80% of the time within the vertical bars on the opposite side of the cue, and 20% of the time on the same side as the cue (Figure 1, right). Subjects performed a two-alternative forced choice task on the orientation of the target using a key press. They were instructed to respond as quickly and as accurately as possible, without moving their eyes from the central fixation cross. Subjects were also explicitly told that the stimulus was much more likely to appear on the opposite side than on the cued side. For a given block of trials, the SOA for the cue and the crowded stimuli was either 40 or 600 ms. At the beginning of each session, subjects completed blocks of 32 practice trials (50% long SOAs and 50% short SOAs) with unflanked targets until they achieved 75% correct performance. Each

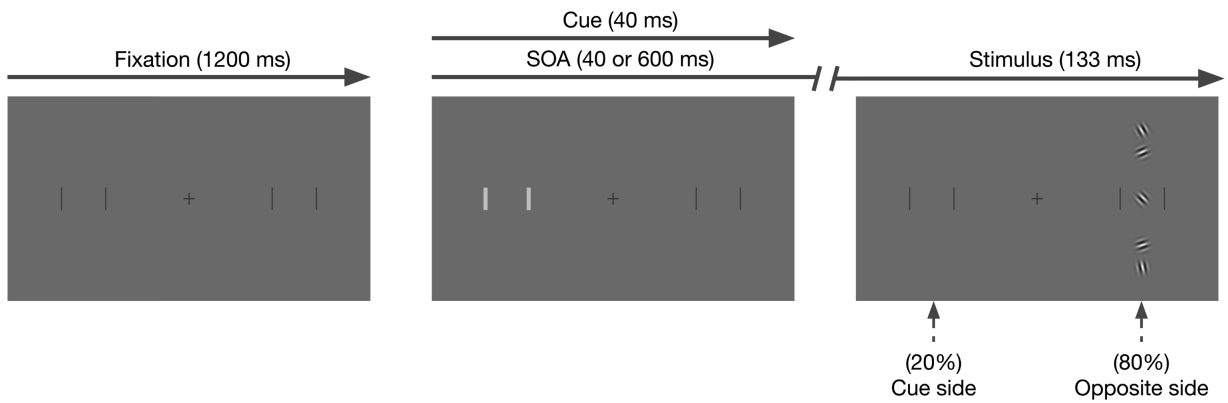


Figure 1. Schematic of the anticueing task. After a fixation interval, one set of vertical bars became thicker and brighter for 40 ms. After an SOA of 40 ms (short) or 600 ms (long), the crowded stimuli appeared for 133 ms within one of the two sets of vertical bars. In 20% of trials, the stimuli appeared on the cued side and in 80% of trials, the stimuli appeared on the opposite side. Stimuli were composed of a central target Gabor patch (45° or 135° orientation) and two sets of two flanking Gabor patches with independent random orientations. Target/flanker spacing was varied over a range of center-to-center distances, and the range of spacings and the size of the Gabor patches were customized for each subject (see Methods). There was also a condition in which the target was presented without flankers. Subjects performed a two-alternative forced choice task on the orientation of the target Gabor patch as quickly and as accurately as possible without moving their eyes from the central fixation cross. We recorded RT and accuracy. Gabor patch and cue sizes shown here were increased for visualization purposes and are not representative of actual experimental values.

subject then completed 8 blocks of 120 trials each (960 trials per session; 3,840 total trials for all 4 sessions). The SOA was fixed for a given block and was randomly ordered across blocks. The eight target/flanker spacing conditions were randomly interleaved within a block and were balanced across each combination of SOA and stimulus location.

Analysis

Critical spacing

A parameterized Weibull function was fit to the accuracy (percent correct) data across the range of target/flanker spacings for each combination of SOA (40 ms or 600 ms) and location (cue or opposite side) (Figure 2, left). Critical spacing, t , was defined as the spacing at 78% accuracy (dashed line in Figure 2). We chose this percent correct value because it was the approximate midpoint of the observed range of percent correct values in this study. Therefore, any effects of attention in critical spacing across conditions would be more likely to be reflected at multiple target/flanker spacing values in the psychometric function. The main effects reported in Figure 3 are not strictly dependent on this particular percent correct value, and they remain significant over a robust range of values (75%–85% correct).

The parameterized Weibull function was:

$$f_{t,b,s}(x) = s - (s - g)e^{-\left(\frac{kx}{t}\right)^b}, \quad (1)$$

where $k = -\ln\left(\frac{s-a}{s-g}\right)^{\frac{1}{b}}$, g was chance performance (50%), a was the percent correct value used to define the critical spacing value (78%), and b and s were the slope and asymptote of the psychometric curve, respectively. Parameters b , s ($\leq 100\%$ correct), and t were optimized using Matlab's `fmincon` for each subject's data. We minimized a squared error cost function that was weighted by the proportion of trials at each target/flanker spacing value and regularized by performance on the unflanked trials. Specifically, the optimization was defined as:

$$\min_{t,b,s \leq 1} \left[\left(\sum_i w_i (f(i) - y_i)^2 \right) + w_{\text{unflanked}} (s - y_{\text{unflanked}})^2 \right], \quad (2)$$

where y_i and $y_{\text{unflanked}}$ were the measured percent correct values for each spacing, i , and the unflanked trials, respectively. Similarly, w_i and $w_{\text{unflanked}}$ were the proportion of trials for each spacing, i , and the unflanked trials, respectively.

Response time

RT was collected for each trial over the range of target/flanker spacings for each subject. As with critical spacing, which is a summary statistic represented by all the percent correct data in the psychometric fit, we computed an RT summary statistic for making

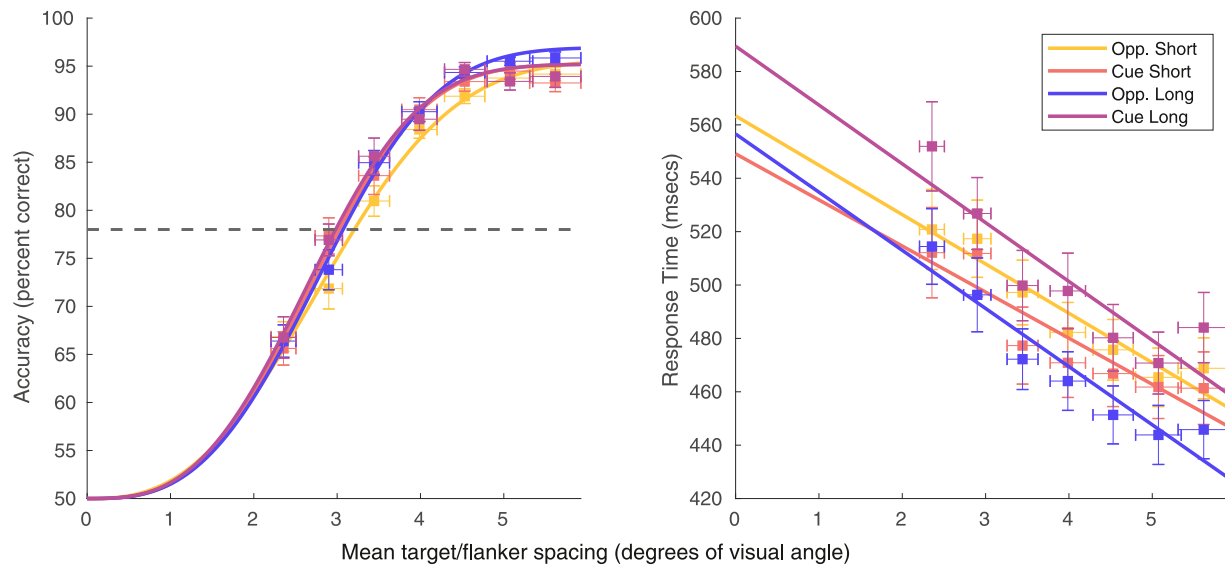


Figure 2. Mean subject task accuracy (left) and mean subject median RT (right) as a function of mean target/flanker spacing for each cue location (opposite or cue side) and SOA (short = 40 ms; long = 600 ms) combination. Note that the range of target/flanker spacing values were customized for each individual subject. Therefore, the displayed target/flanker spacing values are the average across subjects for each of the seven nominal spacings. A Weibull function (Equation 1) and a single line were fit to the averaged data across subjects for accuracy and RT, respectively. Error bars are standard errors of the mean. The black dashed line represents the designated task performance at the critical spacing.

comparisons across conditions. To do this, a single line was fit using least squares regression to median RT values across the range of target/flanker spacings for each combination of SOA and location (cue or opposite side) (Figure 2; right). Only RT values from correct trials were used in the fitting process. For each subject, comparisons across conditions were conducted at the predicted RT (from the fitted line) that corresponded to the critical spacing calculated from all SOA/location trials combined for that subject. We conducted comparisons across conditions at the target/flanker spacing derived from all combined trials rather than at each condition's critical spacing to avoid any possible speed/accuracy trade-offs that could be associated with differences in target/flanker spacings. We also conducted RT comparisons for the unflanked trials.

Statistical analyses

Subjects were removed from analysis if their asymptotic level of performance (s) for at least one of their SOA/location conditions was three or more standard deviations lower than the mean across all conditions (12.5% subjects in total). Trials in which fixation deviated by more than a distance of 3° from the fixation cross during target/flanker presentation were also removed from analysis (2.8% of trials). Mean RT and critical spacing were analyzed with a repeated-measures analysis of variance with SOA (40 or 600 ms) and stimulus location (cue or opposite

side) entered as within-subject factors. We additionally conducted a number of planned comparisons to assess the effects of the cue on RT and critical spacing. Specifically, for each SOA we defined the cueing effects as a pairwise difference between values when the stimulus appeared on the cue side and values when the stimulus appeared on the opposite side. We used two-tailed Student's t tests to assess if the means of the cueing effects were significantly different than zero. Additionally, we computed Cohen's d effect sizes for the paired differences. For the correlation analyses, Pearson's r values were calculated and tested against the null hypothesis of a correlation coefficient value of zero.

Results

Participants performed an orientation discrimination task in which presentation of the cue on one side of the screen predicted that the stimulus would appear on the opposite side of the screen 80% of the time and on the same side of the screen 20% of the time (Figure 1). For all trials, the cue initially directed a participant's involuntary attention to its location. With additional time between cue and stimulus presentation, however, the participant could voluntarily direct their attention to the opposite side of the screen (where the stimulus was more likely to appear). We varied the SOA between cue and stimulus presentations to study the effects of involuntary (40 ms SOA) and voluntary attention (600

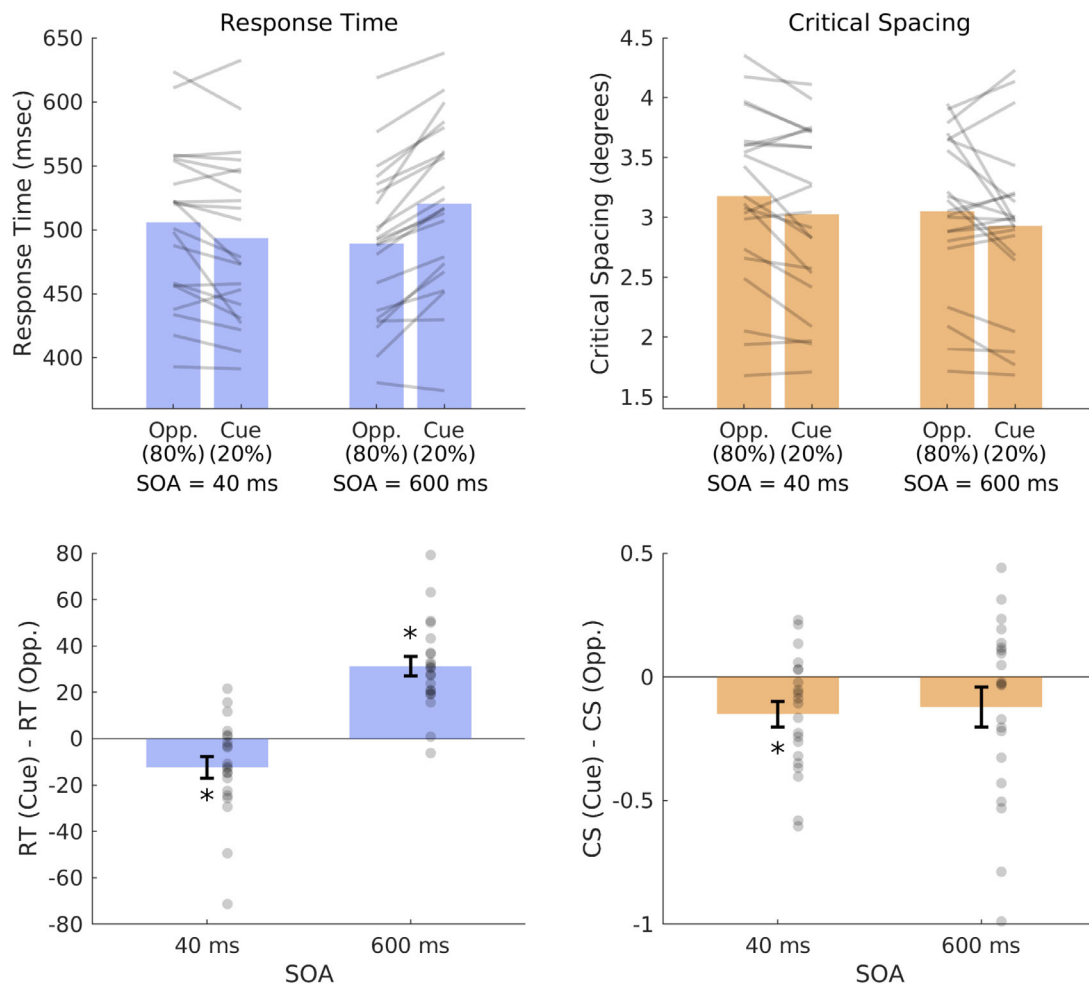


Figure 3. (Top) The effect of stimulus location relative to cue location (opposite or cue side) and SOA (40 or 600 ms) on RT (left; blue) and critical spacing (right; orange) for the crowding task. Gray lines represent matched individual subject data across location conditions. (Bottom) Mean within-subject cueing effects for each metric, defined as the difference between values when the stimulus appeared on the same side as the cue (Cue) and values when the stimulus appeared on the opposite side of the cue (Opp.). Gray dots represent individual subjects, and asterisks indicate significance α level < 0.05 from a planned comparison paired t test. Error bars are standard errors of the mean.

ms SOA) on crowding. Specifically, we compared critical spacing and RT for each combination of SOA (40 ms or 600 ms) and location (cue or opposite side) (Figure 2). For each metric, we also computed the magnitude of the cueing effect by calculating within-subject differences between values when the stimulus appeared on the same side as the cue (“Cue” in Figure 3) and values when the stimulus appeared on the opposite side of the cue (“Opp.” in Figure 3).

For one-half of the blocks, the SOA was 40 ms to maximize involuntary spatial attention directed to the cue location while not allowing enough time for allocation of voluntary attention (Posner, Cohen, & Rafal, 1982; Rokem, Landau, Garg, Prinzmetal, & Silver, 2010). For these trials (Figure 3, top left), the mean RT was faster when the stimulus appeared on the cue side (494 ms) compared with the opposite side (506

ms), indicating that involuntary attention was allocated to the cue side. The magnitude of this cueing effect (cue RT - opposite RT) was -12 ms (Figure 3, bottom left), and this was significantly less than zero ($d = -0.58$, $t_{20} = -2.66$, $p = 0.015$). The mean r^2 values for the lines fit to RT over the range of target/flanker spacings (see Methods) were fairly low (0.75 and 0.47 for the opposite and cue sides, respectively). To confirm that the cueing effect for involuntary attention was not just a consequence of the quality of the linear fit, we computed the effect of cueing on RT for correct trials in the unflanked condition. This mean RT effect was also significantly less than zero (-17 ms; $d = -0.82$; $t_{20} = -3.77$; $p = 0.001$), providing further evidence that the cue was effective in capturing involuntary attention.

For the 40 ms SOA, mean critical spacing was smaller when the stimulus appeared on the cue side (3.03°)

compared with the opposite side (3.18°) (Figure 3, top right). The magnitude of this cueing effect was -0.15° (Figure 3, bottom right), and this was significantly less than zero ($d = -0.64$; $t_{20} = -2.93$; $p = 0.008$). Overall, the Weibull function fit the accuracy (percent correct) data well for the short SOA trials: mean r^2 values were 0.93 and 0.87 for the opposite and cue sides, respectively. Taken together, these results demonstrate that involuntary attention leads to both faster RT and smaller critical spacing in visual crowding.

For the other one-half of the blocks, the SOA was 600 ms, leaving sufficient time for subjects to overcome the initial involuntary capture of attention by the cue and to then allocate voluntary attention to the opposite side, where the stimulus most often appeared (Posner, Cohen, & Rafal, 1982; Rokem, Landau, Garg, Prinzmetal, & Silver, 2010). For these trials (Figure 3, top left), mean RT was faster when the stimulus appeared on the opposite side (489 ms) compared with the cue side (520 ms), indicating that voluntary attention was successfully allocated to the higher probability opposite side. The magnitude of this cueing effect was 31 ms (Figure 3, bottom left), and this was significantly greater than zero ($d = 1.62$; $t_{20} = 7.44$; $p = 3.53e-7$). As for the 40-ms SOA, the r^2 values for the lines fit to RTs for the 600 ms SOA over the range of target/flanker spacings were low: 0.82 and 0.52 for the opposite and cue sides, respectively. However, once again, correct trials from the unflanked condition confirmed a large cueing effect on RT that was significantly greater than zero (43 ms; $d = 1.72$; $t_{20} = 7.87$; $p = 1.49e-7$).

Interestingly, and in contrast with RT, the mean critical spacing was greater when the stimulus appeared on the opposite side (3.05°) compared with the cue side (2.93°) for the long SOA (Figure 3, top right). However, the magnitude of the cueing effect on critical spacing (-0.12°) (Figure 3, bottom right) was not significantly different from zero ($d = -0.33$; $t_{20} = -1.53$; $p = 0.14$). Overall, the Weibull function fit the accuracy (percent correct) data well for the long SOA trials: mean r^2 values were 0.96 and 0.87 for the opposite and cue sides, respectively. Taken together, these results indicate that allocation of voluntary attention to the higher probability opposite side leads to much faster RT but no significant change in critical spacing. A repeated-measures analysis of variance revealed that the interaction of SOA and location was significant for RT ($F_{1,20} = 37.8$; $p = 5.34e-6$), but was not significant for critical spacing ($F_{1,20} = 0.13$; $p = 0.72$). These results indicate that long and short SOAs produced significantly different patterns for RT but not for critical spacing.

We also conducted separate analyses for those participants who had some knowledge of the study design and for those who were completely naive. Seven participants knew that the SOA could be either short or long. For these subjects, mean RT cueing effects for the

short and long SOAs were -5.34 ms (standard error of the mean [SEM] = 11.9 ms) and 37.2 ms (SEM = 7.25 ms), respectively, and the mean critical spacing cueing effects for the short and long SOAs were -0.18° (SEM = 0.075°) and -0.24° (SEM = 0.15°), respectively. For the 14 participants who were completely naive to the study, the mean RT cueing effects for the short and long SOAs were -15.8 ms (SEM = 3.73 ms) and 28.3 ms (SEM = 5.15 ms), respectively, and the mean critical spacing cueing effects for the short and long SOAs were -0.14° (SEM = 0.069°) and -0.064° (SEM = 0.092°), respectively. Overall, the main SOA/location trends were evident when analyzing data either from the 14 naive subjects or from the 7 subjects who had some information about the study design.

The highly significant cueing effect for RTs on the long SOA trials is evidence that the cue was effective at directing voluntary attention to the opposite side. However, one possible explanation for our finding of a nonsignificant negative cueing effect for critical spacing but a significant positive cueing effect for RT for the long SOA trials (Figure 3) is a trade-off between attentional effects on RT and on critical spacing. We, therefore, tested for speed/accuracy trade-offs in cueing effects for both SOAs by correlating the magnitude of individual subjects' RT cueing effect with the magnitude of their critical spacing cueing effect (Figure 4). We found no significant correlation between these two cueing effects for either short SOA (Figure 4, left) ($r = -0.290$; $p = 0.202$) or long SOA (Figure 4, right) ($r = 0.010$; $p = 0.967$) trials. The lack of strong correlations between cueing effects for RT and for critical spacing for both short and long SOAs indicates that subjects in this study likely did not have significant trade-offs between attentional effects on RT and on critical spacing.

Finally, we tested whether the magnitudes of the effects of involuntary and voluntary attention were correlated across subjects. Some studies have described how competition between involuntary and voluntary attention can affect perceptual processing (Berger, Henik, & Rafal, 2005; Fukuda & Vogel, 2009). Perhaps a subject who more successfully overcame the initial involuntary capture of attention by the cue (short SOA trials) was also able to more effectively direct their attention to the opposite side (long SOA trials), where the stimulus most often appeared. To test this relationship, we correlated the magnitude of cueing effects for short and long SOA trials across subjects for both RT and critical spacing. We found no significant correlation between these two cueing effects for either RT (Figure 5, left) ($r = -0.287$; $p = 0.207$) or for critical spacing (Figure 5, right) ($r = 0.347$; $p = 0.123$). These results indicate that the magnitude of an individual's cueing effect for one spatial attention mechanism (involuntary or voluntary) does not reliably predict the other.

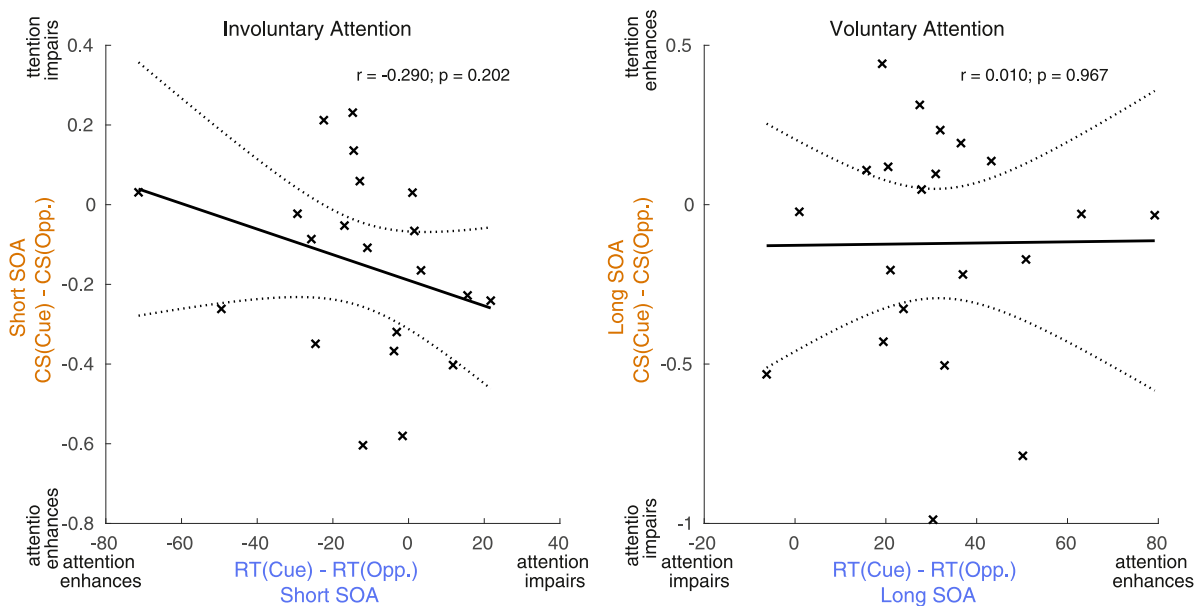


Figure 4. Cueing effects on RT were not strongly correlated with cueing effects on critical spacing for either short SOA (left) or long SOA (right) trials. The 'x's represent individual subjects. The solid and dashed lines represent the linear regression fits and 95% confidence intervals, respectively. Pearson's r and p values for the correlations are displayed in the upper right corner of each plot. Attention "enhances" or "impairs" labels correspond with the direction of the cueing effect for each of these metrics. Specifically, enhanced processing due to attention (i.e., faster RT/smaller critical spacing) is associated with a negative cueing effect (Cue < Opp.) for involuntary attention and with a positive cueing effect (Cue > Opp.) for voluntary attention.

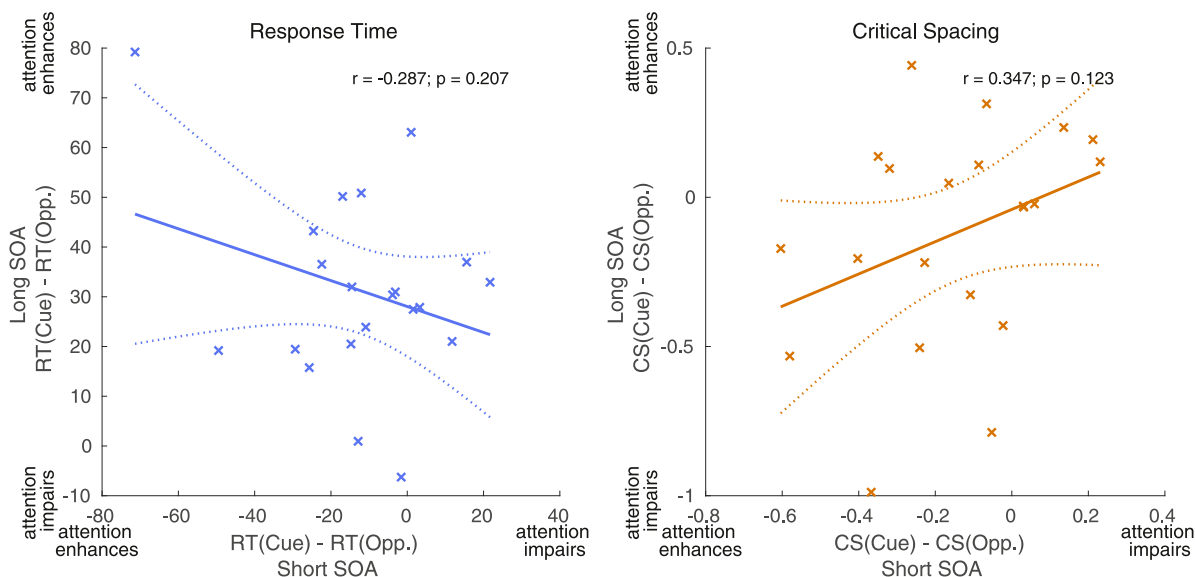


Figure 5. Cueing effects for involuntary (short SOA trials) and voluntary attention (long SOA trials) were not significantly correlated across individual subjects for both RT (left; blue) and critical spacing (right; orange). The 'x's represent individual subjects. The solid and dashed lines represent the linear regression fits and 95% confidence intervals, respectively. Pearson's r and p values for the correlations are displayed in the upper right corner of each plot. Attention "enhances" or "impairs" labels correspond to the direction of the cueing effect for each of these metrics. Specifically, enhanced processing due to attention (i.e., faster RT/smaller critical spacing) is associated with a negative cueing effect (Cue < Opp.) for involuntary attention and with a positive cueing effect (Cue > Opp.) for voluntary attention.

Discussion

We used an anticueing paradigm to measure the effects of involuntary and voluntary spatial attention on a visual crowding task. In our study, all stimulus and task factors were identical for the involuntary and voluntary conditions except for the SOA between the cue and stimulus presentations. Additionally, by customizing the range of target/flanker spacings for each subject, we more effectively avoided floor and ceiling effects on performance compared to other similar studies of attention and crowding. Our data set includes a large number of participants (21 that were included in the analyses presented here) and a substantial amount of data per subject (3,840 trials of the anticueing task). In comparison, recent studies of the effects of spatial attention on crowding (e.g., Yeshurun & Rashal, 2010; Albonico et al., 2018; Kewan-Khalayly, Migó, & Yashar, 2022) included 16 or fewer subjects per main experiment and 1,280 or fewer trials per subject. Our study therefore has high sensitivity for detecting possible cueing effects on RT and critical spacing.

For both involuntary and voluntary attention, we found decreases in RT for target orientation discrimination when spatial attention was directed to the target location compared to when attention was directed elsewhere. We also showed that directing involuntary attention to the target location with a peripheral cue decreased critical spacing compared with when attention was directed elsewhere. Interestingly, we did not find any significant difference in critical spacing when voluntary attention was directed to the target location compared to when it was directed elsewhere, and we showed that this lack of a voluntary attention effect could not be explained by trade-offs between attentional effects on RT and on critical spacing.

Another possibility is that the onset of the stimulus could have led to some capture of involuntary attention at the stimulus location, potentially obscuring a cueing effect on critical spacing for the long SOA trials. However, the fact that twenty of twenty-one subjects showed a positive RT cueing effect for the long SOA (Figure 3) argues against a significant contribution of capture of involuntary attention by the target for long SOA trials. Moreover, when voluntary attention (long SOA) was directed to the opposite side (blue line in Figure 2), overall RTs were faster for this condition compared with any of the other conditions. Taken together, these results suggest that the effects of voluntary attention on RT were much greater than any possible effects of involuntary shifts of attention due to stimulus onset.

Overall, we found that short and long SOAs did not produce significantly different patterns of critical

spacing, even though our RT results provide evidence that the cues effectively engaged involuntary and voluntary attention. If both involuntary and voluntary attention decreased critical spacing, we would have expected to see a significant cross-over interaction between SOA and cue location, with a positive cueing effect (critical spacing greater for cue compared with opposite trials) for the long SOA trials and a negative cueing effect (critical spacing greater for opposite compared to cue trials) for the short SOA trials. Although we did observe such a cross-over interaction for RT (Figure 3, left), we did not observe this for critical spacing (Figure 3, right). This lack of interaction for critical spacing is perhaps unexpected, given voluntary attention's facilitatory effects on performance for a number of visual tasks (Carrasco, 2011). We explore possible differences between the effects of attention on critical spacing and crowding and on other visual tasks in the sections below.

We also showed that critical spacing cueing effect sizes, as measured by Cohen's d , were not very large for either SOA (-0.64 for a short SOA and -0.33 for a long SOA), indicating that neither involuntary nor voluntary attention substantially modulated critical spacing. Finally, we showed that, for both RT and critical spacing, involuntary attention cueing effects were not strongly correlated with voluntary attention cueing effects across participants.

Effects of spatial attention on crowding and critical spacing

There is much debate about how attention affects visual crowding in general and critical spacing in particular. Most studies of the effects of involuntary attention have found enhanced perceptual performance on crowding tasks, and some of these also reported significant effects of involuntary attention on critical spacing (Yeshurun & Rashal, 2010; Rashal & Yeshurun, 2014; Kewan-Khalayly, Migó, & Yashar, 2022) while others did not (Felisberti, Solomon, & Morgan, 2005; Scolari, Kohnen, Barton, & Awh, 2007). Yeshurun and Rashal (2010) hypothesized that they observed a significant decrease in critical spacing with involuntary attention while other investigators did not because their peripheral cue did not act as a forward mask on the processing of the subsequently presented target. For the short SOA trials in our study, we also found a significant decrease in critical spacing when involuntary attention was directed to the target location compared with when it was directed elsewhere, and we avoided forward masking by employing a cue consisting of vertical lines on either side of the possible target locations instead of cueing the target location itself.

Reports in the literature on possible effects of voluntary attention on critical spacing in crowding are more limited. Albonico et al. (2018) used a long SOA

(400 ms) to test the effects of three different cue types (dot, small box, and large box) on critical spacing. They found that only the dot cue significantly decreased critical spacing. However, the goal of their study was to distinguish between orienting and focusing of attention, so they always used a peripheral cue to direct attention to the crowded stimulus. The lack of a symbolic cue makes it difficult to separate the effects of voluntary from those of involuntary attention in their study. Perhaps the large box cue used by [Albonico et al. \(2018\)](#), which encompasses both target and flanker locations, is most conceptually similar to our anticueing approach to isolating involuntary and voluntary attention effects. Although we used differences in cue/target SOA to accomplish this, the large box cue in [Albonico et al. \(2018\)](#) spatially separates the cued region (where involuntary attention is captured) from the stimulus region (where voluntary attention is directed). The lack of a significant cueing effect on critical spacing for the large cue in their study is consistent with what we found for our long SOA trials.

Although studies of the effects of voluntary attention on critical spacing have been limited and inconclusive, this type of attention has been shown to modulate other aspects of crowding. [Freeman and Pelli \(2007\)](#) showed that an attentional cue could provide an escape from crowding in a change detection task for a long SOA (600 ms). In this study, manipulations such as decreasing spacing and adding flankers impaired change detection in uncued trials but not in trials where the object to be changed was precued. [Mareschal, Morgan, & Solomon \(2010\)](#), instead of using a cueing design, instructed participants to attend to different aspects of a crowded stimulus. Specifically, they measured how attending to a radial target/flanker configuration differed from attending to a tangential target/flanker configuration when both were presented at the same time in a cross-shaped stimulus array. In general, flankers along a radial axis crowd more strongly than tangential flankers ([Toet & Levi, 1992](#)), and [Mareschal, Morgan, & Solomon \(2010\)](#) found a similar radial/tangential asymmetry that was based only on allocation of voluntary attention.

Some studies have examined the effects of attention on brain responses to crowded stimuli ([Fang & He, 2008](#); [Chen et al., 2014](#)). Using functional magnetic resonance imaging (fMRI), [Chen et al. \(2014\)](#) found that the magnitude of the behavioral crowding effect was closely linked with a suppressive cortical interaction in V1. Specifically, the peak amplitudes of the fMRI signal were greater for large target/flanker spacings compared with small spacings, indicating that stronger crowding was associated with greater physiological suppression of visual responses. Furthermore, this suppression effect was more prominent when the stimuli were attended versus when they were passively viewed.

Distinct effects of involuntary and voluntary attention on the spatial resolution of perception

Because performance on crowding tasks is dependent on both target/flanker spacing and on the eccentricity of the target ([Bouma, 1970](#); [Whitney & Levi, 2011](#)), it has been thought that it is limited by the spatial resolution of stimulus representations in the visual system ([Parkes, Lund, Angelucci, Solomon, & Morgan, 2001](#); [Balas, Nakano, & Rosenholtz, 2009](#); [Dakin, Cass, Greenwood, & Bex, 2010](#); [Greenwood, Bex, & Dakin, 2010](#); [Freeman & Simoncelli, 2011](#); [Rosenholtz, 2016](#)). Attention has been shown to influence the spatial resolution of texture discrimination, with involuntary and voluntary attention showing distinct effects ([Yeshurun & Carrasco, 1998, 2008](#); [Yeshurun, Montagna, & Carrasco, 2008](#); [Barbot & Carrasco, 2017](#); [Jigo, Heeger, & Carrasco, 2021](#)). Based on these results, it has been hypothesized that involuntary attention always increases perceptual spatial resolution, even when that hinders texture discrimination, whereas voluntary attention can flexibly adapt the spatial resolution of perception to match the demands of the task ([Barbot & Carrasco, 2017](#)).

Physiologically, the effects of spatial attention on the spatial resolution of stimulus representations are related to neuronal RF sizes. Directing spatial attention to one of multiple objects within a single RF biases responses in favor of the attended object ([Desimone & Duncan, 1995](#)). At the single-cell level, these attentional effects have been observed as both a scaling of neuronal responses to an attended stimulus by a gain factor ([McAdams & Maunsell, 1999](#)) and a shrinking of neuronal RFs around an attended stimulus ([Anton-Erxleben, Stephan, & Treue, 2009](#)). Furthermore, RFs in humans and other animals have been observed to both shrink in size and shift toward the locus of attention with sustained spatial attention ([Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006](#); [Klein, Harvey, & Dumoulin, 2014](#)). Using computational modeling approaches, [Baruch and Yeshurun \(2014\)](#) showed that this reconfiguration of RFs with attention could explain a number of attentional effects on neural responses, and [Theiss, Bowen, and Silver \(2021\)](#) showed that a similar mechanism could be implemented in a convolutional neural network, resulting in attentional enhancement of performance on a visual crowding task. Additionally, [He, Wang, and Fang \(2019\)](#) showed that, after perceptual learning of a crowded orientation discrimination task, decreases in RF size of individual fMRI voxels in cortical area V2 correlated with improved performance that resulted from perceptual learning. For a separate group of subjects, training on the orientation discrimination task in the absence of flankers also resulted in improved performance, but this was not correlated with changes in RF size as measured with fMRI.

Given the substantial behavioral, physiological, and computational evidence supporting the beneficial effects of increased spatial resolution by voluntary attention, it is surprising that we saw no significant change in critical spacing when voluntary attention was directed to the target location compared with when it was directed elsewhere. However, we note that we did not include a baseline or neutral cue condition in our study, so fully differentiating possible beneficial and detrimental effects of attention on performance was not possible. Furthermore, we can not rule out possible contributions of inhibition of return (IOR) to the cue location in the long SOA trials. In IOR, RT is slower for cued than for uncued locations for SOAs greater than 300 ms (Posner & Cohen, 1984). In our anti-cueing design, a facilitatory effect of voluntary attention to the opposite location on RT cannot be dissociated from IOR to the cue location. Previous work has shown that IOR is not fully eliminated by voluntary attention that was engaged by informative peripheral cues (Chica & Lupiáñez, 2009). However, the IOR was found to be less prominent for discrimination tasks than detection tasks (Chica, Lupiáñez, & Bartolomeo, 2006), suggesting that it may have played a more minor role in our orientation discrimination task. Overall, given that we did not observe a significant cueing effect on critical spacing for long SOA trials, the IOR likely did not have a large effect on critical spacing, although it may have influenced RT.

One difference between our anticueing study and the texture discrimination tasks described before in this section (Yeshurun, Montagna, & Carrasco, 2008; Barbot & Carrasco, 2017) is that the voluntary attention cue in our crowding task provides less spatial information than the cue in the texture discrimination tasks, given that we used an interleaved range of target/flanker spacings. More specifically, both types of tasks contain a cue that provides information about target location, but in our crowding task, there is also task-irrelevant trial-to-trial uncertainty about the spacing between the target and its flankers. One direction for future work is to investigate how cues that provide information about target/flanker spacing or similarity (Scolari, Byers, & Serences, 2012) impact optimal performance on crowding tasks.

Another possibility is that the critical spacing of visual crowding is not fundamentally determined by the spatial resolution of perception or neuronal RF size. The neurotransmitter acetylcholine decreases excitatory RF size in marmoset primary visual cortex (Roberts et al., 2005), and enhancement of cholinergic signaling with the cholinesterase inhibitor donepezil decreases the spatial spread of the fMRI response to visual stimuli in human visual cortex (Silver, Shenav, & D'Esposito, 2008), a result that is consistent with smaller excitatory RFs. Perceptually, donepezil reduces visual surround suppression in humans (Kosovicheva, Sheremata, Rokem, Landau, & Silver, 2012) and

sharpens visual spatial perception in a contrast decrement detection task in the presence of flankers (Gratton et al., 2017). In contrast with these reports of improved spatial resolution of visual perception in humans after cholinergic enhancement, donepezil was found to have no significant effect on critical spacing of visual crowding in a letter identification task (Kosovicheva, Sheremata, Rokem, Landau, & Silver, 2012). These pharmacological results suggest a possible distinction between critical spacing in crowding and other perceptual and neurophysiological measures of the spatial resolution of stimulus representations.

Finally, it is somewhat surprising that we observed no significant correlation between voluntary and involuntary cueing effects across participants. Other cognitive factors such as memory capacity have been shown to be positively correlated with the ability to resist attentional capture from salient involuntary cues (Fukuda & Vogel, 2009). This result and those from other similar studies (Berger, Henik, & Rafal, 2005) suggest that subjects with stronger voluntary attention may be better able to overcome/ignore capture by involuntary attention. However, we did not observe a significant relationship between a subject's ability to use the peripheral cue to direct their attention to the more likely opposite side (long SOA trials) and their ability to overcome capture by involuntary attention (short SOA trials). It could be informative to conduct a similar correlation study for other tasks that show strong effects of attention on perception. Furthermore, it would be interesting to correlate response amplitudes (Dugué, Merriam, Heeger, & Carrasco, 2020) and RF sizes, as measured physiologically, for voluntary and involuntary attention.

Keywords: visual crowding, critical spacing, exogenous attention, endogenous attention

Acknowledgments

The authors thank Teresa Canas-Bajo and Adeola Harewood-Smith for their early work in developing the ideas and concepts for this study, Ahmad Ahmadzada for help with data collection, and Reem Almagati, Alisa Braun, Kelly Byrne, Elizabeth Lawler, Arjun Mukerji, Julie Self, Justin Theiss, and Devavrat Vartak for helpful discussions.

Supported by National Eye Institute grant R01 EY025278 (M.A.S.) and National Eye Institute Core Grant P30 EY003176.

Commercial relationships: none.

Corresponding author: Michael A. Silver.

Email: masilver@berkeley.edu.

Address: 360 Minor Hall, School of Optometry, University of California, Berkeley 97420-2020, USA.

References

- Albonico, A., Martelli, M., Bricolo, E., Frasson, E., & Daini, R. (2018). Focusing and orienting spatial attention differently modulate crowding in central and peripheral vision. *Journal of Vision*, *18*(3), 4.1–4.17.
- Anton-Erxleben, K., & Carrasco, M. (2013). Attentional enhancement of spatial resolution: Linking behavioural and neurophysiological evidence. *Nature Reviews Neuroscience*, *14*(3), 188–200.
- Anton-Erxleben, K., Stephan, V. M., & Treue, S. (2009). Attention reshapes center-surround receptive field structure in macaque cortical area MT. *Cerebral Cortex*, *19*(10), 2466–2478.
- Balas, B., Nakano, L., & Rosenholtz, R. (2009). A summary-statistic representation in peripheral vision explains visual crowding. *Journal of Vision*, *9*(12), 13.1–13.18.
- Barbot, A., & Carrasco, M. (2017). Attention modifies spatial resolution according to task demands. *Psychological Science*, *28*(3), 285–296.
- Barbot, A., Landy, M. S., & Carrasco, M. (2012). Differential effects of exogenous and endogenous attention on second-order texture contrast sensitivity. *Journal of Vision*, *12*(8), 6.1–6.25.
- Baruch, O., & Yeshurun, Y. (2014). Attentional attraction of receptive fields can explain spatial and temporal effects of attention. *Visual Cognition*, *22*(5), 704–736.
- Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology: General*, *134*(2), 207–221.
- Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature*, *226*(5241), 177–178.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433–436.
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525.
- Chen, J., He, Y., Zhu, Z., Zhou, T., Peng, Y., & Zhang, X. et al. (2014). Attention-dependent early cortical suppression contributes to crowding. *Journal of Neuroscience*, *34*(32), 10465–10474.
- Chica, A. B., & Lupiáñez, J. (2009). Effects of endogenous and exogenous attention on visual processing: an inhibition of return study. *Brain Research*, *1278*, 75–85.
- Chica, A. B., Lupiáñez, J., & Bartolomeo, P. (2006). Dissociating inhibition of return from endogenous orienting of spatial attention: Evidence from detection and discrimination tasks. *Cognitive Neuropsychology*, *23*(7), 1015–1034.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The eyelink toolbox: Eye tracking with MatLab and the psychophysics toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613–617.
- Dakin, S. C., Cass, J., Greenwood, J. A., & Bex, P. J. (2010). Probabilistic, positional averaging predicts object-level crowding effects with letter-like stimuli. *Journal of Vision*, *10*(10), 14.1–14.16.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*(1), 193–222.
- Dugué, L., Merriam, E. P., Heeger, D. J., & Carrasco, M. (2020). Differential impact of endogenous and exogenous attention on activity in human visual cortex. *Scientific Reports*, *10*(1), 21274.
- Fang, F., & He, S. (2008). Crowding alters the spatial distribution of attention modulation in human primary visual cortex. *Journal of Vision*, *8*(9), 6.1–6.9.
- Felisberti, F. M., Solomon, J. A., & Morgan, M. J. (2005). The role of target salience in crowding. *Perception*, *34*(7), 823–833.
- Fernández, A., Okun, S., & Carrasco, M. (2022). Differential effects of endogenous and exogenous attention on sensory tuning. *Journal of Neuroscience*, *42*(7), 1316–1327.
- Freeman, J., & Pelli, D. G. (2007). An escape from crowding. *Journal of Vision*, *7*(2), 22.1–22.14.
- Freeman, J., & Simoncelli, E. P. (2011). Metamers of the ventral stream. *Nature Neuroscience*, *14*(9), 1195–1201.
- Fukuda, K., & Vogel, E. K. (2009). Human variation in overriding attentional capture. *Journal of Neuroscience*, *29*(27), 8726–8733.
- Gratton, C., Yousef, S., Aarts, E., Wallace, D. L., D’Esposito, M., & Silver, M. A. (2017). Cholinergic, but not dopaminergic or noradrenergic, enhancement sharpens visual spatial perception in humans. *Journal of Neuroscience*, *37*(16), 4405–4415.
- Greenwood, J. A., Bex, P. J., & Dakin, S. C. (2010). Crowding changes appearance. *Current Biology*, *20*(6), 496–501.
- He, D., Wang, Y., & Fang, F. (2019). The critical role of V2 population receptive fields in visual orientation crowding. *Current Biology*, *29*(13), 2229–2236.
- Jigo, M., & Carrasco, M. (2020). Differential impact of exogenous and endogenous attention on the contrast sensitivity function across eccentricity. *Journal of Vision*, *20*(6), 11.1–11.25.

- Jigo, M., Heeger, D. J., & Carrasco, M. (2021). An image-computable model of how endogenous and exogenous attention differentially alter visual perception. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(33), e2106436118.
- Kewan-Khalayly, B., Migó, M., & Yashar, A. (2022). Transient attention equally reduces visual crowding in radial and tangential axes. *Journal of Vision*, *22*(9), 3.1–3.9.
- Klein, B. P., Harvey, B. M., & Dumoulin, S. O. (2014). Attraction of position preference by spatial attention throughout human visual cortex. *Neuron*, *84*(1), 227–237.
- Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in Psychtoolbox-3. *Perception*, *36*(14), 1.
- Kosovicova, A. A., Sheremata, S. L., Rokem, A., Landau, A. N., & Silver, M. A. (2012). Cholinergic enhancement reduces orientation specific surround suppression but not visual crowding. *Frontiers in Behavioral Neuroscience*, *6*, 61.
- Levi, D. M. (2008). Crowding - an essential bottleneck for object recognition: A mini-review. *Vision Research*, *48*(5), 635–654.
- Mareschal, I., Morgan, M. J., & Solomon, J. A. (2010). Attentional modulation of crowding. *Vision Research*, *50*(8), 805–809.
- McAdams, C. J., & Maunsell, J. H. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *Journal of Neuroscience*, *19*(1), 431–441.
- Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience*, *4*(7), 739–744.
- Pelli, D. G. (1997). The videotoolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*(1), 3–25.
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma, & D. G. Bouwhuis (Eds.), *Attention and performance X: Control of language processes* (pp. 531–556). Hillsdale: Erlbaum.
- Posner, M. I., Cohen, Y., & Rafal, R. D. (1982). Neural systems control of spatial orienting. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *298*(1089), 187–198.
- Rashal, E., & Yeshurun, Y. (2014). Contrast dissimilarity effects on crowding are not simply another case of target saliency. *Journal of Vision*, *14*(6), 9.1–9.12.
- Roberts, M., Zinke, W., Guo, K., Robertson, R., McDonald, J. S., & Thiele, A. (2005). Acetylcholine dynamically controls spatial integration in marmoset primary visual cortex. *Journal of Neurophysiology*, *93*(4), 2062–2072.
- Rokem, A., Landau, A. N., Garg, D., Prinzmetal, W., & Silver, M. A. (2010). Cholinergic enhancement increases the effects of voluntary attention but does not affect involuntary attention. *Neuropsychopharmacology*, *35*(13), 2538–2544.
- Rosenholtz, R. (2016). Capabilities and limitations of peripheral vision. *Annual Review of Vision Science*, *2*, 437–457.
- Scolari, M., Byers, A., & Serences, J. T. (2012). Optimal deployment of attentional gain during fine discriminations. *Journal of Neuroscience*, *32*(22), 7723–7733.
- Scolari, M., Kohonen, A., Barton, B., & Awh, E. (2007). Spatial attention, preview, and popout: Which factors influence critical spacing in crowded displays? *Journal of Vision*, *7*(2), 7.1–7.23.
- Silver, M. A., Ress, D., & Heeger, D. J. (2007). Neural correlates of sustained spatial attention in human early visual cortex. *Journal of Neurophysiology*, *97*(1), 229–237.
- Silver, M. A., Shenhav, A., & D'Esposito, M. (2008). Cholinergic enhancement reduces spatial spread of visual responses in human early visual cortex. *Neuron*, *60*(5), 904–914.
- Theiss, J. D., Bowen, J. D., & Silver, M. A. (2021). Spatial attention enhances crowded stimulus encoding across modeled receptive fields by increasing redundancy of feature representations. *Neural Computation*, *34*(1), 190–218.
- Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research*, *32*(7), 1349–1357.
- Whitney, D., & Levi, D. M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends in Cognitive Sciences*, *15*(4), 160–168.
- 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*(9), 1156–1160.
- Yantis, S., & Jonides, J. (1990). Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(1), 121–134.
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by

enhancing spatial resolution. *Nature*, 396(6706), 72–75.

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.

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision*, 10(10), 16.1–16.12.