

Predicting bias in perceived position using attention field models

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Attention is the mechanism through which we select relevant information from our visual environment. We have recently demonstrated that attention attracts receptive fields across the visual hierarchy (Klein, Harvey, & Dumoulin, 2014). We captured this receptive field attraction using an attention field model. Here, we apply this model to human perception: We predict that receptive field attraction results in a bias in perceived position, which depends on the size of the underlying receptive fields. We instructed participants to compare the relative position of Gabor stimuli, while we manipulated the focus of attention using exogenous cueing. We varied the eccentric position and spatial frequency of the Gabor stimuli to vary underlying receptive field size. The positional biases as a function of eccentricity matched the predictions by an attention field model, whereas the bias as a function of spatial frequency did not. As spatial frequency and eccentricity are encoded differently across the visual hierarchy, we speculate that they might interact differently with the attention field that is spatially defined.

Introduction

Visual attention is the mechanism through which we select relevant information from our visual environment. Selection of visual information can be based on several of its features, one of which is the location of the information in the visual field, also known as *visual spatial attention*.

Recent models of visual attention describe attention as a Gaussian component that amplifies neural responses (i.e., the attention field). The neural responses in the absence of attention are typically also conceptualized as Gaussians. Consequently, the effect of attention on neural processing is modeled as a Gaussian multiplication representing response amplification (Reynolds & Heeger, 2009; Womelsdorf, Anton-Erxleben, & Treue, 2008). This multiplicative amplification may be followed by a divisive process representing response normalization (Reynolds & Heeger, 2009).

Using functional magnetic resonance imaging (fMRI), we have recently shown that attention attracts receptive fields across the visual hierarchy in humans (Klein, Harvey, & Dumoulin, 2014). We captured this attraction with an attention field model that includes a multiplication between two Gaussian components (i.e., the attention field and the receptive fields) without normalization (Klein et al., 2014). This revealed that the size of the attention field was relatively constant across the visual cortex even though the amount of receptive field attraction increased up the visual hierarchy. As the attention field model predicts a larger attraction for larger receptive fields, we suggested that the increase in the receptive field size up the visual hierarchy was the dominant cause of the increase in receptive field attraction.

On a perceptual level, attention biases the perceived position of stimuli outside the focus of attention away from the attended location (Shim & Cavanagh, 2005;

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Suzuki & Cavanagh, 1997). Assuming that the perceived position of a stimulus is related to its response distribution across a population of neurons tuned for spatial position, a shift of the distribution away from the attended location may produce a bias in perceived position. Suzuki and Cavanagh (1997) proposed three mechanisms through which attention could produce such a shift: (a) response suppression, (b) receptive field shrinkage, and (c) receptive field attraction. Our attention field model, as discussed above, offers a mathematical formalization of receptive field attraction. Therefore, it provides a quantitative framework to assess the contribution of receptive field attraction to the positional bias. We propose that attention attracts receptive fields, moving them from their original location to a position closer to the focus of attention. Consequently, any stimulus located near the focus of attention is now covered by receptive fields that were originally positioned further away from the attended location. This shifts the stimulus's response distribution away from the attended location, which is accompanied by a shift in the perceived position of the stimulus away from the attended location. As our attention field model predicts a larger attraction for larger receptive fields, we expect a larger positional bias when the underlying receptive fields are larger. Specifically, as receptive field size increases with eccentricity (Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Hubel & Wiesel, 1962; Van Essen, Newsome, & Maunsell, 1984) and tuning to lower spatial frequencies (Jones & Palmer, 1987), we expect that attention induces a larger positional bias for stimuli presented at higher eccentricities as well as stimuli containing lower spatial frequencies.

We examined the magnitude of the positional bias as a function of stimulus eccentricity and spatial frequency in two experiments, using an exogenous cueing paradigm to manipulate the focus of attention (Carrasco, Ling, & Read, 2004; Posner, 1980). We measured positional biases by instructing participants to compare the distance between two pairs of Gabor stimuli, one of which was centered on the previously cued location. Based on our model, we expect that when the cued location falls between the two Gabors making up the pair, both Gabors are perceived to be further away from the cued location. This in turn would lead to an increase in the perceived distance between the Gabors of the cued pair. In the first experiment, we varied the eccentricity at which the cue and Gabor pairs were presented and found that positional biases indeed increased with eccentricity, as expected from our model. In the second experiment, we varied the spatial frequency of the Gabor stimuli but did not find any variation in the positional biases across spatial frequency. In sum, the attention field model can explain the bias in perceived position of stimuli outside the

focus of attention as a function of eccentricity, but not spatial frequency. As spatial frequency and eccentricity are encoded differently across the visual hierarchy, we speculate that they might interact differently with the spatially defined attention field.

Methods

Experiment 1: Does the bias in perceived position scale with eccentricity?

The attention field model we used to capture receptive field attraction in human participants (Klein et al., 2014) predicts a larger attraction for larger receptive fields. Because it is known that the average receptive field size increases with eccentricity (Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Hubel & Wiesel, 1962; Van Essen et al., 1984), we expect a larger positional bias for stimuli presented at higher eccentricities.

Participants

Six participants participated in this experiment (all men, age range 26–33). Five participants were naive as to the purpose of the experiment. All participants had normal or corrected-to-normal visual acuity and gave informed consent. Four participants in this experiment participated in at least one other experiment as well.

Experimental setup

Stimuli were generated in Matlab (MathWorks, Natick, MA) using the PsychToolbox (Brainard, 1997; Pelli, 1997) on a PowerMac G5 with an ATI Radeon 9800 XT graphics card. The stimuli were presented on a LaCie 321 monitor (native resolution: $1,600 \times 1,200$; refresh rate: 60 Hz), with a mean luminance background of ~ 75 cd/m². Participants viewed the stimuli from a distance of 90 cm while their head was supported by a chin rest.

Stimuli and task

Throughout the experiment, a black cross ($0.2^\circ \times 0.2^\circ$) positioned at the center of the screen served as a fixation point. Each trial started with a precue period (lasting 750 ms) during which only the fixation cross was visible. On half of the trials, this period was followed by an exogenous cue (black dot, 0.25° in diameter), which flashed on the screen for 50 ms, at 3° , 6° , or 9° either left or right from the fixation cross (cue trials). On the remaining half of the trials, only the

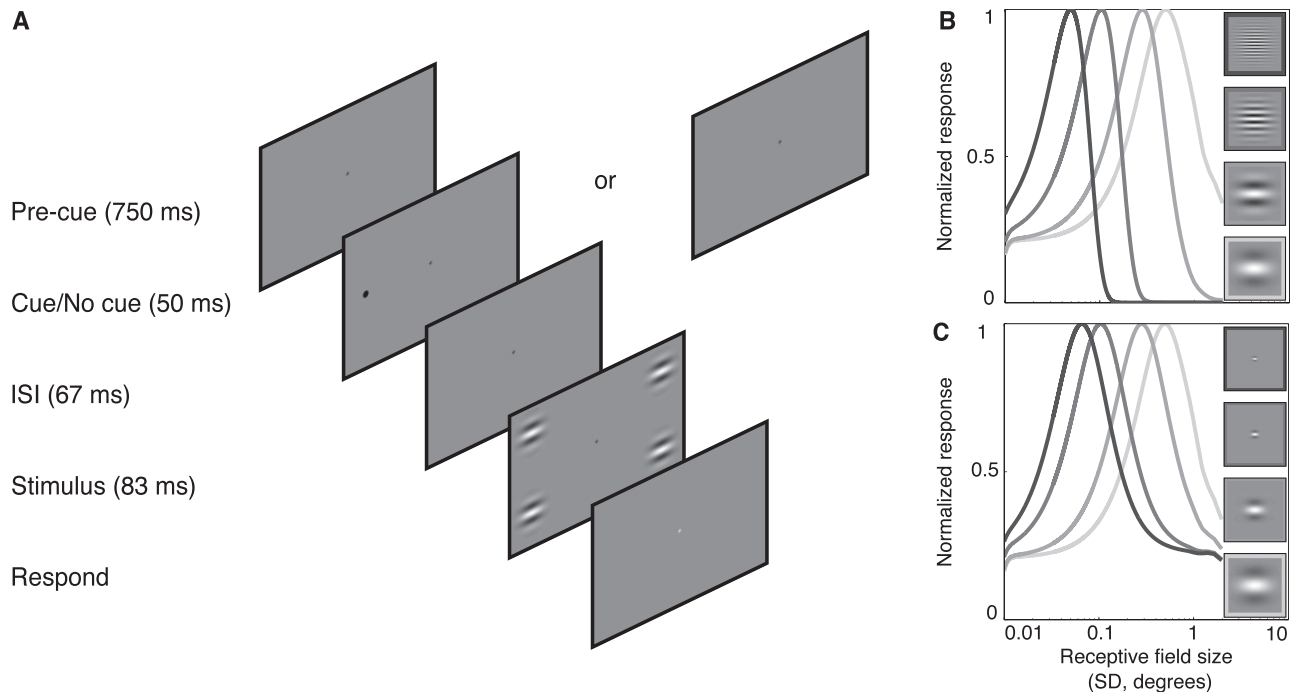


Figure 1. Stimulus and experimental procedure. (A) During the precue period (750 ms), only the fixation cross was presented. On half of the trials, this period was followed by a cue (50 ms), left or right of fixation. On the remaining half of the trials, only the fixation cross was presented during this period. After an interstimulus interval (ISI; 67 ms), two Gabor pairs were flashed on the screen (83 ms), left and right of fixation, centered on the cued location and the location opposite to that. After this period, the fixation cross turned white to prompt the participant to respond. Participants had to report which of the two Gabor pairs they perceived closer together (vertically) by pressing the “F” or “J” button for left and right, respectively. (B) Estimated responses to the Gabors used in Experiment 2 (insets) across a range of receptive field sizes (standard deviation). Responses are computed by convolving the Gabors with a filter model of spatial frequency-selective receptive fields. (C) Similar to (B) but now for the Gabors used in one of the control experiments (insets). The ratio between the spatial frequency and Gaussian standard deviation of the Gabors is kept constant, resulting in a constant width of the estimated responses across receptive field size.

fixation cross was presented (no cue trials). After an interstimulus interval (ISI) of 67 ms, four Gabors (45% Michelson contrast), arranged in two pairs, were presented. The two Gabors within a pair were horizontally aligned, and each pair was centered on the horizontal meridian. During cueing trials, the pairs were presented at the same distance from the fixation cross as the cue. The Gabors consisted of a Gaussian filtered (standard deviation: 0.33° , truncated at 1.8°) and horizontally oriented cosine grating (4.75 cycles per degree [cpd]; Figure 1A). The vertical center-to-center distance between the Gabors within one of the two pairs was fixed at 3° (standard pair), whereas the vertical distance within the other pair was systemically varied (test pair, see below). After presentation of the Gabor pairs, the fixation cross turned white, prompting the participant to respond, after which the next trial started. Both the standard and test pair had a 50% chance of being presented at the previously cued location (cue standard or cue test, respectively). In total, there were 2 (cue/no cue) $\times 2$ (cue standard/cue test) $\times 2$ (cue left/cue right) $\times 3$ (distance from fixation) = 24 conditions.

Participants had to report which of the two Gabor pairs they perceived as vertically closer together by pressing either “F” or “J” for the left or right Gabor pair, respectively. Note that we expect the Gabor pair on the cued side to be perceived further apart (see model below): Participants with a response bias for the cued side would thereby be more likely to show an effect opposite to the expected direction. The vertical distance between the test pair was controlled by a Quest staircase (Watson & Pelli, 1983) for each of the 24 conditions separately. Each staircase terminated after 20 trials and was used to initially estimate the point of subjective equality (PSE): the distance at which the test pair appeared as far apart as the standard pair, for each condition separately. Subsequently, 20 trials were presented for which the vertical distance between the test pairs was randomly jittered around the estimated PSE. The amount of jitter was randomly sampled from a uniform distribution, limited between -0.4° and 0.4° . In sum, 40 trials were presented per condition, resulting in 960 trials per session. Participants completed two sessions, totaling 1,920 trials per subject.

Analysis

We combined the presented vertical distances between the test pair and the participant's corresponding responses from the Quest and jitter trials and collapsed the data from both sessions. We fitted cumulative Gaussians (the distance x at $p = 0.5$: μ and the slope: σ) to each of the no-cue conditions. The value for μ was taken as the distance at which the test pair appears as far apart as the standard pair (PSE). Using bootstrapping (1,000 iterations), we generated a distribution of both fit parameters (μ and σ) and computed the median PSE and slope using these distributions. The median PSE served as a baseline measurement for each cue condition separately. Next, we corrected for any possible bias in perceived distance between the Gabor stimuli that was not due to cueing by subtracting the baseline PSEs obtained for each no-cue condition from the distances presented in the corresponding cue condition. Subsequently, we collapsed the vertical distances and responses from the cue left and cue right conditions. We then fitted cumulative Gaussians to the corrected distances and responses of each cue condition (cue test and cue standard conditions separately) and bootstrapped (1,000 iterations) the median and 95% confidence interval of both fit parameters. In addition, we collapsed the cue test and cue standard conditions together and fitted cumulative Gaussians to the collapsed data. Collapsing was done in such a way that a positive value indicates an increase in perceived distance between the Gabor stimuli due to cueing. Again, bootstrapping was used to obtain the median and 95% confidence interval of the PSE and slope.

Experiment 2: Does the bias in perceived position scale with spatial frequency?

Tuning to lower spatial frequencies is related to larger receptive fields (Jones & Palmer, 1987). As the attention field model predicts a larger attraction for larger receptive fields, we expect that a positional bias resulting from this attraction increases with lower spatial frequencies as well.

Participants

Six participants participated in this experiment (1 woman, age range 25–30). All participants were naive as to the purpose of this experiment. In addition, two participants completed an experiment designed to estimate the contrast differences needed between spatial frequencies to correct for differences in contrast sensitivity (see below). One participant was naive as to the purpose of this experiment. All participants had normal or corrected-to-normal visual acuity and gave

informed consent. All participants participated in at least one other experiment.

Stimulus and task

This experiment was similar to the eccentricity experiment, but now the cue and all Gabor pairs were presented at 3° distance, left and right from fixation. In addition, the stimuli were viewed from a 180-cm distance instead of 90 cm. The Gabors varied in spatial frequency between trials: either 1, 1.75, 4.75, or 10 cpd. Both pairs within the same trial had the same spatial frequency. This 10-fold range (~ 3.3 octaves) in spatial frequencies ensured stimulation of different-sized receptive fields (DeValois, Albrecht, & Thorell, 1982). We verified this by convolving the Gabors with a filter model resembling spatial frequency selective receptive fields (Jones & Palmer, 1987; Figure 1B). The contrasts of the Gabors were 17%, 21%, 33%, and 60% Michelson for the 1, 1.75, 4.75, and 10 cpd, respectively. These values were chosen to make all Gabors appear similar in contrast and were estimated in a separate experiment (see below). This experiment had 32 conditions and a total of 2,560 trials. Participants completed the experiment in two sessions.

To account for differences in perceived contrast across the range of spatial frequencies used in this experiment, we adjusted the contrast of the 1, 1.75, and 4.75 cpd Gabors to appear similar in contrast to that of the 10 cpd Gabor, which was fixed at 60% Michelson. The contrasts needed to achieve this were estimated in a separate experiment. This experiment used a similar procedure as the main experiments but differed in several ways. First, a cue was never presented prior to the Gabor pairs. Second, the Gabor pairs within one trial differed in spatial frequency and contrast: One was always 10 cpd and set to 60% Michelson contrast (standard pair), and the other pair was one of the remaining spatial frequencies, and its contrast was systematically varied (test pair). Participants were instructed to report which of the two Gabor pairs appeared higher in contrast by either pressing “F” or “J” for the left or right Gabor pair, respectively. Initially, Quest staircases were used to control the contrast of the test pair and estimate the contrast at the PSE after 25 trials, for each condition separately. Subsequently, 75 trials were presented in which the amount of contrast of the test pair was randomly jittered around the PSE estimated for the corresponding condition. The amount of jitter was randomly sampled from a uniform distribution, limited between -15% and 15% Michelson. This experiment had 2 (standard left/standard right) $\times 3$ (each of the three remaining spatial frequencies) = 6 conditions. One hundred trials were presented for each condition, totaling 600 trials per experiment. Two participants

completed the experiment. Data were analyzed by collapsing the responses and contrasts from the standard left and standard right conditions together, fitting cumulative Gaussians to the collapsed data and bootstrapping the median PSE values.

Control Experiment 1: Does the size of the Gabor influence the results?

In Experiment 2, we increased the spatial frequency of Gabors that had a constant size in the spatial domain. Doing so introduces more cycles of the cosine with higher spatial frequencies, narrowing the Gabors in the frequency domain. In this control experiment, we examine whether this confounding factor may have affected the results in Experiment 2 by fixing the size of the Gabors in the frequency domain and thus varying their size in the spatial domain.

Participants

Six participants participated in this experiment (1 woman, age range 25–31). Five participants were naive as to the purpose of this experiment. In addition, two participants completed an experiment designed to estimate the contrast differences needed between spatial frequencies to correct for differences in contrast sensitivity. One participant was naive as to the purpose of this experiment. All participants had normal or corrected-to-normal visual acuity and gave informed consent. All participants participated in at least one other experiment.

Stimulus and task

This experiment was similar to the spatial frequency experiment, except that the standard deviation of the Gabor's Gaussian filter was a set to one third of the Gabor's wavelength. This reduces the size of the Gabors with increasing spatial frequency and made the 10 cpd Gabors difficult to observe. We replaced this condition with the 7.5 cpd condition, reducing the range of spatial frequencies to ~ 2.9 octaves. This range is still sufficient to stimulate different-sized receptive fields between conditions (DeValois et al., 1982). We verified the size of the Gabors and the separation of the peaks in the frequency domain by applying the filter model (Jones & Palmer, 1987; Figure 1C). The Gabors' standard deviations were 0.33°, 0.19°, 0.07°, and 0.04°, and their contrasts were 23%, 26%, 41%, and 60% Michelson for 1, 1.75, 4.75, and 7.5 cpd, respectively. The contrast values were chosen to make all Gabor stimuli look similar in contrast and were estimated in an experiment identical to the contrast experiment conducted prior to Experiment 2. Participants com-

pleted 2,560 trials for this experiment, which were distributed across two sessions.

Control Experiment 2: Was spatial attention prompted by presenting a cue?

Effects of exogenous attention on perception should peak about 80 to 130 ms after the onset of the cue (Cheal & Lyon, 1991; Nakayama & Mackeben, 1989). Our initial ISI (67 ms) ensured a stimulus presentation in this window. If attention does indeed underlie our results, effects of cuing should become weaker on both shorter and longer intervals. Note that we do not expect the effect of cuing to completely disappear on both shorter and longer intervals. The positional bias can still be present even when the cue and stimulus are simultaneously presented or the cue and stimulus are separated by 1500 ms (Suzuki & Cavanagh, 1997). The important thing to notice here is that the increase in perceived distance due to cuing should be reduced for shorter and longer intervals. In this experiment, we verify this prediction.

Participants

Six participants participated in this experiment (1 woman, age range 22–31). Five participants were naive as to the purpose of this experiment. All participants had normal or corrected-to-normal visual acuity and gave informed consent. Four participants participated in at least one other experiment.

Stimulus and task

This experiment was similar to Experiment 1, but now the cue and Gabor stimuli were always presented at 3° left and right from fixation and the interval between cue offset and stimulus onset was either 0 ms, 67 ms, or 600 ms. The contrast was set to 33% Michelson. Participants completed two sessions, totaling 1,920 trials per subject.

Attention field model

The attention field model is summarized in Equation 1 below and is identical to the model that captures receptive field attraction in human subjects (Klein et al., 2014) and in macaques (Womelsdorf et al., 2008). The model consists of a multiplication between two Gaussian components but has no normalization process as in the attention field model proposed by Reynolds and Heeger (2009).

In the model, the onset of the cue attracts attention toward its location, which we model as a Gaussian-shaped attention field at the cued location. This attention field attracts receptive fields toward the cued location. We model the receptive field as a Gaussian as well; therefore, the receptive field attraction is given by a Gaussian multiplication:

$$\text{RF attraction} = \mu_{\text{or}} - \frac{\mu_{\text{or}}\sigma_{\text{af}}^2}{\sigma_{\text{af}}^2 + \sigma_{\text{rf}}^2} \quad (1)$$

where σ_{rf} and σ_{af} represent the size of the receptive field and the size of the attention field, respectively (i.e., the standard deviation of the Gaussian components). Furthermore, μ_{or} represents the receptive field's original location relative to the attention field.

All parameters in Equation 1 needed to obtain a prediction for the receptive field attraction, except for the attention field size, can be derived from our stimulus design and data. We model the original position of the receptive field relative to the attention field as the center-to-center distance between the cue and one of the Gabors, plus the receptive field attraction (i.e., half the increase in perceived distance measured for a specific condition). Estimating the receptive field sizes underlying the increase in perceived distance requires us to make assumptions about the relation between receptive field size and eccentricity and the relation between receptive field size and spatial frequency tuning. Receptive field size increases with eccentricity (Dumoulin & Wandell, 2008; Harvey & Dumoulin, 2011; Hubel & Wiesel, 1962; Van Essen et al., 1984), which we model as a linear function:

$$\text{Receptive field width} = a + bx \quad (2)$$

where x stands for the eccentricity. Furthermore, a and b are the intercept and slope coefficients, which we estimate to be 0.58 and 0.15, respectively. This estimate is based on data from V1, obtained in our fMRI study (Klein et al., 2014). Spatial frequency tuning is related to receptive field size: Larger receptive fields are tuned to lower spatial frequencies. Using a biological plausible relation between receptive field size and spatial frequency tuning (Jones & Palmer, 1987), we obtain an estimate of the receptive field size tuned to the spatial frequency in every spatial frequency condition:

$$\text{Receptive field width} = \frac{1}{\omega 3.3} \quad (3)$$

where ω represents the spatial frequency of the Gabors. As we know the receptive field attraction in every condition (half of the increase in perceived distance) and have an estimate of the receptive field size and original receptive field location in every condition, we can compute the attention field size necessary to produce the increase in positional bias in every condition separately:

$$\sigma_{\text{af}} = \sigma_{\text{or}} \sqrt{\frac{\mu_{\text{at}}}{\text{RF attraction}}} \quad (4)$$

We assess how model predictions for the increase in perceived distance compare to the positional biases we measure. As we do not have an independent estimate of the attention field size, we choose to make a qualitative rather than quantitative comparison. We compute the attention field size needed to produce the increase in perceived distance measured in every condition of the eccentricity and spatial frequency experiment (Equation 4). We use these attention field sizes to compute the receptive field attraction across a range of receptive field sizes (Equation 1) and multiply this by 2 to give the predicted increase in perceived distance. Doing so illustrates how well model predictions using the attention field size measured in one condition compare to perceived distance increments in the remaining conditions.

Results

The attention field model predicts an increase in perceived distance between the Gabors on the cued side

Our predictions are based on the following logic: The onset of the cue will attract attention to its location, leading to a receptive field attraction toward the cued location. As a consequence of the attraction, receptive fields whose original location was at the side of the Gabor's center opposite to the cued location (original RF location, Figure 2A) will move to a location that is aligned with the Gabor's center (RF location with attention field, Figure 2A). This receptive field attraction moves the cortical representation (solid and dashed circles, Figure 2B) of both Gabors within the pair away from the cued location (change in cortical location, Figure 2B). This change in cortical location increases the distance between the representations of the Gabors within the pair, leading to an increased perceived distance between the Gabors on the cued side. An attention field model predicts that this increase in perceived distance depends on the size of both the attention field and the receptive fields underlying the positional bias (Figure 2C). In sum, the attention field model predicts larger increases in perceived distance with larger receptive fields and smaller attention fields.

Experiment 1: The bias in perceived position scales with eccentricity

To assess the effect of cueing on the perceived distance between the two Gabors within a pair, we

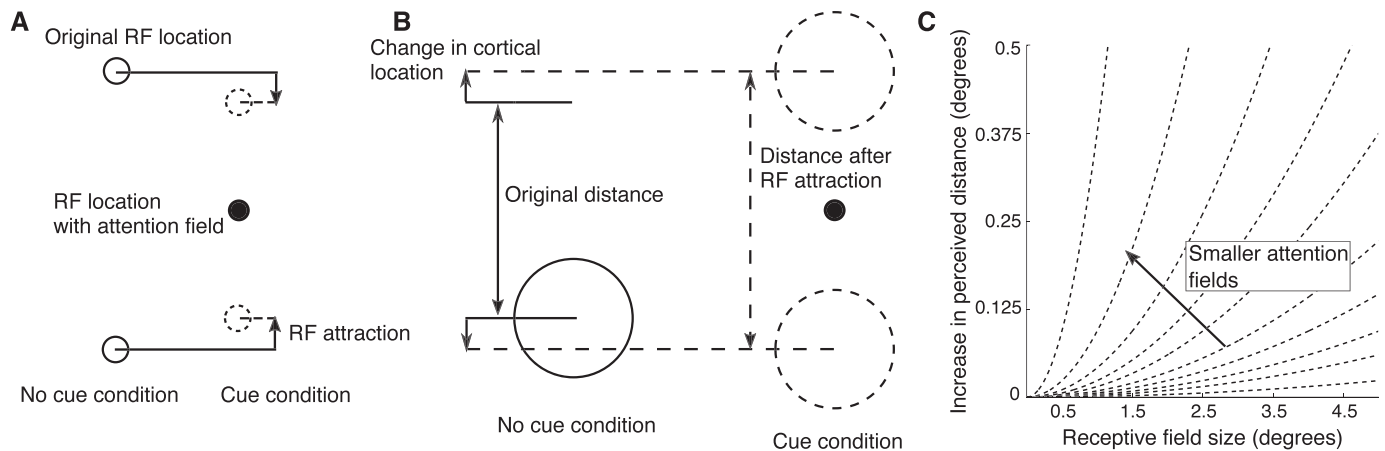


Figure 2. Proposed model. (A) When no cue is presented, receptive fields are aligned with their original location (solid circles). The onset of a cue attracts attention toward its location, which we model as a Gaussian-shaped attention field at the cued location (black dot). The interaction between the attention field and receptive field results in a receptive field attraction toward the cued location (RF attraction). (B) Without a cue, the cortical representation of the Gabors (solid circles) corresponds to the location at which the Gabors were presented. Consequently, the distance between the representations of Gabors within a pair corresponds to their physical distance in visual space (original distance). Because of the receptive field attraction toward the attention field (black dot), receptive fields whose original location is further away from the cued location now cover the Gabors. As a consequence, the cortical representations move away from the cued location at the center of the Gabor pairs (change in cortical location), resulting in an increase in the distance between the cortical representations (distance after RF attraction). We propose that this increase in distance between the cortical representations leads to an increase in perceived distance between the Gabors on the cued side. (C) The attention field model predicts an increase in perceived distance between the Gabors on the cued side. The predicted increases are larger for larger receptive fields (x axis) and *smaller* attention field sizes (separate lines).

fitted cumulative Gaussians to the corrected distances (see the Methods section) and responses from the cue conditions. Figure 3A shows the median fit and the 95% confidence intervals obtained by bootstrapping for the cue standard and cue test conditions separately. The data are taken from one subject and one eccentricity condition (6°). We plot the probability that the participant reports seeing the test pair closer together than the standard pair as a function of the difference in distance between the test pair and standard pair. As expected, the curve fitted for the cue test condition (black lines) is shifted to the left, demonstrating that when presented at a previously cued position, the test pair has to be closer together to appear as far apart as the standard pair. An effect in the opposite direction is observed for the cue standard condition (red lines). This demonstrates that the participant perceived the Gabor pair on the cued side farther apart than the pair on the noncued side. Figure 3B shows the difference in distance between the test and standard pair at the PSE and the 95% confidence intervals for both the cue test and cue standard conditions (dark and light gray bars, respectively) for all three eccentricity conditions for the same participant. The effects of cueing on the perceived distance between the Gabor pairs are in the expected direction for both the cue test and cue standard conditions. To assess the magnitude of the effect of cueing across

eccentricity conditions, we collapsed the cue test and cue standard conditions (Figure 3C, D) for this participant. Figure 3C shows the probability that the participant reports seeing the noncued pair closer together than the cued pair, as a function of the difference in distance between the cued and noncued pair. The curve is shifted to the right, meaning that the noncued pair had to be further apart than the cued pair, to appear equally far apart. Figure 3D shows the difference in distance between the cued and noncued pair at the PSE for the collapsed data for all eccentricity conditions. We interpret this as the magnitude of the effect of cueing on the perceived distance between the Gabor pair across eccentricity. Figure 3E shows the magnitude of the effect of cueing on the perceived distance between the Gabor pair across eccentricity, for all participants separately (gray lines) and the average across all participants (solid line), together with the standard error of the mean (SEM, gray area). A one-way repeated-measures analysis of variance (ANOVA) revealed a significant effect of eccentricity on the magnitude of the cueing effect, $F(2, 10) = 7.98$, $p < 0.01$. A linear regression confirmed a significant increase of the cueing effect with eccentricity (slope coefficient = 0.0244, $p = 0.01$).

To illustrate how model predictions for increases in perceived distance resemble the perceived distance increments measured in this experiment, we compute

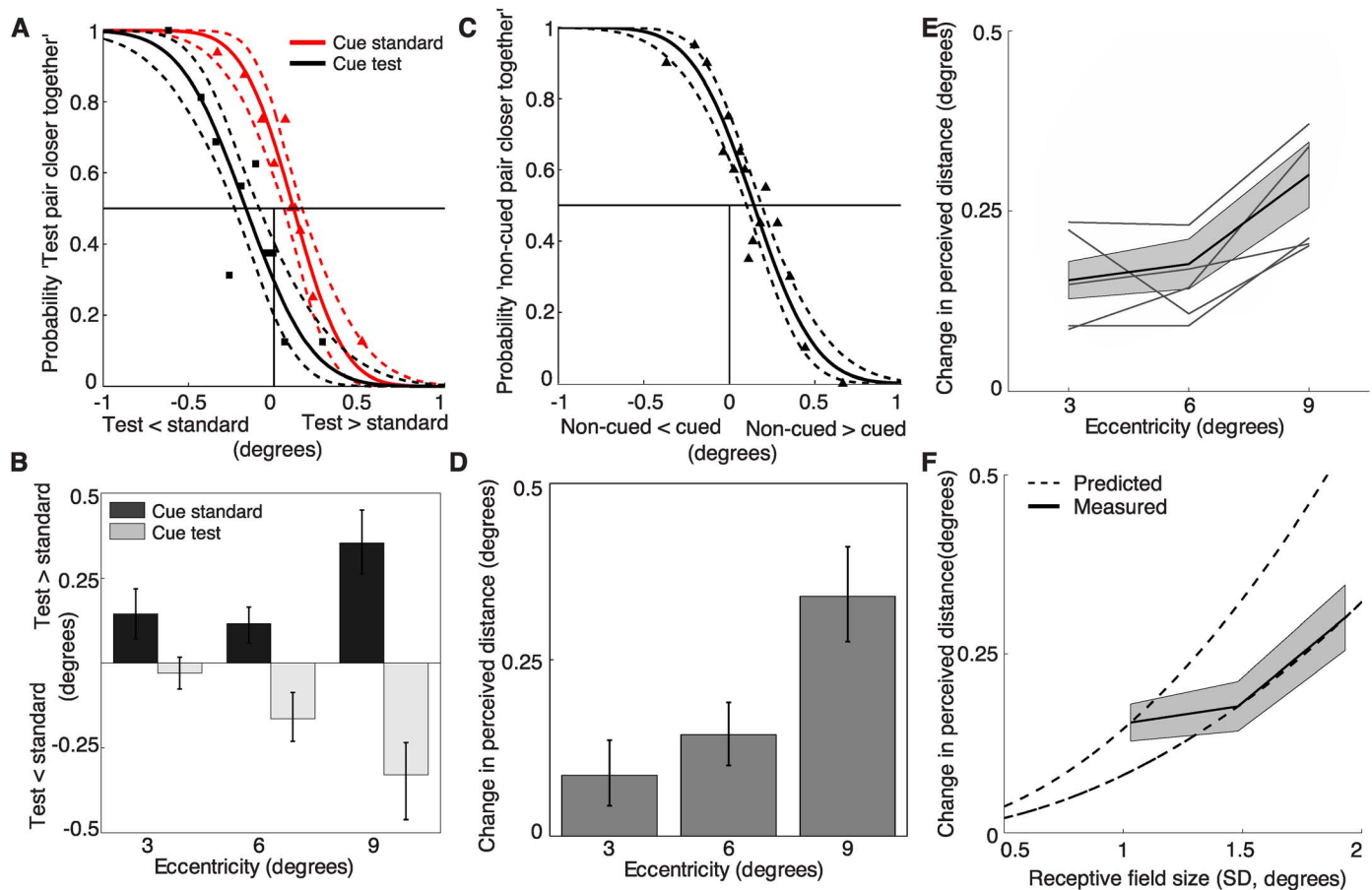


Figure 3. Results eccentricity experiment. (A) The probability that a participant reports seeing the test pair closer together than the standard pair, as a function of the difference in distance between the two pairs. Curves are the median cumulative Gaussian fits (solid lines) and the 95% confidence intervals (dashed lines) for the cue standard and cue test conditions separately. The data are from a single participant collected for the 6° condition. When the test pair is cued, it has to be closer together to appear as far apart as the standard pair (black curves). When the standard pair is cued, the test pair has to be further apart to appear as far apart as the standard pair (red curves). This indicates an increase in perceived distance when the Gabor pair appears at a previously cued location. The solid black, thin lines mark the $p = 0.50$ (PSE) and the point of equal presented distance between the test and standard pair. (B) The difference in distance between the test and standard pair at the PSE of every eccentricity condition separately. Data are from the same subject as in (A). (C) Similar to (A) but now the cue standard and cue test conditions are collapsed. The plot shows the probability that the participant reports seeing the noncued pair closer together than the cued pair, as a function of the difference in distance between the cued and noncued pair. (D) Similar to (B) but now the cue standard and cue test conditions are collapsed. This shows that the magnitude of the effect of cueing on the perceived distance between the cued pair increases with increasing eccentricity. (E) The magnitude of the effect of cueing on the perceived distance between the cued pair for every participant separately (thin gray lines). The thick solid line marks the average across all participants; the gray area represents the standard error of the mean (SEM). (F) The average effect of cueing on the perceived distance between the Gabor stimuli across participants (solid line), together with the SEM (gray area) as function of the estimated receptive field size underlying the increases in perceived distance. Dashed lines represent increases in perceived distance predicted by the attention field model. All error bars in panels (B) and (D) are 95% confidence intervals obtained by bootstrapping. The triangles and squares in panel (A) and (C) represent binned averages of the raw data; cumulative Gaussians were fit on the raw, unbinned data. Cueing results in larger perceived distances between the Gabor pair, and this effect increases with eccentricity, as expected based on predictions from our attention field model.

the attention field size necessary to produce the increase in perceived distance for every eccentricity condition separately (Equation 4). The computed attention field sizes are 4.54° for the 3° condition and 6.10° for both the 6° and 9° condition. We used these attention field sizes to compute the predicted increase in perceived

distance across a large range of receptive field sizes. Figure 3F presents the measured effect of cueing on the perceived distance between the Gabor pairs (solid line, average across subjects, together with the SEM [gray area]) as a function of estimated receptive field size (Equation 2). The dashed lines represent model

predictions of perceived distance increments, computed for each of the three attention field sizes. The predicted increases in perceived distance follow a similar increase with eccentricity as the measured increase in perceived distance.

Experiment 2: Perceived distance does not scale with spatial frequency

The data from this experiment were analyzed in the same way as those for the eccentricity experiment. Figure 4A shows the probability that a participant reports seeing the test pair closer together than the standard pair, as a function of the difference in distance between the test and standard pair. Data are from the 4.75 cpd condition collected for one participant. Figure 4B shows the difference in distance between the test and standard pair at the PSE and the 95% confidence intervals for both the cue test and cue standard conditions (dark and light gray bars, respectively) for all four spatial frequency conditions from the same participant. We collapsed the cue test and cue standard conditions in Figure 4C and D for the same participant. This reveals the magnitude of the effect of cueing on the perceived distance between the Gabor pairs. Figure 4E shows the magnitude of the effect of cueing on the perceived distance between the Gabor pair across spatial frequency for all participants separately (dashed lines) and the average across participants (solid line), together with the *SEM* (gray area). A one-way repeated-measures ANOVA revealed a significant effect of spatial frequency on the magnitude of the cueing effect, $F(3, 15) = 5.31$, $p = 0.011$, but post hoc testing revealed no significant differences between the spatial frequency conditions.

Again, we illustrate how model predictions for increases in perceived distance resemble those measured in this experiment. Using an estimate for the receptive field size tuned to the spatial frequency in every condition separately (Equation 3), we compute the attention field size for every condition (Equation 4). The computed attention field sizes are 1.54° , 0.93° , 0.28° , and 0.14° for the 1, 1.75, 4.75, and 10 cpd conditions, respectively. We used these attention field sizes to compute the predicted increase in perceived distance for every condition, across a large range of receptive field sizes. Figure 4F presents the measured effect of cueing on the perceived distance between the Gabor pairs (solid line, average across subjects, together with the *SEM* [gray area]). The dashed lines represent model predictions of perceived distance increments, computed for each of the three attention field sizes. An attention field model using these attention field sizes clearly predicts an increase of the

increase in perceived distance between the Gabor stimuli that is not present in our data.

Control experiments: Perceived distance increments depend on stimulus timing but are independent from stimulus size

Data analyses for the control experiments were similar to that of the main experiments. Figure 5A shows the increase in perceived distance between the cued pair when controlling for the size of the Gabors in the frequency domain. Gray lines mark the results for each participant separately; the solid black line and the gray area mark the average across participants and the *SEM*, respectively. A one-way repeated-measures ANOVA reveals no significant differences between the spatial frequency conditions, $F(3, 15) = 1.58$, $p = 0.235$.

Figure 5B shows the increase in perceived distance as a function of ISI for every participant separately (gray lines) and the average across all participants (black line), together with the *SEM* (gray area). A one-way repeated-measures ANOVA shows a significant effect of ISI on the perceived distance between the Gabors, $F(2, 10) = 18.849$, $p = < 10^{-6}$. Post hoc testing reveals a significant reduction in the effect of the cue for the ISI = 600 ms, compared with the ISI = 0 ms and ISI = 67 ms condition ($p = 0.024$ and 0.02 , respectively). In addition, a marginally significant reduction of the increase in perceived distance was found for the ISI = 0 ms compared with the ISI = 67 ms condition ($p = 0.054$). All p values are corrected using false discovery rates (Benjamini & Hochberg, 1995). The increases in perceived distance do not depend on the size of the Gabors, but do depend on the interval between the cue and Gabors.

Discussion

We have demonstrated that the positional bias of Gabors outside the focus of attention, measured by an increase in perceived distance between the two Gabors, increases with eccentricity. Perceived distance increments, however, do not vary with the spatial frequency content of the Gabors. Control experiments verify that attention underlies the observed positional bias in this experiment. In addition, the size of the Gabors in the frequency or the spatial domain did not affect the magnitude of the bias.

Several models have been proposed that can account for the positional bias examined here. Suzuki and Cavanagh (1997) proposed three mechanisms through which attention can lead to a positional bias, namely, response suppression, receptive field shrinkage, and

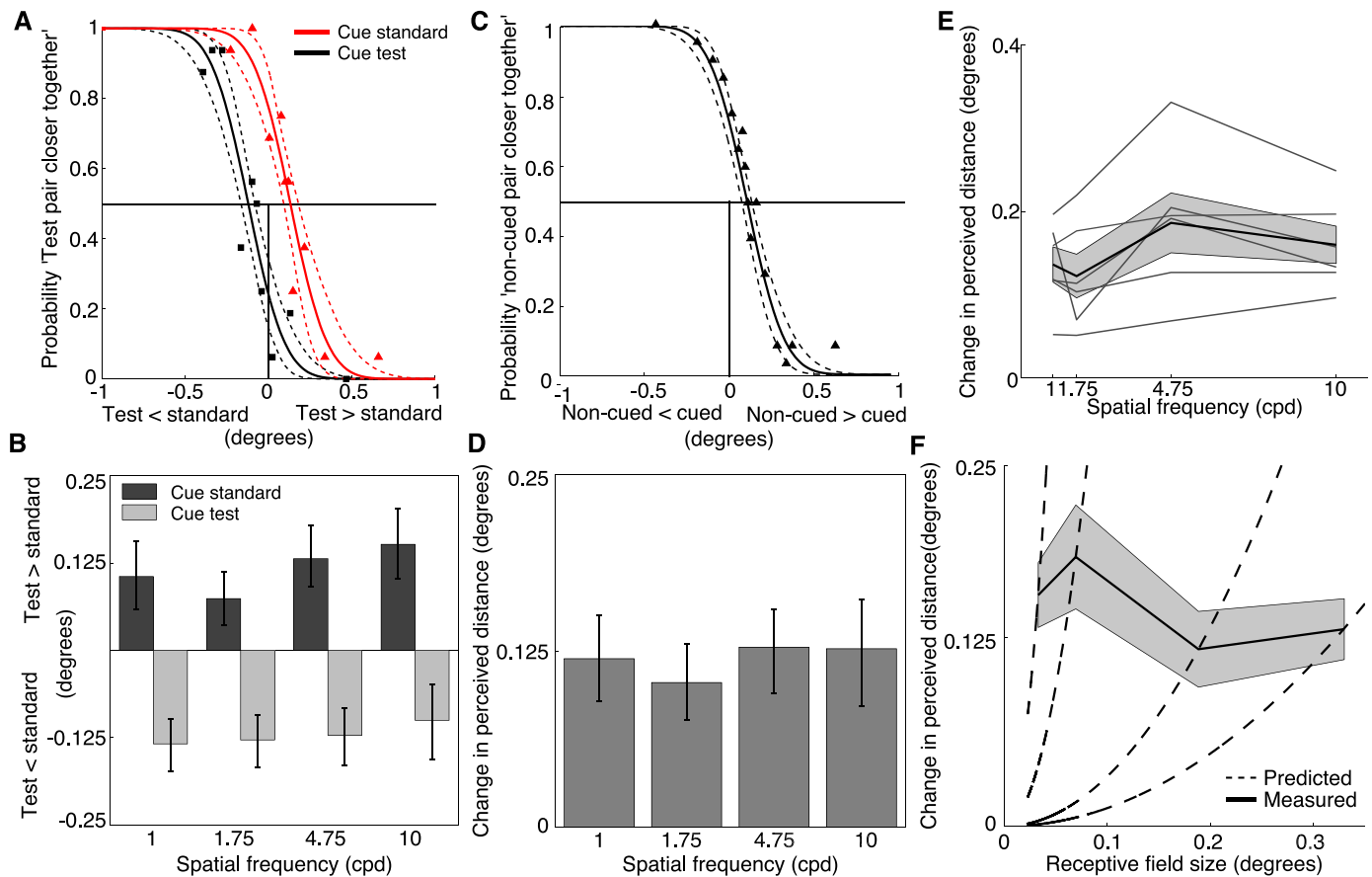


Figure 4. Results spatial frequency experiment. (A) The probability that a participant reports seeing the test pair closer together than the standard pair, as a function of the difference in distance between the two pairs. Curves are median cumulative Gaussian fits (solid lines) and the 95% confidence interval (dashed lines) for the cue standard and cue test conditions separately. The data are from a single participant collected for the 4.75 cpd condition. The solid black, thin lines mark the $p = 0.50$ (PSE) and the point of equal presented distance between the test and standard Gabor pairs. (B) The difference in distance between the test and standard pair at the PSE of every spatial frequency condition separately. Data are from the same subject as in (A). (C) Similar to (A) but now the cue standard and cue test conditions are collapsed. The plot shows the probability that the participant reports seeing the noncued pair closer together than the cued pair, as a function of the difference in distance between the cued and noncued pair. (D) Similar to (B) but now the cue standard and cue test conditions are collapsed. This shows that the magnitude of the effect of cueing on the perceived distance between the cued pair is about constant across spatial frequencies. (E) The magnitude of the effect of cueing on the perceived distance between the cued pair for every participant separately (thin gray lines). The thick solid line marks the average across all participants; the gray area represents the standard error of the mean (SEM). (F) The average effect of cueing on the perceived distance between the Gabor stimuli across participants (solid line), together with the SEM (gray area) as function of the estimated receptive field size underlying the increases in perceived distance. Dashed lines represent increases in perceived distance predicted by the attention field model. All error bars in panels (B) and (D) are 95% confidence intervals obtained by bootstrapping. The triangles and squares in panel (A) and (C) represent binned averages of the raw data; cumulative Gaussians were fit on the raw, unbinned data. Based on our model, we expected that increasing the spatial frequency of the Gabors leads to a smaller increase in perceived distance. However, we find that the positional bias does not vary as a function of Gabor spatial frequency.

receptive field attraction. More recently, Baruch and Yeshurun (2014) proposed the attentional attraction field model. This model explains the positional bias as a consequence of receptive field attraction. Our model as presented here explains the positional bias as a consequence of receptive field attraction as well. However, our model includes receptive field size as an important parameter, which is not the case for the models proposed by Suzuki and Cavanagh (1997) and

Baruch and Yeshurun (2014). Here, we attempted to examine the dependence of the positional bias on receptive field size, a key prediction from our model. Our experiments were not designed to distinguish between different models, and as such, our results do not permit differentiation between models.

Within our model, the positional bias is the consequence of an interaction between the attention field, representing the strength of attentional modula-

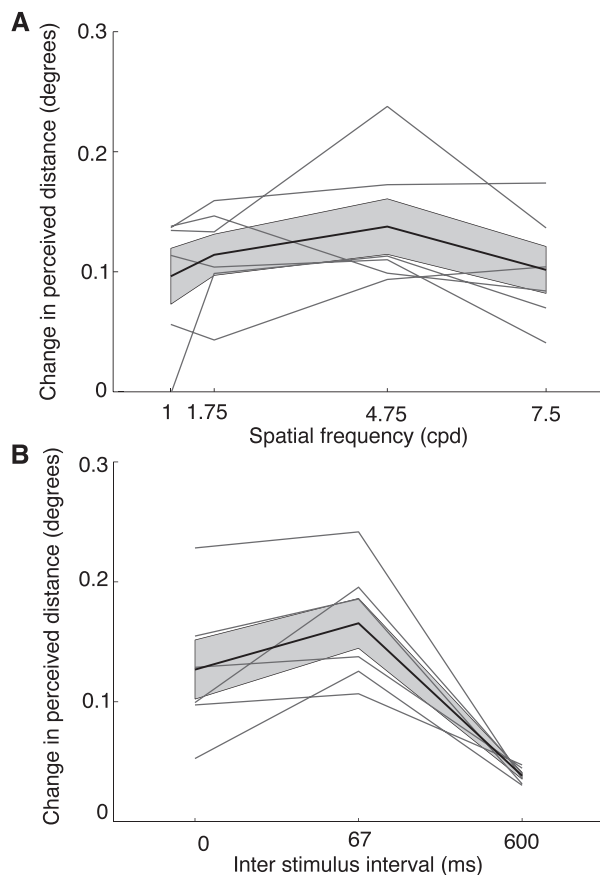


Figure 5. Results control experiments. (A) The magnitude of the effect of cueing on the perceived distance between the cued Gabor pair when controlling for the size of the Gabor stimuli in the frequency domain. Gray lines represent data from every participant separately. The black line represents the average across subjects, the gray area the SEM. (B) Similar to (A) but now when the timing between the cue and Gabors is varied. Data presented in this figure are analyzed in the same way as those presented in Figures 3 and 4. The increase in perceived distance does not depend on the size of the Gabors but does depend on the timing between the cue and Gabors.

tion and the receptive field. We find that the positional bias increases with eccentricity, which we interpret as a consequence of larger receptive fields at higher eccentricities. Within this interpretation, larger receptive fields are more susceptible to attentional modulation and are thus attracted more. This assumes that variation in attentional modulation, and thus attention field size, between the conditions in the eccentricity experiment cannot explain the increase in positional bias. We have several reasons to assume that this is indeed the case.

First, the size of the attention field typically varies with experimental parameters, such as spatial uncertainty (Belopolsky, Zwaan, Theeuwes, & Kramer, 2007; Hernández, Costa, & Humphreys, 2010; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010) and

may depend on the specific task and stimulus used in an experiment (Intriligator & Cavanagh, 2001). Each condition in our eccentricity experiment used the same stimulus and participants performed the same task, only the eccentricity at which the stimulus was presented varied. Moreover, stimuli were equally likely to appear at each of the three eccentricities, thus minimizing variation in spatial uncertainty about the stimulus position between conditions. Therefore, we expect little variation in attention field size between our conditions because of variation in spatial uncertainty and stimulus or task characteristics. Second, in our model, the attention field represents a Gaussian-shaped multiplicative amplification of neural responses (Klein et al., 2014; Reynolds & Heeger, 2009; Womelsdorf et al., 2008). Within this framework, stronger attentional modulation is predicted when response amplification increases and when this amplification is spread over a narrower range of visual space. Thus, if attention elicits stronger response amplification at higher eccentricities, or if this amplification is spread over a smaller extent of visual space, the attentional modulation may be stronger at higher eccentricities. This could then explain the larger positional bias we measure at higher eccentricities. However, fMRI studies suggest that higher eccentricities are related to *less* response amplification in most, but not all, visual areas (Bressler, Fortenbaugh, Robertson, & Silver, 2013) and possibly to an *increased* spread of this amplification (Puckett & DeYoe, 2015). Although far from conclusive, within the framework of our model, this suggests a weaker attentional modulation of receptive fields at higher eccentricities, which would lead to a reduced attraction of receptive fields and thus predict a smaller positional bias. In sum, we expect little variation in attention field size between the conditions of our eccentricity experiment due to task and stimulus characteristics. In addition, higher eccentricities may be related to reduced attentional modulation of receptive field position. Therefore, we assume that variation in attention field size cannot account for the increase in positional bias with eccentricity but that increases in receptive field size underlie this result.

The increase of receptive field size with eccentricity accounts for other eccentricity-dependent effects of attention as well. For example, whether attention improves or impairs performance on a texture segmentation task depends on the match between the spatial scale of the segmentation task and the receptive field size at the eccentricity at which the task is presented (Yeshurun & Carrasco, 1998). We varied the eccentricity of both the cue and target to examine the effects of eccentricity on the magnitude of the positional bias. Other studies manipulated only the eccentricity of the cue to examine how the positional bias varies with cue–target distance. They found that

the positional bias peaks for cue–target distances of approximately 2° – 4° and decreases for shorter and longer distances (Kosovicheva, Fortenbaugh, & Robertson, 2010; Suzuki & Cavanagh, 1997). As presented here, our model predicts an increasing positional bias with increasing distance but not a decrease. To be able to account for a decreasing effect with distance, our model can be extended to include a parameter that attenuates receptive field attraction as a function of distance to the attended location.

Although an attention field model predicts variation of the positional bias with spatial frequency, we did not find such an effect. There can be several explanations for the lack of variation in perceived position across spatial frequency. First, it should be noted that the model predictions for the spatial frequency experiment are derived using another model describing the relation between spatial frequency and receptive field size in V1 (Jones & Palmer, 1987). This assumes that changes in receptive field position at the level of V1 affect the positional bias examined here. However, some psychophysical evidence suggests that the positional bias may be induced at levels prior to binocular integration in V1 (DiGiacomo & Pratt, 2012). Thus, varying the spatial frequency of our stimulus may lead to changes in underlying receptive field size and consequently to variation in receptive field attraction at the level of V1. However, it is possible that these changes at the level of V1 are not translated to changes in the positional bias. In contrast, every visual field map across the visual processing hierarchy displays an eccentricity by receptive field size relationship. Consequently, increasing the eccentricity at which a stimulus is presented would vary the underlying receptive field size at every level of the visual hierarchy and thus induce variation in receptive field attraction throughout the visual hierarchy. This makes it more likely that the level of visual processing at which the positional bias is induced shows variation in receptive field attraction as well. Thus, the different ways by which eccentricity and spatial frequency are encoded across the visual hierarchy may have led to the difference between the results of the eccentricity and spatial frequency experiment.

Second, the attention field model described in this study is based on fMRI results obtained using endogenous attention. In this study, however, we test its perceptual consequences with exogenous attention. Exogenous and endogenous attention might be controlled differently in the primate brain (Buschman & Miller, 2007; Busse, Katzner, & Treue, 2008; Corbetta & Shulman, 2002) and may have some different effects on perception (Briand, 1998; Briand & Klein, 1987; Lu & Doshier, 2000; Yeshurun, Montagna, & Carrasco, 2008). However, we do not believe that differences between exogenous and endogenous attention are responsible for the discrepancy between the predicted

and measured positional biases in Experiment 2. Both exogenous and endogenous attention affect visual processing as early as the primary visual cortex (Gandhi, Heeger, & Boynton, 1999; Liu, Pestilli, & Carrasco, 2005; Motter, 1993; Somers, Dale, Seiffert, & Tootell, 1999), where spatial frequency–selective cells have been well described (Jones & Palmer, 1987). In addition, an attention field model captures the effects of both exogenous and endogenous attention on contrast sensitivity in human perception (Herrmann et al., 2010), suggesting that they affect visual processing in very similar ways. Moreover, positional biases have been found using both exogenous and endogenous attention (Suzuki & Cavanagh, 1997). Finally, using exogenous attention, we did find an increase in positional biases with eccentricity in the current study, as predicted by the model.

Third, if different spatial frequencies are affected by a positional bias to differing extents, this may brake phase alignment across different spatial frequencies and disrupt accurate edge detection. Therefore, the visual system could correct for spatial misalignment across spatial frequencies. This correction may be conceptually similar to the correction imposed on retinal motion due to eye movements (Sommer & Wurtz, 2008; Wurtz, 2008). Therefore, local mechanisms may correct for the spatial misalignment of different spatial frequencies.

Fourth, it is possible that the magnitude of the positional bias we measure here is not related to variation in receptive field shifts but to uncertainty about the distance difference between the Gabor stimuli. Within this framework, participants are more susceptible to a positional bias when they are more uncertain about the distance difference between the two Gabor stimuli. This task uncertainty is represented by the slope (sigma) of the cumulative Gaussians we fit to our data. Indeed, we find that the slopes of our functions are significantly related to the measured bias in both the eccentricity and spatial frequency experiment but not in the control experiment, where we varied the spatial extent of the Gabor stimuli. Therefore, position uncertainty can explain some, but not all, of our results.

Finally, it is important to consider that our task was spatial in nature. Our cue was spatially localized, and we examined its effect on the spatial position of the Gabor stimuli. In the spatial frequency experiment, we manipulated the spatial frequency of the Gabor stimuli, a stimulus dimension that is orthogonal to and independent of the stimulus position. This discrepancy between the nature of the task and the nature of the varied stimulus property could be responsible for the lack of an effect of spatial frequency on perceived position. Thus, the attention field we employed may operate only in the spatial domain and not in the spatial frequency domain. Similarly, attention may

operate independently from the spatial domain in feature space (Çukur, Nishimoto, Huth, & Gallant, 2013; David, Hayden, Mazer, & Gallant, 2008; Hayden & Gallant, 2009).

Conclusions

We examined biases in the perceived position of objects surrounding the focus of spatial attention. An attention field model predicts a larger positional bias when underlying receptive fields are larger. We found that positional biases increase with eccentricity but are relatively constant across a range of spatial frequencies. We have discussed several reasons that might explain why positional biases do not vary with spatial frequency. The discussed mechanisms can potentially be incorporated into an attention field model to increase its explanatory power in the perceptual domain. The attention field model is therefore a useful way to bridge neural mechanisms of attention with perception.

Keywords: attention, perceived position, positional bias, attention field model

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