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The Many Mappings of Visual Space:

Examining the Perception and Representation of Space in the Visual Periphery

By

Francesca Cowden Fortenbaugh

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Psychology

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Lynn C. Robertson, Chair
Professor Michael A. Silver
Professor Jack L. Gallant
Professor Martin S. Banks

Spring 2012

The Many Mappings of Visual Space:

Examining the Perception and Representation of Space in the Visual Periphery

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by

Francesca Cowden Fortenbaugh

Abstract

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Francesca Cowden Fortenbaugh

Doctor of Philosophy in Psychology

University of California, Berkeley

Professor Lynn C. Robertson, Chair

It can be argued that individuals are most often concerned with the objects that exist in an environment, as it is these objects that are recognized, localized and acted upon. However, the space between objects plays as critical a role in activities of daily living as the objects themselves because without the perception of an underlying spatial structure, accurate localization, navigation, and manipulations of objects would not be possible. To date, questions still exist as to how space is perceived across the visual field as a function of eccentricity (i.e., where an object is located within the visual field) and the factors that influence space perception in the visual periphery. In particular, conflicting reports have been found in the literature regarding inherent biases in peripheral localization and the modulating affect of attention on the perceived structure of visual space. The aim of these studies was to help resolve some of these issues. In the first two chapters it is argued that perception of both the locations and shapes of objects presented in the periphery are influenced by voluntary and involuntary attention. In Chapter 2, the results of three experiments demonstrate that changes in the distribution of sustained voluntary attention alter the perceived locations of target dots presented at different eccentricities along the cardinal axes. Specifically, the results show that when attention is focused on a region of space, targets appear to be located more peripherally than when attention is distributed across the visual field. The next three experiments in Chapter 3 show that rapid shifts in the location of involuntary attention can distort the perceived shape of an oval. These studies support the assertion that changes in attention alter the underlying structure of visual space, and thus, alter the perceived locations and/or shape of any object presented in that space. The experiments in Chapter 4 investigate the role of visual boundaries in spatial localization and argue that different classes of borders are associated with the different reference frames and metrics used in defining the underlying perceptual structure of visual space. The results of these experiments show that when spatial localization occurs relative to the intrinsic borders of the visual field, participants show a peripheral bias and a non-linear scaling of target locations across eccentricity. The introduction of external boundaries first leads to a linear scaling of target locations and can change the pattern of mislocalization from a peripheral to a foveal bias. In Chapter 5, it is argued that the borders of the visual field are used to compute location in a more natural metric (percentage of visual field extent) than degrees of visual angle for determining spatial location within a retinotopic reference frame, and that this metric may determine the allocation of processing resources across the visual field. Using a crowding paradigm in which participants perform significantly better when target gratings are presented along the lower vertical meridian than the upper vertical meridian, the results of the final experiment show that both inter-subject and intra-subject variability can be accounted for by this new metric. Collectively, these experiments highlight the fact that visual space is not a stable mapping of the external environment. Rather, the perceived structure of visual space is flexible and can be altered by both the borders that define a space as well as the attentional state of an observer.

Table of Contents

Title Page

Copyright

Abstract...1

Table of Contents...i

List of Figures..iv

Acknowledgments..vi

1. Introduction...1

2. The Influence of Sustained Attention on Spatial Localization…………………………....4

2.1. Introduction to the Effect of Attention on Spatial Localization……………………...4

2.1.1. The Affect of Attention on Visual Processing….……………..……………4

2.1.2. Previous Research on Peripheral Localization………………...…………...5

2.2. Experiment 1:Sustained Attention Alters Foveal Bias……………………………….6

2.2.1 Methods……………………….………………………………….……............7

2.2.2 Results.…………………………………………………………………….…...9

2.2.3 Discussion………………………………………………………….........13

2.3. Experiment 2: Dissociating Attentional Distribution From the Number of Target Locations…………………………………………………………......................17

2.3.1 Methods……………………….………………………………….……..............17

2.3.2 Results.……………………………………………………………….........18

2.3.3 Discussion………………………………………………………….........21

2.4. Experiment 3: The Relationship Between the Magnitude of Foveal Bias and Visual Angle………………………………………..……..................................22

2.4.1 Methods……………………….………………………………….……..............23

2.4.2 Results.……………………………………………………………….........23

2.4.3 Discussion………………………………………………………….........27

2.5. General Discussion of Experiments 1-3……………….…………………………29

2.5.1 Models of Attention and Localization……………………………….....30

2.5.2 Source of the Foveal Bias……………………………………………….33

3. The Influence of Involuntary Shifts of Attention on Object Structure...…………….........35

3.1. Introduction to Rapid Shifts of Attention on Space Perception……………..........36

3.2. Experiment 4: Demonstrating Distortions in Object Shape……......……….....……36

3.2.1 Methods…………………….…………………………….…..............36

3.2.2 Results and Discussion………………………………………….........38

3.3. Experiment 5: The Influence of Cue Timing on Distortions……………….........40

3.3.1 Methods…………………….…………………………….…..............40

3.3.2 Results and Discussion………………………………………….........41

3.4. Experiment 6: Dissociating Figural Aftereffects From Shifts of Attention...............44

3.4.1 Methods…………………….…………………………….…..............44

3.4.2 Results and Discussion………………………………………….........45

3.5. General Discussion of Experiments 4-6……………….………………………........46

4. The Role of Visual Boundaries on Spatial Localization……………….………...……47

4.1. Introduction to Spatial Localization in the Peripheral Visual Field………………..47

4.1.1 Foveal and Peripheral Biases in Peripheral Localization………..............47

4.1.2 Resolving Discrepancies: The Influence of Visual Boundaries…...………48

4.2. Experiment 7: Border Type Alters Localization Bias and Spatial Scaling……..........49

4.2.1 Methods…………………….…………………………….…..............49

4.2.2 Results.………………………………………………………….........51

4.2.3 Discussion……………………………………………………….........56

4.3. Experiment 8: Demonstrating Peripheral Biases with Verbal Response...........……58

4.3.1 Methods…………………….…………………………….…..............58

4.3.2 Results……………………………………………………………………..........59

4.3.3 Discussion…………………………………………………………….........61

4.4. Experiment 9: External Borders Introduce Foveal Bias……...................................62

4.4.1 Methods……………………….………………………………….…..............62

4.4.2 Results………………………………………………………………..........63

4.4.3 Discussion…………………………………………………………….........65

4.5. General Discussion of Experiments 7-9…...……………………….…………….............66

5. Redefining the Metric of the Retinotopic Coordinate System...70

5.1. Introduction to Modeling Metrics of Visual Space...70

5.2. Experiment 10: Perceptual Asymmetries and the New Metric of Retinotopic Visual Space...71

5.2.1 Methods……………………….………………………………….…..............72

5.2.2 Results and Discussion………………………………………………….........74

5.3. General Discussion of Experiment 10……………………………….……………...........78

6. General Conclusions..……………….……………….…………….……….………..…............80

7. References…………………….……………………………….…………………..………......84

List of Figures

Figure 1. Experiment 1: Trial Sequence……………..…………..…………………...……….....7

Figure 2. Experiment 1: Magnitude Errors……………………..………………....................10

Figure 3. Experiment 1: Positional Uncertainty...………………..…...………..………............11

Figure 4. Experiment 1: Slope Parameters……………………….…..………………………13

Figure 5. Experiment1: Eye-Movement Control Results…………………………………......16

Figure 6. Experiment 2: Magnitude Errors……………………..………………....................19

Figure 7. Experiment 2: Positional Uncertainty...………………..…...………..………............20

Figure 8. Experiment 2: Slope Parameters……….……………….…..…………………………...21

Figure 9. Experiment 3: Magnitude Errors……………………..………………....................24

Figure 10. Experiment 3: Positional Uncertainty...………………..…...………..………............25

Figure 11. Experiment 3: Slope Parameters…….………………….…..………………………26

Figure 12. Comparison of Errors Across Experiments 1 and 3…...………………………… ……28

Figure 13. Experiment 4: Experimental Predictions……………..………………………….…...35

Figure 14. Experiment 4: Trial Sequence……………..…………..…………………...….……37

Figure 15. Experiment 4: Results……………………..…………..…………………...……......39

Figure 16. Experiment 5: Post-Cue Results……………………...………….……….....………......42

Figure 17. Experiment 5: Simultaneous-Cue Results……………………..…………….....……....43

Figure 18. Experiment 6: Trial Sequence and Results………………………..…………..….………45

Figure 19. Photograph of Goldmann Perimeter……...……………………..…………….....……....50

Figure 20. Experiment 7: Localization Errors……………………..…...………......................52

Figure 21. Experiment 7: Spatial Uncertainty……………………..…...…...……....................53

Figure 22. Experiment 7: Normalized Magnitude Estimates………………………………….54

Figure 23. Experiment 7: Power Function Parameters…………………………...………...55

Figure 24. Experiment 8: Localization Errors……………………………………………...59

Figure 25. Experiment 8: Power Function Parameters……………………………….......60

Figure 26. Experiment 9: Localization Errors……………………………………………...64

Figure 27. Experiment 9: Slope Parameters……………………..……………………….……65

Figure 28. Two Models of Retinotopic Visual Space……………………………………………71

Figure 29. Experiment 10: Behavioral Paradigm…………………………………………......73

Figure 30. Experiment 10: Correlation of Visual Field and Average Performance Ratios……...75

Figure 31. Experiment 10: Correlation of Visual Field and Performance Ratios……………......76

Figure 32. Experiment 10: Equating Performance Using New Metric……………………….....77

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1. Introduction

Physical space, at least at the level with which humans interact with it, is Euclidean. However, visual space, defined as the visual perception of space, is not necessarily a veridical representation of the external environment (Indow, 2004; Robertson, 2004; Wagner, 1985, 2006). This is due to the fact that in the normal-vision observer many factors outside of the primary sensory constraints (i.e., optical blur, acuity, diplopia) determine how the world is perceived, and in particular, where objects are seen. The many visual illusions and documented distortions in the perception literature provide ample evidence that our perception of space does not always have a one-to-one correspondence with the external environment. Factors such as attention (Simons & Chabris, 1999), expectations and prior experiences (Palmer, 1999), environmental factors (Cutting & Vishton, 1995; Da Silva & Fukusima, 1986; He, Wu, Ooi, Yarbrough, & Wu, 2004; Howard & Rogers, 2002; Norman, Crabtree, Clayton, & Norman, 2005), context (Murray, Boyaci, & Kersten, 2006), and perceived effort (Proffitt, Stefanucci, Banton, & Epstein, 2003) have all been shown to influence our perception of the world.

Previously, attempts have been made to model the 3-dimensional structure of visual space and the factors that influence distance perception along the depth plane (Cutting, Bruno, Brady, & Moore, 1992; Cutting & Vishton, 1995; Indow, 1982, 1991, 2004; Luneburg, 1947, 1950; Wagner, 1985, 2006). However, significantly less research has been conducted that attempts to model visual space as a function of eccentricity and the factors that influence space perception in the peripheral visual field[1]. Taking into account the numerous factors that have been shown to influence location perception mentioned above, in a review of the space perception literature, Wagner (2006) concluded that there is no one underlying metric of visual space. That is to say, there is no one distance function that can be applied to account for errors in perceived location across all dimensions and experimental or task settings. While this is surely the case, the fact that the structure of visual space varies across tasks, instructions, and environments only increases the need for a better understanding of the properties of these spaces. The evidence for flexible representations of visual space does not mean that regularities in the underlying structure of visual space, or consistent biases induced by various factors, do not exist. Nor do multiple mappings of visual space imply that research attempting to characterize the underlying structure of visual space is limited in nature. Rather, the evidence for distortions in space perception suggest that visual space itself cannot be considered to be a constant in perception and that investigations into how individuals perceive objects in an environment need to be coupled with research investigating where those objects are perceived to exist.

The overall goal of the research presented here was to develop paradigms that allow inferences to be made about the underlying metrics used by normal-vision individuals across various tasks where inconsistencies have previously been observed. The research focuses on two factors: the role of visual-spatial attention and visual boundaries on space perception. In order to obtain a more complete understanding of visual space and how these factors influence the

[1] In the literature, definitions of what constitutes the central visual field and the peripheral visual field vary. Based on physiological work of the retina (Osterberg, 1935; Schwartz, 2010), we define the central visual field as less than 10º from fixation (where fixation corresponds to the fovea). This region is approximately equal to the macular region, which consists of the foveola, the fovea, the parafoveal region, and the perifoveal region. All remaining parts of the visual field will be considered to be part of the peripheral visual field.

development of perceptual metrics, it is important first to conceptualize what defines a space. In mathematics and physics, a space is defined through two concepts: a reference frame, which defines an origin and directions from the origin, and a metric, which is a distance function that allows one to assess how far away an object is along a particular direction. Given a reference frame and a metric it is possible to define coordinate systems, such as the Cartesian coordinate system used in defining spatial layouts of a scene, with the observer at the origin, or the polar coordinate system used to describe spatial location in retinal coordinates, with the point of fixation defining the origin. Accurate spatial localization requires that both a reference frame and a metric be defined for the space in which localization occurs. This can be thought of as defining a coordinate system, given the frame of reference that is employed to generate the task response. Reference frame selection has been well described in the psychology literature (Bridgeman, Peery, & Anand, 1997; Klatzky, 1998; Paillard, 1991). Depending on the type of localization required, this process could involve the transformation of retinal input from retinal coordinates to eye-based, head-based, body-based, or allocentric reference frames. The present research focuses on the corresponding issue of how visual-spatial attention and visual boundaries alter the metric used to assess where objects are presented and how objects are represented at various distances from fixation. Thus, rather than focusing on the direction in which objects are perceived or the reference frame selected for task completion, the present work focuses on the distance functions that are coupled to the reference frames used.

Chapter 2 investigates the influence that changes in the distribution of sustained attention have on the perceived location of small stationary targets presented at various eccentricities along the cardinal meridians. Conflicting reports have been found in the literature regarding whether attention alters perceived location in the visual periphery. In this study we show that focusing attention on a specific region of space alters biases in perceived location and reduces the magnitude of previously reported foveal biases.

Chapter 3 investigates the role of involuntary shifts in the focus of spatial attention on the perceived shape of oval frames presented in the visual periphery. While several studies have previously reported shifts in the perceived location of targets away from cues that draw involuntary attention prior to target onset, the consequence of these shifts on the underlying structure of visual space has not been fully explored. In particular, this phenomenon, called the attentional repulsion effect, has previously been described as evidence for transitory distortions in the underlying structure of visual space, but the tasks used to measure the attentional repulsion effect have involved relative location judgments between two target lines. Thus, to date, it remains unclear whether the attentional repulsion effect is measuring errors in relative position coding of multiple objects or distortions in the underlying structure of visual space itself. We help to resolve this issue by testing errors in the perceived shape of a single object under various cue configurations. The results show that rapid shifts in the focus of attention distort the perceived shape of the oval, supporting the assertion that the errors resulting from shifts in involuntary attention reflect transient distortions in the underlying structure of visual space.

Chapter 4 takes a different approach than previous studies on localization in the visual periphery by examining the role that visual boundaries play in perceived location. Within the peripheral localization literature, two classes of biases have been reported: foveal biases, where targets are mislocalized closer to fixation than they were, and peripheral biases, where targets are mislocalized as being farther from fixation than they were. Using a Goldmann perimeter and asking participants to judge the perceived location of a briefly presented target dot relative to different classes of visual boundaries, we are able to resolve this issue by demonstrating that peripheral biases tend to occur when target locations are judged within an egocentric reference frame. When external boundaries, such as an aperture or computer monitor, are present, there are foveal localization biases. By modeling how target locations are judged across eccentricity, we are also able to show changes in the metric of visual space as a function of eccentricity. In particular, we found that when no external boundaries are present, a non-linear metric is used, and that the introduction of external boundaries enables participants to employ a linear metric with which to judge target locations.

Finally, Chapter 5 questions whether the appropriate metric has been used to describe retinotopic visual space. Many experimental paradigms describe space in the units that are applied to the external environment. We define distances and sizes in terms of inches or centimeters. In vision, we also describe distances in terms of degrees of visual angle. The use of visual angles falls naturally out of the fact that the retina is approximately spherical in shape with the fovea at the center of a half dome. Understanding the metric of visual space as a function of eccentricity may aid our understanding of other visual processes and how visual-processing capabilities vary across the visual field. In this study, we propose that the units of retinotopic visual space are best defined in terms of the boundaries enclosing the regions in which tasks are completed. While we are not often aware of our visual field extents and cannot always perceive the boundaries themselves, the edges of the visual field provide a natural boundary to visual space, and percent of visual field extent may be a more natural unit of measurement than degrees of visual angle. Here we measured the visual field extents along the vertical meridian of participants and had them complete a crowding task. Previous reports have shown that participants are better able to discriminate the orientation of a crowded grating in the lower visual field than the upper visual field. By altering the locations of the gratings according the new proposed metric and considering the differences in visual field extent across participants, we are able to account for the magnitude of the performance asymmetry both across and within participants.

2. The Influence of Sustained Attention on Spatial Localization

2.1. Introduction to the Effect of Sustained Attention on Spatial Localization

Over the course of a day we continually alter the degree to which our attention is focused or dispersed across the visual field. This ability to voluntarily adjust the focus of attention allows humans to optimize information processing, given the optical and processing limitations of the visual system and current behavioral goals. Despite much progress in understanding how different attentional states change the way information is processed, this progress has also highlighted new complexities and interactions between attentional operations and resulting perceptions.

2.1.1. The Affect of Attention on Visual Processing

Studies looking at rate of processing have shown that visually attending to a stimulus location or feature speeds target detection time (Carrasco, Giordano, & McElree, 2006; 1990; Posner, Snyder, & Davidson, 1980; Treisman & Gelade, 1980). Other lines of study have shown that directing voluntary attention toward an object can alter object perception. For example, accuracy in speeded target discrimination tasks increases when voluntary attention is directed to a cued location and the target is presented there (Prinzmetal, McCool, & Park, 2005). Another study examined changes in the physical appearance of objects when voluntary attention is focused on or away from an object and found that directing the locus of attention toward a circular array of moving dots increased the perceived size of the array (Anton-Erxleben, Henrich, & Treue, 2007). Spatial attention has also been shown to increase the processing abilities of the visual system, enhancing spatial resolution (Carrasco, Williams, & Yeshurun, 2002; Yeshurun & Carrasco, 1998), texture segmentation (Yeshurun, Montagna, & Carrasco, 2008) and contrast thresholds (Carrasco, Ling, & Read, 2004) relative to conditions when attention is directed away from a target item.

In contrast to studies looking at reaction time and accuracy measures, less is known about what effect attention may have on the perceived location of objects themselves. To date, most studies examining the effect of attention on spatial localization have used visual cues to direct attention preferentially to one region of space or another (Kosovicheva, Fortenbaugh, & Robertson, 2010; Suzuki & Cavanagh, 1997; Tsal & Bareket, 1999, 2005), or dual-task methods that manipulate attentional load or resources (Adam, Davelaar, van der Gouw, & Willems, 2008; Adam, Ketelaars, Kingma, & Hoek, 1993; Prinzmetal, 2005; Prinzmetal, Amiri, Allen, & Edwards, 1998). One line of studies (Prinzmetal, 2005; Prinzmetal, et al., 1998) tested perceived location of briefly presented target dots presented within a circular region while participants completed easy or hard dual-tasks at fixation. Participants were required to move a cursor to the perceived location of the target dot, and results showed that increasing attentional demands at fixation increased the variability of perceived location but not its the mean. However, another study (Adam, et al., 2008) using a dual-task paradigm found evidence for a foveal bias in perceived location that was modulated by the difficulty of the secondary task at fixation. Here participants were required to move a cursor to the perceived location of a target presented along the horizontal meridian. The secondary task was a digit identification task at fixation in which participants were required to report one, two, or three numbers presented prior to the target onset. Results showed that participants mislocalized the targets as being closer to the point of fixation than they really were (i.e., a foveal bias), and that the degree of foveal bias increased with the true distance of the target from fixation. Furthermore, increasing the demand of the secondary task from one to three letters or reducing the target duration both increased the size of the foveal bias for a given target location.

2.1.2. Previous Research on Peripheral Localization

While the studies discussed above provide important information on the effects of attentional processing on perceived target location, in all cases targets were presented within 10° of fixation. Thus, by the criteria of Bishop and Henry (1971), these studies only provide information about localization effects within the parafoveal region of the central visual field. However, a significant amount of research has shown systematic biases in localization of targets presented in both the parafoveal and peripheral regions of the visual field. In one early study, Mateeff and Gourevich (1983) presented small, circular targets that were briefly flashed at various eccentricities above a stable, numbered scale along the horizontal meridian. They found a foveal bias when estimating the target's location, consistent with the results of Adam et al. (2008). That is, while the numbered scale used to reference the target location was visible throughout a trial, observer's reported the location of the target to be at a smaller distance from the fovea than it actually was, and this tendency to underestimate the eccentricity of the stimulus increased as targets were presented more peripherally. Though one study (Mapp, Barbeito, Bedell, & Ono, 1989) failed to replicate these findings (although see Rose & Halpern, 1992), other studies (Eggert, Ditterich, & Straube, 2001; Müsseler & Van der Heijden, 2004; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999) using relative and absolute localization judgments of successively presented peripheral targets found results that are consistent with a foveal bias.

Of particular interest to the current paper are the results of studies looking at the effect of placing landmarks or distracter items in the visual display while participants report the perceived location of briefly presented peripheral targets. Results from these studies (Diedrichsen, Werner, Schmidt, & Trommershäuser, 2004; Eggert, et al., 2001; Kerzel, 2002; Makovski, Swallow, & Jiang, 2010; Uddin, Kawabe, & Nakamizo, 2005a; Werner & Diedrichsen, 2002; Yamada, Kawabe, & Miura, 2008) have shown that in many cases distortions in perceived location are shifted toward the location of the distracter items, reducing the foveal bias that is otherwise seen when the distracters are located at further eccentricities than the target. Currently, there is a proposal that the underlying cause of this attraction effect is due to attention being shifted toward the location of the distracter item (Kerzel, 2002; Yamada, et al., 2008). Under this model, the largest foveal biases occur when attention is focused at the point of fixation and no landmarks or distracters are present in the display. However, alternative models for these effects have been proposed, including a spatial memory averaging hypothesis in which the perceived location of the target stimulus is a weighted average of the true location of the target and salient neighboring landmarks (Hubbard & Ruppel, 2000). Given that alternative stimulus-based proposals exist for alterations in perceived location when landmarks are present and that prior studies on attention have always manipulated stimulus qualities, it is important to develop new paradigms that can manipulate aspects of visual attention without introducing distracters or altering the physical qualities of landmarks in the display.

2.2. Experiment 1: Sustained Attention Alters Foveal Bias

The purpose of the present study was to further explore changes in perceived location over a large range of eccentricities under different attentional conditions. However, in contrast to studies that have used dual-task or cueing paradigms in which multiple objects beside the target are present in the display, we investigated how changes in the distribution of sustained attention could alter the perceived location of targets across the visual field in the absence of foveal distracter items and landmarks. A single target dot was briefly presented (150 ms) in the parafoveal or peripheral visual field across several different eccentricities. We used a measure similar to those reported initially by Temme et al. (1985) and Mateeff and Gourevich (1983) in which participants made verbal magnitude judgments about the perceived location of a target dot briefly flashed along one of the cardinal axes. In addition, we manipulated the distribution of voluntary attention across the visual field by telling participants before each block along which of the four cardinal axes the target could appear. The number of relevant axes was systematically varied: 1) all four axes, to induce a broad distribution of attention (Attend All), 2) the vertical or horizontal meridian (between blocks), to induce a more narrowed, elongated distribution of attention (Attend Meridian) and 3) one of the 4 axes (between blocks) to induce an even more narrowed distribution of attention (Attend Axis). The attention manipulation was therefore a sustained attention task related to the area of space that the participants attended to throughout a block of trials, while allowing for comparison between different regions of the visual field under the different attention conditions. As this paradigm was designed to test perceived location, and not detection ability, white target dots were presented on a black background to maximize stimulus contrast. This assured that the target's visibility was always above threshold.

Magnitude estimates were made relative to the edge of a circular aperture placed over the monitor and, thus, all targets were presented within the same defined area. This removed the need for visible scales across the regions or multiple stimuli on each trial. While the ability of individuals to accurately make magnitude judgments varies, the present experiment was designed to examine how magnitude judgments to the exact same stimulus location change as attentional distribution varies. Moreover, while this task is a type of relative judgment task, it differs from previous designs (Mateeff & Gourevich, 1983; Müsseler & Van der Heijden, 2004; Müsseler, et al., 1999) in which localization judgments were made relative to a comparison object or landmark present within the display. It was also not possible for participants to direct attention solely to the edge of the aperture to make a magnitude judgment. Rather, their judgments had to be based on the entire length of the axis on which a target appeared. It is this aspect of the design that enabled us to manipulate the distribution of attention rather than just shifts of attention from one region of the display to another within a block of trials and control for any extra distracter objects in the display.

Based on previous findings (Mateeff & Gourevich, 1983) it was hypothesized that participants would show a foveal bias: underestimating perceived target locations and the degree of error increasing with the true eccentricity of the target. More importantly, if sustained attention not only alters perceived stimulus qualities but also perceived location as suggested by the results of Adam et al. (2008), foveal biases should be reduced or eliminated as attention is focused on smaller regions of visual space.

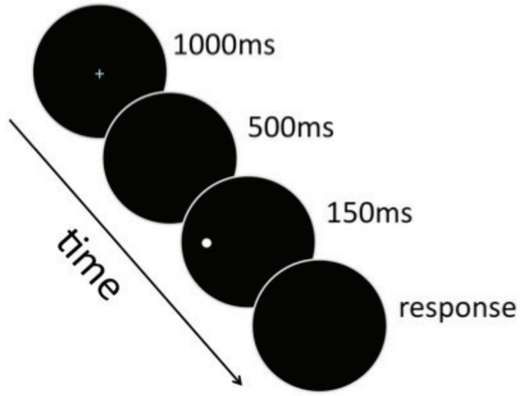

Figure 1. Experiment 1 Trial Sequence. The monitor was covered with a large, black piece of cardboard with a circular aperture (30° radius) cut out. Every trial began with a blue fixation cross in the center of the screen. This was followed by a blank screen and then a 1° diameter target was briefly presented at one of 7 equally spaced eccentricities between 4° and 28° along the four cardinal axes. Fixation cross and target are shown at a larger scale here for clarity.

2.2.1. Methods

Participants. Twelve healthy undergraduates (9 females; mean age: 19.4 years) participated in the main experiment for course credit. An additional four undergraduates (3 females; mean age: 21.5 years) participated at a later time in the eye-movement control condition for course credit. All reported normal or corrected-to-normal vision and no ocular disorders. Participants with corrected-to-normal vision wore contact lenses. Glasses, astigmatism, or any indication of ocular disease were means for exclusion. All participants gave informed consent, and the University of California's Committee for the Protection of Human Subjects approved the experimental protocol (#2010-04-1159).

Materials and Procedure. Participants sat 25.4cm from the computer monitor (ViewSonic G225f, refresh rate = 100Hz). A chin and forehead rest stabilized head position. A large black piece of cardboard, 91.5cm x 61.5cm, with a circular aperture (14.67cm or 30° radius) cut out was centered over the computer screen. The experiment was run in a dark room. The only border visible to the participants was the edge of the circular aperture due to the glow of the computer screen. Aside from adjusting the distance to the computer screen, care was taken before running each participant to assure that the height and lateral placement of the monitor were centered such that participants could fixate a cross at the center of the screen with their eyes in primary position. A digital level was used to check that the monitor was not tilted and participants verbally confirmed with the lights on that the monitor appeared centered.

All experimental parameters were executed using Presentation® software (Version 11.1, www.neurobs.com). Figure 1 shows an example of a trial sequence. On every trial, participants first viewed a blue fixation cross (1° in visual angle; 10 cd/m^2) for 1000ms on a black background (0.3 cd/m^2). After a 500ms blank a white target dot (1° diameter; 84 cd/m^2) appeared for 150ms in the participant's peripheral visual field, and participants verbally estimated how far out from fixation the target appeared to be by giving magnitude estimates between 0 (central fixation) and 100 (edge of aperture). The experimenter sat next to the participant in the room and recorded all of the responses. The ISI was long enough to eliminate apparent motion between the fixation cross and target dot but short enough that participants were able to maintain fixation on the cross. The fixation cross was colored blue to help eliminate apparent motion.

After the experimenter recorded the participant's response for a given trial there was a fixed inter-trial interval of 500ms before the next trial started. As participants made verbal responses and the experimenter recorded each response, it was not possible to determine reaction times in this task. This is because any measure of reaction time would be contaminated with variations in how long it took the experimenter to enter the participant's response on a given trial.

There were seven blocks of trials with three levels of attentional distribution along the horizontal and vertical meridians as follows. 1) Attend Axis condition: four blocks in which the target appeared only along the left, right, upper, or lower axis. 2) Attend Meridian condition: two blocks in which the target appeared only along the horizontal or vertical meridian. 3) Attend All condition: one block in which the target appeared randomly along any of the four axes. Before beginning each block, participants were verbally informed about the axis/axes on which the target could appear and a large white cross was also displayed at this time with the axis/axes that the participants were to attend to highlighted in blue. In every block, seven eccentricities were tested along each axis (4°, 8°, 12°, 16°, 20°, 24°, and 28°) for a total of 28 possible target locations in the Attend All block, 14 target locations in each of the Attend Meridian blocks, and 7 target locations in each of the Attend Axis blocks. Because the possible axes on which the target might appear did not change within a block and the target locations spanned almost the entire length of each axis, the task manipulated the distribution of sustained attention across the visual field over long periods of time as opposed to other studies of voluntary attention in which participants are cued to move the focus of their attention to a different location on every trial. Target locations were randomly tested with 5 repeats per location. Before beginning the experiment participants first completed 10 practice trials in the Attend All condition in order to familiarize them with the task. Participants were also informed that they should respond as quickly and accurately as possible. It was explained that the study was designed to examine where participants' perceived the target locations and that it was important for them to give a response as soon as possible after the target was presented. Feedback was given regarding response times after the practice trials. Block order was randomized across subjects to control for possible learning effects across blocks.

Eye-movement control condition: Four new, naïve participants completed the task at a later time while eye movements were monitored. The paradigm for this test was exactly the same at that in the main experiment with one exception. A commercial infrared camera (LTCMW304C5 by LTS, Houston, TX) was set up in front of the aperture with a monitor off to the side such that the experimenter was able to continuously monitor the right eye of participants. If participants made an eye-movement before a magnitude estimate was given during a trial, the experimenter pressed the spacebar, a tone was sounded, and no magnitude estimate was recorded for that trial. The discarded trial was then repeated at a random time later during that block. This assured that five valid repeats for each target location tested were still obtained at the end of each block.

2.2.2. Results

Localization Errors. The task required participants to give magnitude estimates of the perceived target location relative to the aperture's edge and fixation. This type of relative judgment is essentially a percentage reflecting the ratio of the perceived target eccentricity relative to the perceived total extent of the stimulus space (i.e. the perceived eccentricity of the aperture edge). For the seven target eccentricities tested here (4°, 8°, 12°, 16°, 20°, 24°, and 28°) with the aperture edge located at 30° eccentricity, the true magnitudes of the targets relative to the aperture edge were 13.3, 26.7, 40, 53.3, 66.7, 80, and 93.3, respectively. Magnitude errors were calculated by subtracting the true magnitude of each target location from participants' magnitude estimates. Thus, a negative magnitude error indicates an underestimation of the true target location (i.e. a foveal bias) and a positive magnitude error indicates an overestimation (i.e. a peripheral bias). As the true eccentricity of the aperture edge and target locations are known, it was possible to recover errors in terms of degrees of visual angle as well. Therefore, to aid in comparisons with previous studies and provide a more meaningful unit of measurement, all figures show errors in degrees of visual angle as well as magnitude units. Figure 2 shows the mean magnitude errors as a function of Eccentricity and Axis for each of the three attention conditions. As can be seen, participants showed a foveal bias with a general tendency to underestimate the distance of the target from fixation. A 3(Attention) x 4(Axis) x 7(Eccentricity) Repeated Measures ANOVA (using the Greenhouse-Geisser correction when appropriate) was run on the mean magnitude errors. This analysis resulted in a main effect of Eccentricity, with participants showing larger underestimations the farther the target was from fixation, $F(2.1,22.6) = 4.58$, $p = 0.02$. Underestimations also increased the more attention was distributed across the visual field as seen in the significant main effect of Attention condition, $F(2, 22) = 6.83$, $p < 0.01$. A main effect of Axis was also found with greater underestimations along the horizontal meridian than the vertical meridian, $F(3,33) = 12.62$, $p < 0.01$. All two-way interactions also reached significance, showing that the degree of underestimation with Eccentricity depended on the Axis and Attention condition (Attention x Eccentricity: $F(12,132) = 2.93$, $p < 0.01$, Attention x Axis: $F(6,66) = 2.74$, $p = 0.02$, Eccentricity x Axis: $F(18,198) = 2.96$, $p < 0.01$). The pattern of errors across the eccentricities tested differs along the horizontal and vertical meridians in the three Attention conditions. However, the three-way interaction did not reach significant levels, $F(36, 396) = 1.38$, $p = 0.08$. A trend analysis showed an overall linear increase in foveal bias with Eccentricity, $F(1,11) = 8.02$, $p = 0.02$. Tests for quadratic and cubic trends did not reach significant levels ($p > 0.86$ for both).

Uncertainty in Perceived Location. As the attention conditions were designed to manipulate uncertainty in where targets could appear within a block of trials but not the location where they did appear on a given trial, the targets were presented at the maximum contrast possible (Weber contrast = 278%). However, in order to test for systematic changes in positional uncertainty, analyses were conducted on the standard deviations of the participants' magnitude errors. Figure 3 shows the standard deviations of the magnitude errors as a function of Eccentricity and Axis for the three attention conditions. The standard deviations were submitted to a 3(Attention) x 4(Axis) x 7(Eccentricity) Repeated-Measures ANOVA. As can be seen in Figure 3, standard deviations did not significantly differ across the three Attention conditions, $F(2,22) = 0.21$, $p = 0.81$. However, there were significant main effects of Axis, $F(3,33) = 4.24$, $p = 0.01$, and Eccentricity, $F(6,66) = 3.57$, $p < 0.01$. None of the interactions reached significant levels (ps > 0.46). A trend analysis on the standard deviations revealed a significant quadratic trend for Eccentricity, $F(1,11) = 10.10$, $p < 0.01$. The linear and cubic trends were not significant

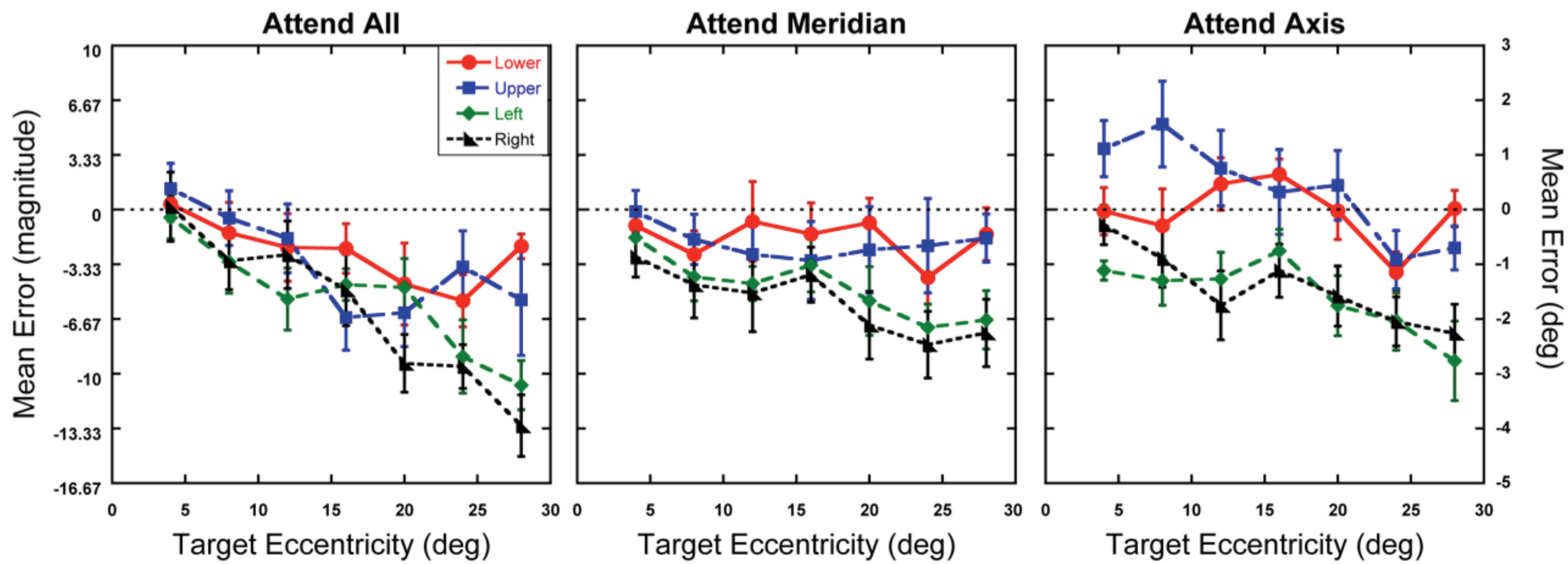

Figure 2. Experiment 1 Magnitude Errors. Mean magnitude errors for each of the four axes tested as a function of Target Eccentricity in degrees for the three Attention conditions. The right y-axis shows the errors in units of degrees of visual angle. The Lower Axis is shown as circles, the Upper Axis as squares, the Left Axis as diamonds, and the Right Axis as triangles. Error bars represent ±1 S.E. The dotted lines at zero represent expected performance if no distortion exists.

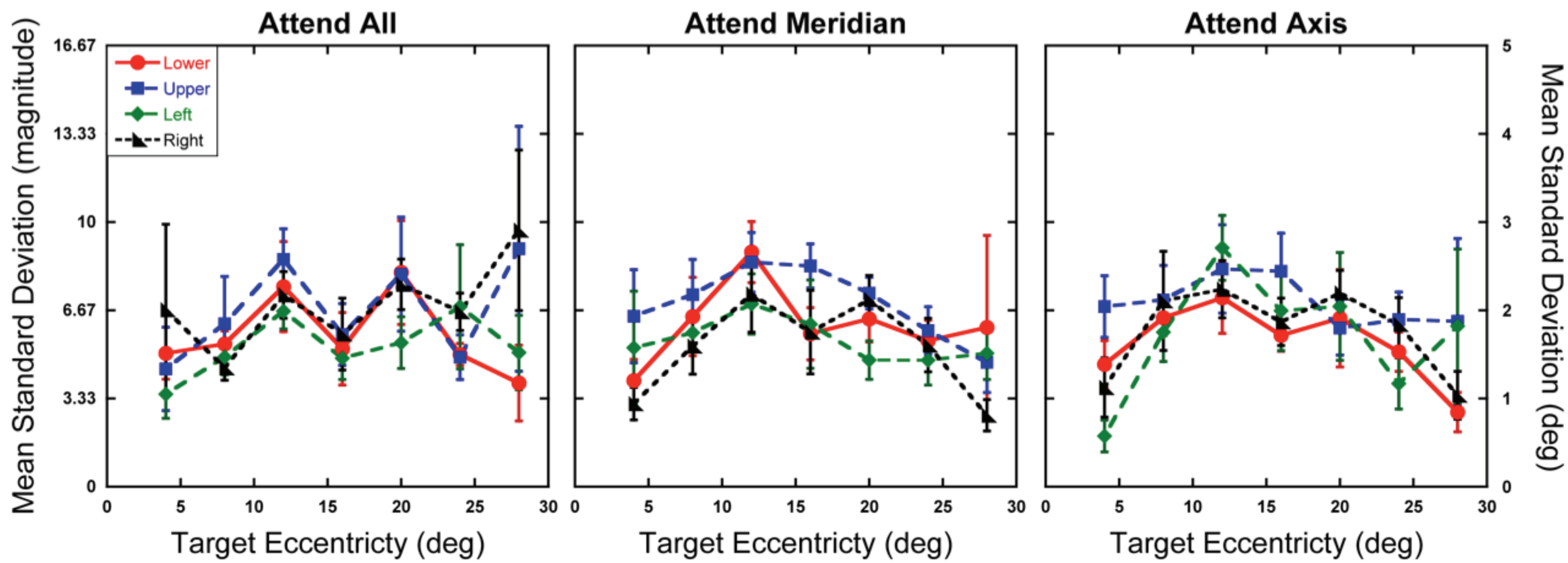

Figure 3. Experiment 1 Positional Uncertainty. Standard deviations of the magnitude errors as a function of Target Eccentricity in degrees and Axis tested for the three Attention conditions. The same formatting from Figure 2 is used here. Error bars represent ±1 S.E.

(linear: $p = 0.86$; cubic: $p = 0.15$). Post-hoc comparisons, using the Sidak-Bonferroni correction for multiple comparisons ($\alpha_{S\text{-}B} = 0.0085$), revealed that the main effect of Axis was driven by larger standard deviations along the upper axis relative to the left and right axes (*ps* ≤ 0.008), but not the lower axis ($p = 0.04$). Standard deviations did not differ among the other three axes (*p*s $\geq$ 0.21).

Spatial Metric(s) Underlying Localization Errors. While the localization errors showed differences in spatial distortion that varied with attentional distribution, eccentricity, and axis tested, it was not possible to determine from the errors alone whether this distortion reflected a deviation from a linear mapping, a change in scaling, or some combination of the two. In order to assess the underlying source of these changes, a hierarchical modeling scheme was applied in fitting a 2-parameter power function to the raw subject data. The predefined origin (the fixation point) was presented on every trial, eliminating the need for a constant parameter in the model. For every participant, power functions as shown in Equation 1 were fit to the 35 magnitude estimates (7 Eccentricities x 5 Repeats) for each of the 12 conditions (3 Attention conditions x 4 Axes).

$$J = \lambda D^{\alpha} \text{ (1)} \qquad (1)$$

In this equation, J = the magnitude estimate; D = the targets' true magnitude; λ = a global scaling factor that compresses or expands all values by a constant amount; α = an exponent that determines whether the metric is linear (i.e. when $\alpha = 1$). For every subject two functions were fit, one in which both the λ and α parameters were free to vary and one in which the α parameter was fixed at $\alpha = 1$ (GraphPad Prism, San Diego, CA). The quality of fits was assessed by comparing the change in the amount of variance explained relative to the change in degrees of freedom using an F-ratio. For the 1-parameter model the average adjusted R^2 was 0.91 (range: 0.42 to 0.97). For the 2-parameter model the average adjusted R^2 was 0.92 (range: 0.6 to 0.98). Across the 12 conditions for each of the 12 participants, 51% of the 144 functions showed a significantly better fit by the 2-parameter model. While half of the models showed a better fit when exponents were allowed to vary from 1, the increase in variability explained was modest. The average R^2 results showed only a 1% increase on average for the 2-parameter model over a 1-parameter model. Based on the high level of explained variance for the 1-parameter model and the only modest increase in variance explained when the exponent was treated as a free parameter, these results suggest that the magnitude estimates are best fit by a linear model. The estimates from this model were therefore used in further analyses.

Figure 4 shows the mean estimated slopes (λ) across the three Attention conditions for each of the four axes tested. In order to further examine the effect of attention on perceived location, a 3(Attention) x 4(Axis) Repeated Measures ANOVA was used to analyze the estimated slopes with Greenhouse-Geisser corrections applied where appropriate. The results show a main effect of Attention, with slopes increasing monotonically as attention was focused on smaller regions of space, $F(2,22) = 6.79$, $p < 0.005$. There was also a main effect of Axis,

$F(3,33) = 16.69$, $p < 0.001$. The Attention x Axis interaction was not significant, $F(3.42,37.64) = 0.73$, $p = 0.56$.

2.2.3. Discussion

Attentional Effects on Foveal Bias. Previous studies have found that targets flashed in the peripheral visual field tend to be mislocalized toward the fovea (Mateeff & Gourevich, 1983; Müsseler, et al., 1999). The results of Experiment 1 both replicate this finding and extend it to include measurements based on magnitude estimates relative to a stable external visual boundary (i.e. an aperture's edge). More importantly, the results demonstrate that changes in the distribution of sustained voluntary attention across the visual field, independent of other landmarks present in a display, can alter the degree to which such targets are mislocalized. As seen in Figure 2, the Attention x Eccentricity interaction reflects the different rates of underestimation with eccentricity across attention conditions. This effect is most evident when comparing the magnitude errors in the Attend All and Attend Axis conditions, with small errors for the close eccentricities but large underestimations at the farther eccentricities in the Attend All condition. In contrast, errors for the Attend Axis condition were small for both close and far eccentricities. Interestingly, the magnitude estimates in the Attend Meridian condition showed a pattern that was similar to the Attend All condition for the closer target eccentricities (< 12°) but resembled the Attend Axis condition for the farther eccentricities.

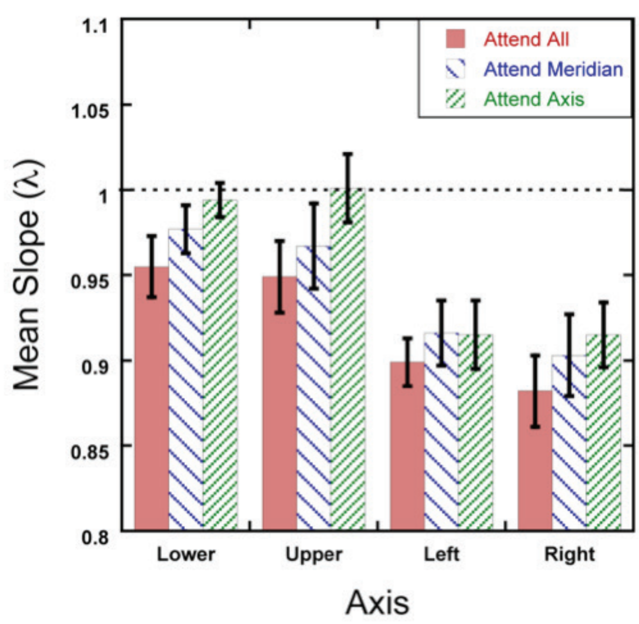

Figure 4. Experiment 1 Slope Parameters. Mean estimated slope parameters, λ, as a function of Axis tested for the three attention conditions after fitting the individual magnitude estimates to the function $J = \lambda D$. Error bars represent ±1 S.E. The dotted line at one represents the expected performance if the mapping is undistorted.

The effect of attentional distribution on perceived location is further seen in the slope estimates of Figure 4, which show a global decrease in scaling when attention is distributed across the entire visual field relative to when attention is focused on a specific region. Previous studies (Adam, et al., 2008; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999) have reported that the degree to which participants underestimate the distance of a target from fixation is approximately 10% of the eccentricity of that target. In both of these studies targets were only presented along the horizontal meridian and inspection of Figure 4 shows a similar degree of underestimation for targets presented along the horizontal meridian here with slopes around 0.90. Similar degrees of underestimation were not, however, found for targets along the vertical meridian. These results will be discussed more fully below.

One concern that could be raised about the magnitude errors is whether the differential distributions of the eccentricity effects across attention conditions are the result of a true distortion in perceived location or arise from degradation in stimulus quality due to changes in sampling and cortical processing in the peripheral visual field (Banks, Sekuler, & Anderson, 1991; Bishop & Henry, 1971; Goldstein, 2002; Horton & Hoyt, 1991; Johnston, 1986; Mullen, Sakurai, & Chu, 2005). The analyses of the standard deviations addressed this question and showed a quadratic inverted-U trend, verifying that the linear increase in foveal bias across eccentricity cannot be explained by uncertainty in perceived target location per se. Rather, the results are more consistent with the participants using the fixation point and edge of the aperture as landmarks, with uncertainty in estimates reaching a maximum at the points most distant from these two landmarks. However, unlike previous studies (Diedrichsen, et al., 2004; Kerzel, 2002; Uddin, et al., 2005a; Werner & Diedrichsen, 2002; Yamada, et al., 2008), which have shown that the presence of landmarks or distracter elements in a display can reduce foveal bias (i.e. they induce a bias in localization towards the landmark), the results of the present study show that the edge of the aperture and point of fixation served only to reduce variability in responses. Errors in localization consistently showed the largest foveal bias for target locations closest to the aperture edge. Thus, the edge of the aperture was not able to serve as a landmark in the same manner that has been reported previously in the literature. Importantly, the lack of any main effect or interaction with Attention condition in the analysis of the standard deviations suggests that uncertainty in perceived location did not vary systematically as attention was spread across the visual field.

Vertical/Horizontal Differences. While the three-way interaction for the magnitude errors did not reach significant levels, a trend was observed. Specifically, the pattern of results seen in Figure 2 suggests that there was a qualitative difference in performance along the horizontal and vertical meridians across the three attention conditions. Magnitude errors tended to be smaller along the vertical meridian in all three of the attention conditions, and the rate at which magnitude errors changed with eccentricity also tended to be smaller along the vertical meridian. The largest dissociation in performance along the horizontal and vertical meridians is seen in the Attend Axis condition. Here, participants actually overestimated target locations along the upper axis for most of the points, and there was almost no error along the lower axis. Differences in foveal bias across the two meridians are also visible in the slope parameters. As can be seen in Figure 4, slope estimates were higher for the upper and lower axes than the left and right axes across the three attention conditions. Moreover, the slope estimates for the Attend Axis condition show a near perfect scaling across eccentricity along the vertical meridian, with slopes approaching a value of one (lower axis = 0.994, upper axis = 1.001). In contrast, slopes estimates along the horizontal meridian ranged from 0.882 to 0.916.

This result is important as it shows that participants were able to give accurate verbal estimates of the target locations, at least under some circumstances. This increases confidence that errors along the other axes and different attention conditions reflects distortions in perceived target locations and not just an inability to give accurate verbal judgments, as the same eccentricities were tested in all cases.

No predictions were made prior to testing about variations in localization performance across the two meridians. In the peripheral localization literature, no definitive evidence exists for differences in performance across the two meridians. One study by Temme et al. (1985) found that for eccentricities larger than 20º, overestimations in perceived eccentricity were greater along the upper axis than the lower axis, and larger overall along the vertical meridian when compared to estimates along the horizontal meridian. However, this study differs from the present study in that participants made judgments relative to their perceived visual field extent and the results show a consistent peripheral bias in perceived location. Moreover, another study (Bock, 1993) that found peripheral biases in perceived eccentricity using a pointing task found comparable biases across the two meridians, though only locations within the central 10º were tested. While it is not clear why performance varied across the horizontal and vertical meridians in the present task, both neurobiological and visual distinctions between the two meridians and across the lower and upper axes have been found in a variety of tasks (Carrasco, Giordano, & McElree, 2004; Carrasco, Talgar, & Cameron, 2001; McAnany & Levine, 2007; Previc, 1998; Previc & Intraub, 1997). At least one study (Mackeben, 1999) has also found greater cueing benefits when stimuli are presented along the horizontal meridian than the vertical meridian in a letter identification task. Similarly here, the largest changes in localization errors across the three attention conditions occurred along the horizontal meridian. However, it has also been shown that individual differences exist in the degree to which attentional facilitation occurs in different regions of the visual field for a given eccentricity (Altpeter, Mackeben, & Trauzettel-Klosinski, 2000; Mackeben, 1999). As most studies on localization in the visual periphery have only tested along the horizontal meridian, it is not possible to determine whether the present results reflect an inherent anisotropy across the meridians in this type of task, a property of the subject population used in the study, or some combination of the two. While the horizontal-vertical anisotropy may appear to add undue complexity to the question of how attention changes representations of visual space, these results show that different effects of attention along the horizontal and vertical meridians can be isolated by analyzing parameters that tease apart the underlying spatial metric.

Potential Confounds. One concern about the present data is whether or not eye-movement patterns differed across the three attention conditions, as it is well documented that eye-movements toward target locations can improve localization performance (Adam, et al., 1993; Enright, 1995; Uddin, 2006). However, previous studies that have examined localization and attention with and without eye movements have found only modest benefits for localization performance with eye-movements at the target duration used in the present study (Adam, et al., 2008; Adam, et al., 1993). This is supported by another study examining shifts of attention and eye movements that found typical saccade latencies of around 200ms (Hoffman & Subramanian, 1995). In the current study the presentation time of the target was kept very brief (150ms) to help prevent participants from making eye-movements to the targets once they appeared. A more problematic issue is whether participants moved their eyes before the target appeared. While the instructions emphasized maintaining fixation at the center of the screen, the optimal strategy to locate an object in a given region would be to fixate in the center of the region along which the target might appear. For the Attend All and Attend Meridian conditions, eye movements were not of great concern since the optimal location corresponded to the center of the screen. Eye-movements are of greater concern in the Attend Axis condition in which participants knew the direction in which the target would appear. Thus, while the timing of target presentations were the same across the attention conditions, it is possible that in the Attend Axis condition, when participants knew the direction in which the target would appear, participants made eye-movements along the tested axis prior to target onset on some trials and this reduced their errors. The eye-movement control condition was run in order to address this concern.

Figure 5 shows the mean errors for the eye-movement control condition as a function of Eccentricity and Attention condition. Given the small number of participants who completed this task, statistical analyses on the data were not completed. However, inspection of Figure 5 shows that the pattern of errors replicates the overall pattern found in the main experiment, with errors both increasing with increasing eccentricity and larger errors found as attention was distributed across more of the visual field. If participants did move their eyes along the attended axis in the

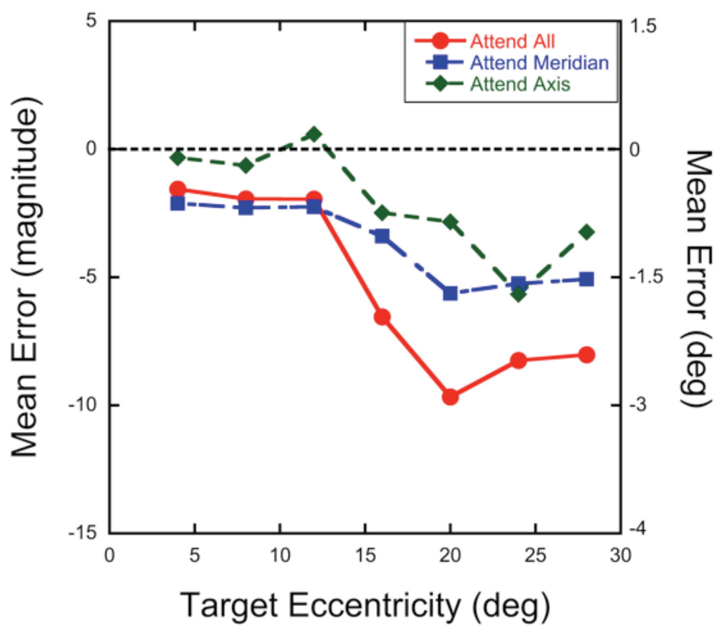

Figure 5. Experiment 1 Eye-Movement Control. Mean magnitude errors for the four participants who completed the eye-movement control condition as a function of Target Eccentricity in degrees for the three Attention conditions. The right y-axis shows the errors in units of degrees of visual angle. Means for the Attend All condition are shown as circles, the Attend Meridian condition are shown as squares, and the Attend Axis condition are shown as diamonds. The dotted line at zero represents expected performance if no distortion exists.

main experiment and this in turn lead to reductions in foveal bias, the data from the eye-movement control condition should not show significant differences across the three attention conditions. Rather, the same degree of underestimations would be expected across the three attention conditions. The fact that the expected differences were found in the control condition therefore suggests that the differences in localization errors across the three Attention conditions in the main experiment cannot be explained by systematic differences in eye-movement patterns.

Another potential confound in the original design is that the number of possible target locations co-varied with the attention manipulation. While participants were informed before each block that the target could appear anywhere along the attended axes, and they should therefore maintain attention across the space, it is possible that variations in the number of target locations tested influenced the responses of participants. As the number of target locations tested in each block and changes in the distribution of attention cannot be untangled in the present design, a second experiment was conducted to address this issue.

2.3. Experiment 2: Dissociating Attentional Distribution From the Number of Target Locations

This experiment followed the same procedure as the previous experiment with the following exceptions. In the Attend All condition, only four eccentricities were tested along each axis resulting in a total of 16 target locations tested. The same seven eccentricities tested in Experiment 1 were tested in the two Attend Meridian conditions, resulting in a total of 14 target locations in each of the two blocks. Finally, in the four Attend Axis blocks, 14 eccentricities were tested along each axis. Thus, the total number of target locations tested in each block of trials was either 16 or 14 locations. If the attention effects found in Experiment 1 are the result of changes in the number of target locations tested within a block, no differences across the three Attention condition should be found. On the other hand, if changes in the errors seen in Experiment 1 are due to changes in the distribution of attention *across* the axes being attended, then the same pattern of errors observed in Experiment 1 should be observed here.

2.3.1. Methods

Participants. Eleven undergraduates (7 females; mean age: 19.6 ± 1.0 years) participated in this experiment for course credit. None of the participants had participated in the previous experiment and the same exclusion criteria as before applied. All gave informed consent as approved by the University of California before participating.

Materials and Procedure. The same stimulus parameters and apparatus as in Experiment 1 were used. For the Attend All condition, the eccentricities tested were: 4°, 12°, 20°, and 28°. In the Attend Meridian condition, seven eccentricities tested were: 4°, 8°, 12°, 16°, 20°, 24°, and 28°. Finally, in the Attend Axis condition, eccentricities were sampled every 2deg to include: 2°, 4°, 6°, 8°, 10°, 12°, 14°, 16°, 18°, 20°, 22°, 24°, 26°, and 28°. As the total number of targets across all attention conditions increased from 84 in Experiment 1 to 100 in this experiment, the number of repetitions for each target location was reduced to 4 repetitions per block. Therefore, there were a total of 400 experimental trials in this experiment. As before, all participants completed 10 practice trials before beginning the experiment, and block order was varied across participants.

2.3.2. Results

Localization Errors. Magnitude errors were calculated in the same way as in Experiment 1 and the mean localization errors are shown in Figure 6. Only four eccentricities (4°, 12°, 20°, and 28°) were tested in all three of the attention conditions. The mean magnitude errors for these four eccentricities were therefore run in a 3(Attention) x 4(Axis) x 4(Eccentricity) Repeated Measures ANOVA (using the Greenhouse-Geisser correction when appropriate). As in the previous experiment, there was a significant effect of Attention, with larger underestimations observed when attention was distributed across the visual field, $F(2, 20) = 11.87$, $p < 0.001$. Magnitude errors also increased with Eccentricity, $F(3,30) = 13.31$, $p < 0.001$. In contrast to Experiment 1, no difference was found in magnitude errors across the four axes tested, $F(2.04,20.42) = 1.03$, $p = 0.40$. Moreover, none of the interactions were significant ($ps \geq 0.32$). Contrary to the first experiment, a trend analysis for the Eccentricity factor showed a significant linear trend, $F(1,10) = 25.13$, $p = 0.001$, and a significant cubic trend, $F(1,10) = 6.11$, $p = 0.03$. The quadratic trend was not significant, $F(1,10) = 1.67$, $p = 0.23$.

Uncertainty in Perceived Location. As in Experiment 1, analyses on the standard deviations were conducted to assess whether positional uncertainty increased with Eccentricity or across the different Attention conditions. Figure 7 shows the mean standard deviations as a function of Axis and Eccentricity for the three attention conditions. A 3(Attention) x 4(Axis) x 4(Eccentricity) Repeated-Measures ANOVA was used to analyze the mean standard deviations for the four eccentricities tested in all attention conditions, with Greenhouse-Geisser corrections applied where necessary. Analyses revealed a significant effect of Eccentricity, $F(3,30) = 24.81$, $p < 0.001$. There was no main effect of Axis, $F(3,30) = 1.50$, $p = 0.24$, and no main effect of Attention, $F(2,20) = 0.40$, $p = 0.68$. The Axis x Attention interaction was also not significant, $F(6,60) = 1.06$, $p = 0.39$. However, the Attention x Eccentricity interaction was significant with a shift in the peak standard deviations from 12º in the Attend All condition to 20º in the Attend Meridian and Attend Axis conditions, $F(6,60) = 2.57$, $p = 0.03$. The Axis x Eccentricity interaction was also significant, $F(9,90) = 2.50$, $p = 0.01$. The three-way interaction was not significant, $F(18,180) = 1.36$, $p = 0.16$. As in Experiment 1, a trend analysis run on the main effect of Eccentricity showed a significant quadratic trend, $F(1,10) = 51.44$, $p < 0.001$. The linear and cubic trends were not significant (linear: $F(1,10) = 0.13$, $p = 0.72$; cubic: $F(1,10) = 0.03$, $p = 0.87$).

Spatial Metric(s) Underlying Localization Errors. In order to assess the spatial metric the participants used to make magnitude judgments across eccentricity the same fitting procedure described in Experiment 1 was applied. For the 1-parameter model the average adjusted R^2 was 0.92 (range: 0.66 to 0.98). For the 2-parameter model the average adjusted R^2 was 0.93 (range: 0.77 to 0.99). Across the 12 conditions for each of the 11 participants, only 39% of the 132 functions showed a significantly better fit by the 2-parameter model. In part, this difference can be explained by the smaller number of eccentricities tested in the Attend All condition. With only four eccentricities, the increase in the number of free parameters increases the risk of model over-fitting. Regardless, given that 61% of the conditions showed a better fit with the 1-parameter model, these results suggest that the magnitude estimates are best fit by a linear model as found in Experiment 1. The estimates from this model were therefore used in further analyses.

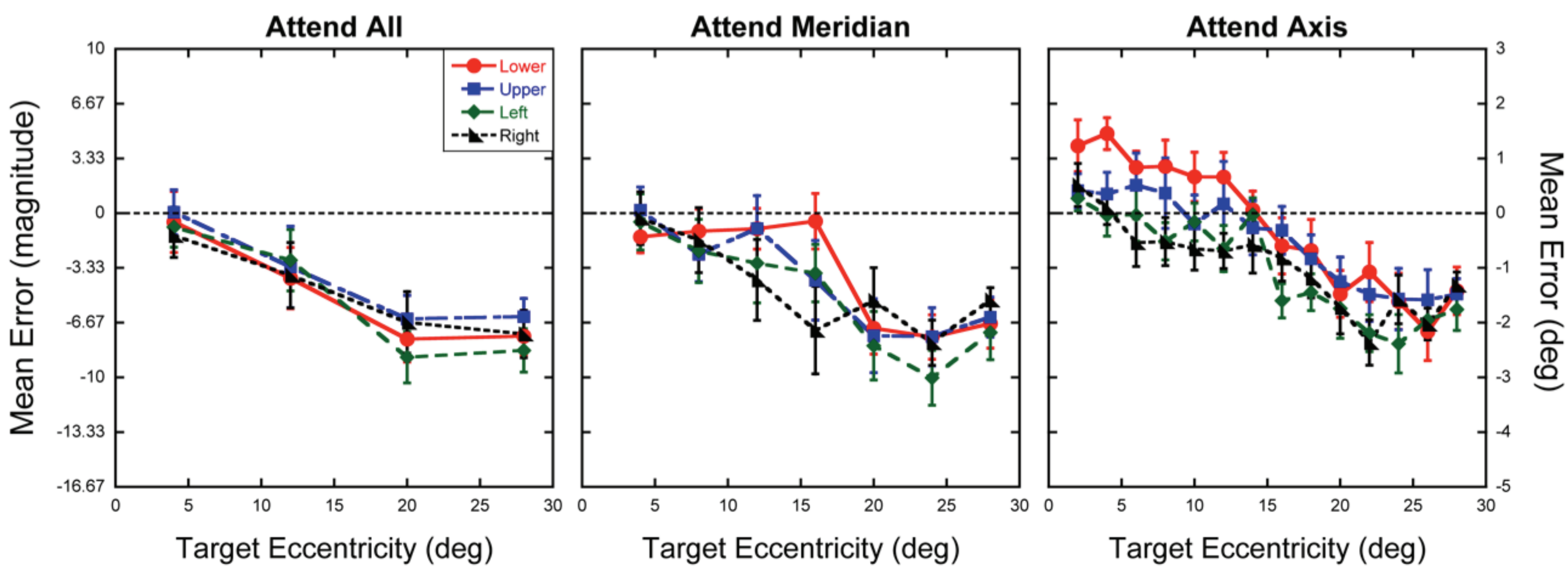

Figure 6. Experiment 2 Magnitude Errors. Mean magnitude errors for each of the four axes tested as a function of Target Eccentricity in degrees for the three Attention conditions. The right y-axis shows the errors in units of degrees of visual angle. The Lower Axis is shown as circles, the Upper Axis as squares, the Left Axis as diamonds, and the Right Axis as triangles. Error bars represent ±1 S.E. The dotted lines at zero represent expected performance if no distortion exists.

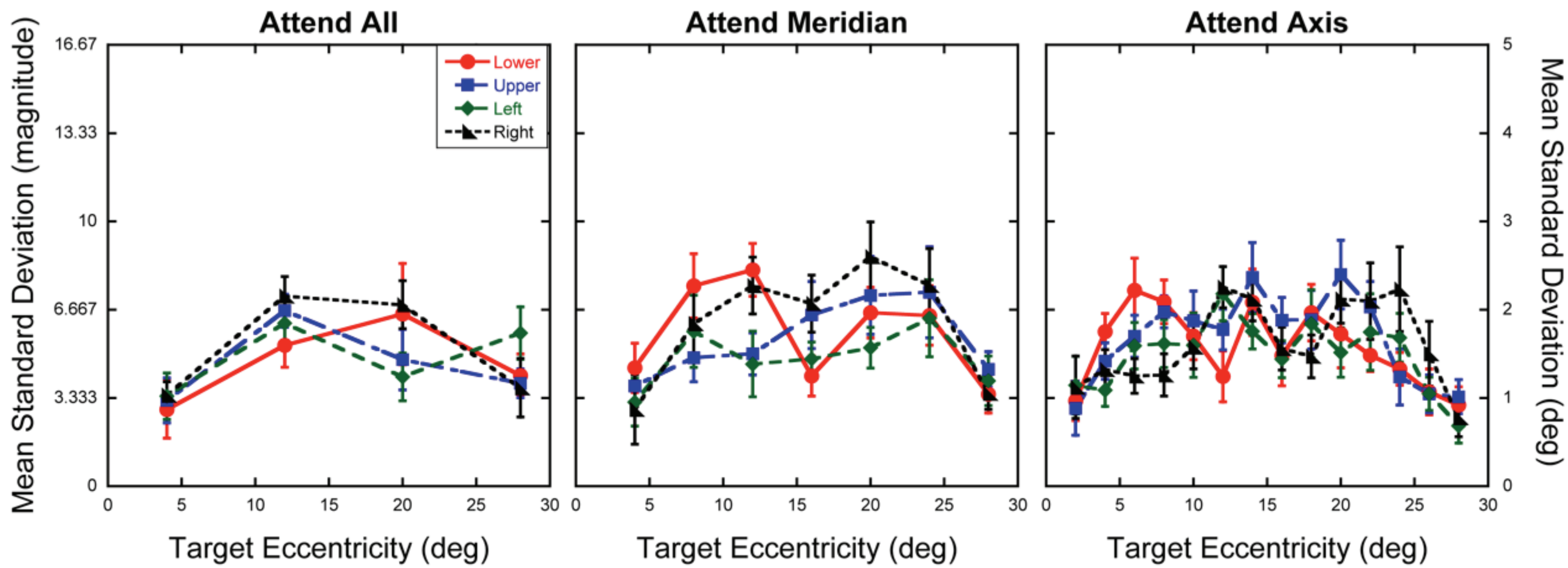

Figure 7. Experiment 2 Positional Uncertainty. Standard deviations of the magnitude errors as a function of Target Eccentricity in degrees and Axis tested for the three Attention conditions. The same formatting from Figure 6 is used here. Error bars represent ±1 S.E.

Figure 8 shows the mean estimated slopes (λ) across the three Attention conditions for each of the four axes tested. A 3(Attention) x 4(Axis) Repeated Measures ANOVAs was used to analyze the estimated slopes. The results showed a main effect of Attention, with slopes increasing as attention was focused on smaller regions of space, $F(2,20) = 4.87$, $p = 0.02$. As expected given the pattern of the magnitude errors, the slopes did not differ across the four axes tested, $F(3,30) = 1.27$, $p = 0.30$. The Attention x Axis interaction was also not significant, $F(6,60) = 0.52$, $p = 0.79$.

2.3.3. Discussion

The findings of Experiment 2 support the hypothesis that changes in the distribution of attention modulate foveal biases in peripheral localization. In contrast to Experiment 1, the number of target locations was equated as best as possible across the three Attention conditions. Significant reductions in foveal biases were again found in the Attend Axis condition relative to the Attend All and Attend Meridian conditions. This is supported both by changes in the magnitude errors themselves, as well as changes in the slope parameters.

There were a couple of differences found in the pattern of errors across the two experiments. Inspection of Figures 2 and 6 suggest a reduction in foveal bias for the farthest eccentricity tested in the Attend All condition along the horizontal meridian. While there were a total of 16 target locations in this block across the four axes, only four distinct eccentricities were tested. Given the small number of distinct eccentricities, it is plausible that in this condition

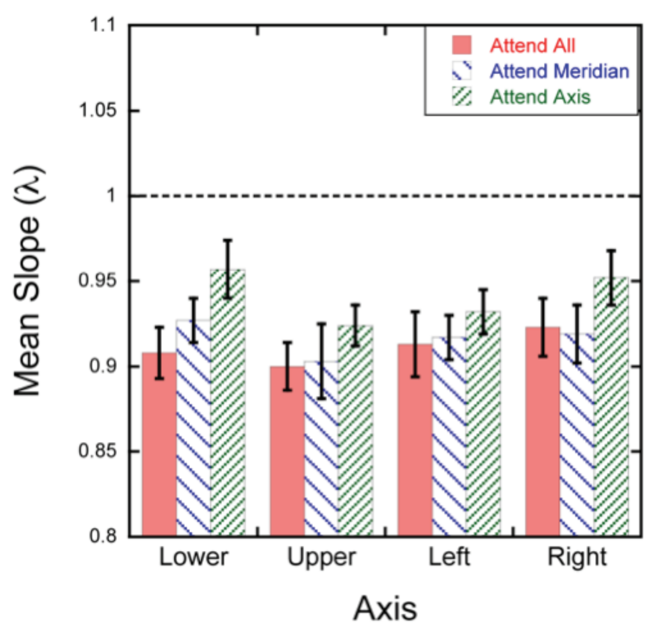

Figure 8. Experiment 2 Slope Parameters. Mean estimated slope parameters, λ, as a function of Axis tested for the three attention conditions after fitting the individual magnitude estimates to the function J = λD. Error bars represent ±1 S.E. The dotted line at one represents the expected performance if the mapping is undistorted.

participants were more likely to be aware that the same eccentricities across each axis were repeatedly tested. This, in turn, may have caused a reduction in target uncertainty *once the target appeared* over the coarse of the block. This interpretation is supported by a slight reduction in the average standard deviations of responses in the Attend All condition across the two experiments, which is not seen for the other two attention conditions.

A more significant difference across the two experiments is the lack of a main effect of Axis or an interaction between Axis and Attention condition for either the magnitude errors or the slope parameters. In the first experiment foveal biases were significantly smaller along the vertical meridian than the horizontal meridian. In the current experiment, no differences in magnitude errors were observed in the Attend All condition across the two meridians. Across all attention conditions, the magnitude of errors along the horizontal meridian closely matched those found in the first experiment with the exception of the farthest eccentricity tested in the Attend All condition. The largest changes in magnitude errors across the two experiments occurred for target locations along the vertical meridian. In the Attend Axis condition, an overestimation of target locations was still observed for the target eccentricities closest to the point of fixation along the lower axis. However, for the farther eccentricities tested, magnitude errors showed comparable foveal biases across all axes tested. The lack of a horizontal-vertical anisotropy is also clearly seen in the slope parameters. While the slope parameters for the left and right axes matched those found in Experiment 1, the slope parameters for the upper and lower axes showed a large reduction in this experiment that is apparent across all three Attention conditions. The only difference between the first experiment and the current one was the number of locations tested in each Attention condition and there is no apparent reason why changes in the number of target locations across the three Attention conditions would influence the horizontal-vertical anisotropy found in Experiment 1. However, as noted previously, there are known individual differences in attentional facilitation across the visual field (Altpeter, et al., 2000; Mackeben, 1999). The lack of any significant variation in localization performance across the two meridians in this experiment therefore suggests that the previous dissociation may have been due to individual differences on the part of the participants.

In sum, the present results support the hypothesis that changes in the distribution of attention across the visual field modulate foveal biases when localizing peripheral targets. One further question is whether the degree to which targets locations are underestimated depends on the relative location of the targets within the display or the true eccentricity of the targets. Magnitude errors were comparable in size across the previous two experiments and both of these experiments were run at the same viewing distance so the magnitudes and target eccentricities remained constant. Given a fixed aperture width, it is possible to dissociate the true magnitudes of the targets from the target eccentricities by manipulating the viewing distance to the screen. The last experiment used this technique to look at the influence of target eccentricity and relative location on the magnitude of foveal biases.

2.4. Experiment 3: The Relationship Between the Magnitude of Foveal Bias and Visual Angle

This experiment was the same as Experiment 1 except for one change in the design: the viewing distance of the participants was doubled from 25.4cm to 50.8cm. This change essentially halved the eccentricities of the target locations. If the degree to which participants underestimate the locations of targets depends on the true eccentricity of the target item, (independent of the relative position along each axis in the display) then localization errors should be smaller overall than the errors observed in the first experiment but should match the pattern observed within the first four testing locations (i.e. 4°-16°). On the other hand, if the degree of foveal bias depends on the relative location of the targets within the display, the localization errors in this experiment should be of the same magnitude and follow the same pattern as the results from the first experiment.

2.4.1. Methods

Participants. Fourteen undergraduates (7 females; mean age: 20.4 ± 3.3years) participated in this experiment for course credit. None of the participants had participated in the previous two experiments and the same exclusion criteria as before applied. All gave informed consent as approved by the University of California before participating.

Materials and Procedure. The same stimulus parameters and apparatus as in Experiment 1 were used. Participants viewed the monitor from 50.8cm. Given that targets were presented on a flat monitor, doubling the viewing distance did not exactly halve the eccentricities of the targets. The new eccentricities of the seven target locations along each axis were: 2.0°, 4.0°, 6.1°, 8.2°, 10.3°, 12.6°, and 14.9° of visual angle. The aperture, with a radius of 14.67cm, was now located at 16.1° eccentricity. Thus, the true magnitudes of the targets in this experiment were 12.4, 25, 37.7, 50.7, 64.1, 78, and 92.5, respectively. As before, all participants completed 10 practice trials before beginning the experiment. In order to better control for learning effects, 14 participants completed the experiment, and block order was counterbalanced across participants with the constraint that each of the seven blocks be presented twice at a given temporal order. In other words, two of the participants completed the Attend All condition in the first block; two completed it during the second block of trials, etc.

2.4.2. Results

Localization Errors. Magnitude errors were calculated in the same way as in Experiment 1 and the mean localization errors are shown in Figure 9. A 3(Attention) x 4(Axis) x 7(Eccentricity) Repeated Measures ANOVA (using the Greenhouse-Geisser correction when appropriate) was used to analyze mean magnitude errors. As in the previous experiment, there was a significant effect of Attention, with larger underestimations observed when attention was distributed across the visual field, $F(2, 26) = 16.52$, $p < 0.001$. There was also a main effect of Axis, $F(3,39) = 4.75$, $p = 0.01$. The main effect of Eccentricity did not reach significant levels, $F(1.68,21.77) = 3.05$, p = 0.07. However, Eccentricity did interact with Attention condition, $F(5.48,71.22) = 3.42$, $p = 0.006$, and the Axis tested, $F(18,234) = 3.00$, $p < 0.001$. The Attention x Axis interaction was also significant, $F(6,78) = 3.53$, $p = 0.004$. The three-way interaction was not significant, $F(36, 468) = 1.07$, $p = 0.36$. Contrary to the first experiment, a trend analysis for the Eccentricity factor did not reach significant levels for the linear trend, $F(1,13) = 3.81$, p = 0.07. The quadratic and cubic trends were also not significant (quadratic: $F(1,13) = 1.04$, p = 0.33; cubic: $F(1,13) = 0.44$, p = 0.52).

Uncertainty in Perceived Location. As in Experiment 1, analyses on the standard deviations were conducted to assess whether positional uncertainty increased with Eccentricity or across the different Attention conditions. Figure 10 shows the mean standard deviations as a function of Axis and Eccentricity for the three attention conditions. A 3(Attention) x 4(Axis) x

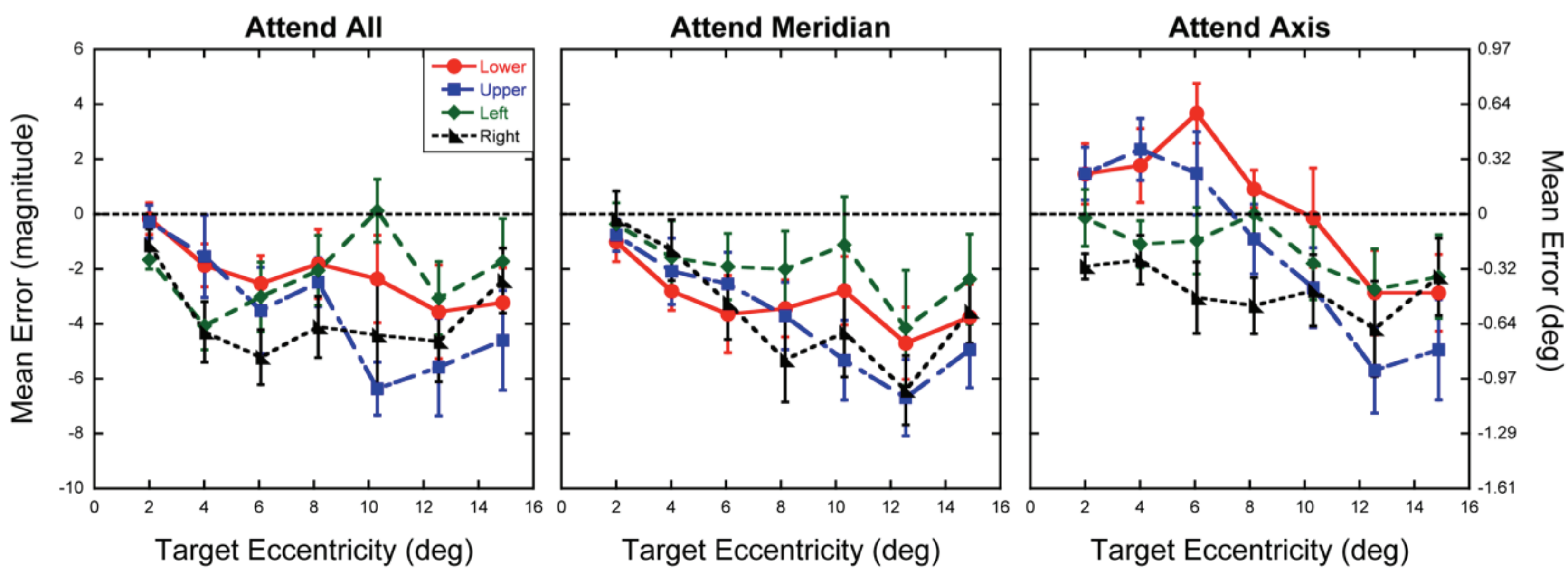

Figure 9. Experiment 3 Magnitude Errors. Mean magnitude errors for each of the four axes tested as a function of Target Eccentricity in degrees for the three Attention conditions. The right y-axis shows the errors in units of degrees of visual angle. The Lower Axis is shown as circles, the Upper Axis as squares, the Left Axis as diamonds, and the Right Axis as triangles. Error bars represent ±1 S.E. The dotted lines at zero represent expected performance if no distortion exists.

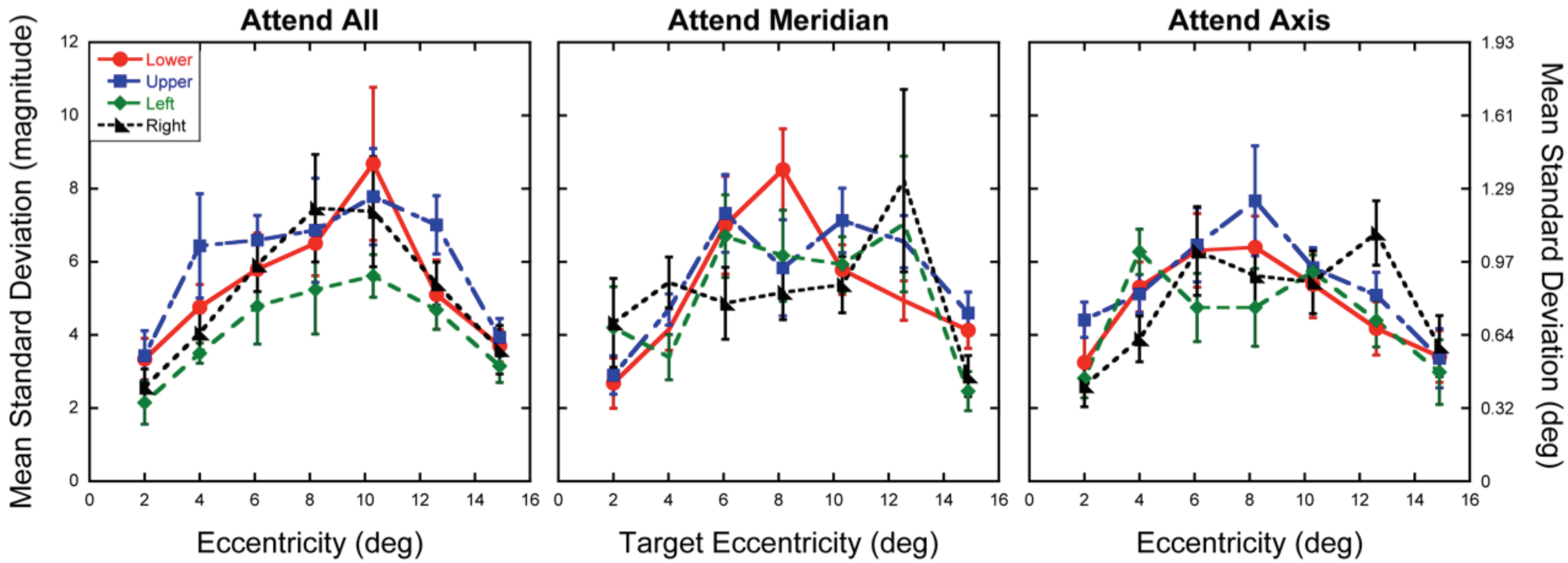

Figure 10. Experiment 3 Positional Uncertainty. Standard deviations of the magnitude errors as a function of Target Eccentricity in degrees and Axis tested for the three Attention conditions. The same formatting from Figure 9 is used here. Error bars represent ±1 S.E.

7(Eccentricity) Repeated-Measures ANOVA was used to analyze the mean standard deviations with Greenhouse-Geisser corrections applied where necessary. The pattern of results mirrored that found in Experiment 1. Analyses revealed a significant effect of Eccentricity, $F(2.24,29.08) = 14.09$, $p < 0.001$, and a main effect of Axis, $F(3,39) = 4.43$, $p = 0.01$. There was no main effect of Attention, $F(2,26) = 0.11$, $p = 0.90$, although the Axis x Attention interaction did show a trend, $F(6,78) = 2.09$, $p = 0.06$. The Axis x Eccentricity interaction was not significant, $F(18,234) = 0.95$, $p = 0.52$, nor was the Attention x Eccentricity interaction, $F(12,156) = 1.32$, $p = 0.21$. Finally, the three-way interaction was not significant, $F(36,468) = 1.22$, $p = 0.19$. A trend analysis run on the main effect of Eccentricity showed significant linear and quadratic trends (linear: $F(1,13) = 15.55$, $p = 0.002$; quadratic: $F(1,13) = 38.26$, $p < 0.001$). The cubic trend did not reach significance, $F(1,13) = 4.39$, $p = 0.06$.

Spatial Metric(s) Underlying Localization Errors. The spatial metric used by participants to make magnitude judgments across eccentricity was assessed with the same fitting procedure described in Experiment 1. For the 1-parameter model the average adjusted R^2 was 0.94 (range: 0.73 to 0.98). For the 2-parameter model the average adjusted R^2 was 0.95 (range: 0.84 to 0.98). Across the 12 conditions for each of the 14 participants, 52% of the 168 functions showed a significantly better fit by the 2-parameter model. As in Experiment 1, while half of the models showed a better fit when exponents were allowed to vary from 1, the increase in variability explained was modest. The average R^2 results showed only a 1% increase on average

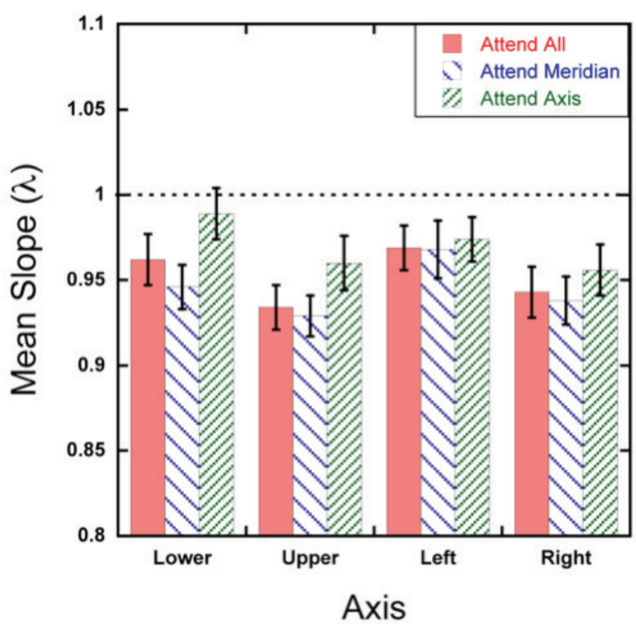

Figure 11. Experiment 3 Slope Parameters. Mean estimated slope parameters, λ, as a function of Axis tested for the three attention conditions after fitting the individual magnitude estimates to the function $J = \lambda D$. Error bars represent ±1 S.E. The dotted line at one represents the expected performance if the mapping is undistorted.

for the 2-parameter model over a 1-parameter model. Based on the high level of explained variance for the 1-parameter model and the modest increase in variance explained when the exponent was treated as a free parameter, these results suggest that the magnitude estimates are best fit by a linear model as found in Experiment 1. The estimates from this model were therefore used in further analyses.

Figure 11 shows the mean estimated slopes (λ) across the three Attention conditions for each of the four axes tested. A 3(Attention) x 4(Axis) Repeated Measures ANOVAs was used to analyze the estimated slopes. The results showed a main effect of Attention, with slopes increasing as attention was focused on smaller regions of space, $F(2,26) = 7.19$, $p = 0.003$. There was also a main effect of Axis, $F(3,39) = 4.6$, $p = 0.007$. The Attention x Axis interaction was not significant, $F(6,78) = 1.58$, $p = 0.16$.

2.4.3. Discussion

The results of the last experiment mirror those found in Experiment 1 in several respects. First, the foveal bias was replicated with a new group of participants and at a new viewing distance. As seen in Figure 9, across both meridians and the three attention conditions participants showed consistent underestimations in perceived target location, and the degree of underestimation tended to increase with eccentricity. Second, the degree to which participants exhibited a foveal bias was modulated by the extent to which the participants' distributed their attention across the display, again confirming the main finding in Experiment 1. Relative to the Attend All and Attend Meridian conditions, the foveal bias was significantly reduced in the Attend Axis condition. The pattern of variability in magnitude estimates for a given target also showed a similar inverted-U pattern to that observed in the previous experiments, with the smallest variability seen in estimates to the targets closest to the fovea and aperture edge.

There are a few ways in which the pattern of errors in the present study diverged from those observed in Experiment 1. First, magnitude error tended to be smaller in this experiment relative to the first, particularly when the errors were calculated in degrees of visual angle. The rate at which errors increased across eccentricity was also smaller than in the previous experiments. This is reflected in the main effect of Eccentricity not reaching significant levels and the higher slope estimates along the horizontal meridian. However, in the current experiment the locations of the targets in degrees of visual angle were approximately half the size as in the first experiment. This suggests that the size of the foveal bias exhibited by participants depends to some extent on the retinal location of the target and not just the relative location of the targets within the display. To more easily compare the magnitude errors across Experiment 1 and Experiment 3, Figure 12 shows the mean errors in degrees of visual angle as a function of Eccentricity and Experiment for the three Attention conditions. As can be seen in Figure 12, both the pattern and size of errors across eccentricity are similar in both experiments in the Attend Axis and Attend Meridian conditions. Thus, despite a global reduction in the size of magnitude errors found in the second experiment, the absolute size of these errors in terms of degrees of visual angle was comparable when target eccentricities were matched. Less consistency in the pattern of errors across eccentricity was found in the Attend All condition, with participants showing a more constant level of underestimation in this experiment than Experiment 1. One possible explanation for the difference in patterns may be how participants utilized the edge of the aperture as a landmark. Several studies (Diedrichsen, et al., 2004; Kerzel, 2002; Uddin, et al., 2005a; Werner & Diedrichsen, 2002; Yamada, et al., 2008) have found a reduction in foveal bias

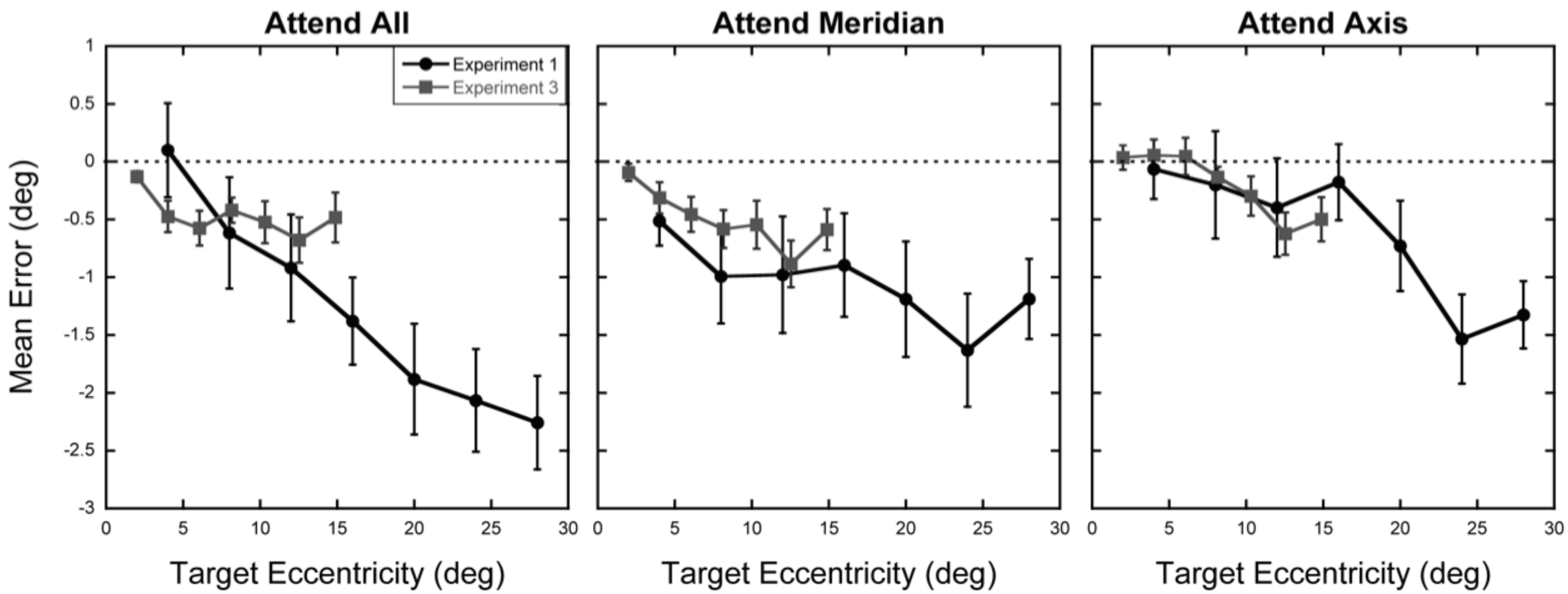

Figure 12. Comparison of Errors Across Experiment 1 and Experiment 3. Mean errors in degrees of visual angle as a function of Experiment and Target Eccentricity in degrees for the three Attention conditions. Errors from Experiment 1 are shown as circles while the errors from Experiment 3 are shown as squares. Error bars represent ±1 S.E. The dotted lines at zero represent expected performance if no distortion exists.

or a bias in perceived location toward a peripherally placed distracter item. Importantly, the degree to which such a distracter influences the perceived location of a target depends on the distance between the target and distracter. While the physical distance of the targets relative to the aperture edge did not vary across experiments, the distance in terms of degrees of visual angle did. It is possible that by reducing the angular distance of the targets to the aperture edge in the last experiment, an attraction effect as found in previous studies was introduced for the more peripheral targets. Such an effect would counteract the foveal bias and lead to the pattern of errors observed in the present study. Moreover, errors for the farthest target tested showed a slight reduction relative to the second farthest target across all attention conditions, which is consistent with a larger attraction effect toward the aperture edge for the most peripheral target locations, as noted in Adam et al. (2008).

As seen in Figure 9, the magnitude errors are nearly identical for the most peripheral target across all axes and attention conditions in the third experiment, despite varying degrees and patterns of errors across the other eccentricities tested. As seen in Figure 12, this pattern was not observed in Experiment 1, with errors in the Attend All condition increasing even for the farthest target. While the exact form of the attentional distribution in the Attend All condition is unknown, this difference could be related to qualitative differences in the spread of attention across one and two dimensions as well as changes in the effect of attention across eccentricity.

As in Experiment 2, a horizontal-vertical anisotropy was not observed in this experiment. This is reflected in the pattern of magnitude errors shown in Figures 2 and 9 and the slope parameter estimates in Figures 4 and 11. Of particular note is the change in scaling across the left axis. In the Attend All and Attend Meridian conditions the smallest errors appear for targets along the left axis. In contrast, errors along the right axis continue to show some of the largest underestimations. Though the initial variations were striking, the lack of a replication of this finding across the second and third experiments suggests that differences in performance along the horizontal and vertical meridian are most likely due to variations in the individual participants who completed the task rather than some underlying bias in localization performance across the two meridians. If such underlying biases do exist, it may also be that a more sensitive measure than verbal magnitude estimates is needed to reliably measure such effects. More importantly, across all three experiments changes in scaling were found across the three attention conditions while differences in scaling across the horizontal and vertical meridian were only found in Experiment 1.

2.5. General Discussion of Experiment 1-3

The three experiments in this study used a new method that blends approaches used to study localization across eccentricity (Mateeff & Gourevich, 1983; Temme, et al., 1985) but added variations that produce differences in the distribution of attention to determine how attention affects the underlying metric of visual space. Importantly, the "objects" in the field were kept constant (in this case the only objects were the surrounding aperture edge and fixation point). We found that the distribution of spatial attention itself modulates the metric of visual space. The results showed significant and replicable distortions of the spatial metric as a function of how attention was allocated over the visual field, consistent with previous reports using different types of attentional manipulations (Adam, et al., 2008; Bocianski, Müsseler, &

Erlhagen, 2010). We also provide support in the third experiment that the size of errors and the degree to which they are modulated by the distribution of attention depends on the retinal location of targets, not just their relative location within a display.

One question that may be raised is to what extent memory played a role in the current findings. It is known that spatial distortions occur when observers are asked to remember the layout of a scene (Intraub, 2002; Intraub, Hoffman, Wetherhold, & Stoehs, 2006; Intraub & Richardson, 1989). Foveal biases have also been demonstrated when observers are asked to report the location of a previously seen target (Sheth & Shimojo, 2001) and distortions in memory are known to increase as the interval between target presentation and response increases (Diedrichsen, et al., 2004; Werner & Diedrichsen, 2002). The study by Sheth and Shimojo (2001) is of particular importance because the general bias to remember locations as being closer to the fovea than they really were matches the observed pattern of responses in the present studies. The participants in the present studies were encouraged to respond as quickly as possible and explicitly told that the purpose of the study was to determine where they perceived target location and not where they remembered them to be. However, making magnitude estimates without a visible scale on which to rely takes a longer time to formulate than other measures such as reaction times and relative comparisons. As a result it is difficult to rule out a memory component. It beyond the scope of this paper to determine whether the foveal biases observed here and in other studies of peripheral localization (Mateeff & Gourevich, 1983) are due to processes of retaining spatial representations in memory. The primary interest of the present study was to examine how changes in the distribution of attention alter localization performance in the periphery. To our knowledge, there is no evidence in the spatial memory literature that the modulations in errors observed in the present experiment varies with how participants' distribute their attention across the display.

2.5.1. Models of Attention and Localization

While the results of the three experiments all suggest that changes in the distribution of sustained attention across the visual field lead to consistent modulations in the magnitude of peripheral mislocalization, questions remain as to how these findings fit with current theories of how attention influences location perception. The following section describes some of the relevant models and their applicability to the current findings.

Many models of attention have postulated that attention is required in order for accurate localization and identification to occur, such as Feature Integration Theory (Treisman & Gelade, 1980). However, it has also been shown that while directing attention to a location can significantly improve the precision of localization (Prinzmetal, 2005; Prinzmetal, et al., 1998; Tsal & Bareket, 1999, 2005), localization is still possible when attention is directed away from the location of a target. This finding led Tsal and colleagues to propose the Attentional Receptive Field Hypothesis (Shalev & Tsal, 2002; Tsal & Bareket, 1999, 2005; Tsal & Shalev, 1996). Under this model, coarse localization is possible when attention is directed away from a target location. However, because position information is pooled over many receptive fields the ability of the visual system to localize positions is limited by the ability to perform computations across multiple, overlapping receptive fields. Using theoretical receptive fields, the Attentional Receptive Field Hypothesis predicts that information about length and position from any one receptor is determined by the size of that receptive field. Precision can be improved, however, by comparing responses across multiple receptive fields and this process is thought to occur, or at least improve, when attention is directed toward the location of the target. While this model can capture findings of increased length of stimuli (Tsal & Shalev, 1996) or increased dispersion in localization responses (Tsal & Bareket, 1999, 2005) when attention is directed away from a target, it is not clear how the model in its current form can account for systematic biases to localize a target toward or away from the fovea and changes in mean perceived location under different attentional conditions.

It is of interest to note that in one study (Tsal & Bareket, 1999) changes in localization errors consistent with the current study were found. In this study participants were required to localize briefly presented targets within large circles that were either located at the center of the screen or offset 9º to the left or right side. Pointing responses were used to indicate the perceived target location. Participants were also cued to the possible circle in which the target could appear. The results showed peripheral biases for the validly cued targets presented in the peripheral circles that were not seen in the invalidly cued condition. The researchers suggest that the introduction of a peripheral bias may have been due to the participants making eye-movements in the direction of the target when it was validly cued. While peripheral biases are not usually found in localization tasks using computer-based displays, other studies using manual responses with different experimental set-ups have found peripheral biases when eye movements were controlled (Bock, 1993; Temme, et al., 1985; Uddin, 2006). Of more relevance to the current study is the direction of the shift in errors. As attention shifted from another circle in the invalidly cued condition to the circle in which the target actually appeared (the validly cued condition), localization errors shifted peripherally. While the current study found consistent foveal biases, the direction in which errors moved from the Attend All condition to the Attend Axis condition was also more peripheral (i.e. a reduction in foveal bias).

Another possible mechanism that may be able to account for the present findings has to do with spatially localized changes in baseline activity of neurons in attended regions of space. Increases in baseline activity when attention is directed to specific regions of space have been found using both single-cell recordings in monkeys (David, Hayden, Mazer, & Gallant, 2008; Luck, Chelazzi, Hillyard, & Desimone, 1997) and functional magnetic resonance imaging in humans (Driver & Frith, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Silver, Ress, & Heeger, 2007). In the present study, no visual cues were used to manipulate spatial attention. Rather, within a given block of trials spatial uncertainty in where the target might appear was altered to affect the distribution of attention. Thus, it seems plausible that the underlying mechanisms responsible for altering perceived location in the present paradigm are not stimulus-locked but rather occur in the absence of visual stimulation. Previous work in fMRI has shown such spatially specific increases in baseline activity prior to target onset (Kastner, et al., 1999; Silver, et al., 2007). Moreover, while the spatial extent over which baseline activity can be modulated is not fully understood, shifts in baseline activity over an entire quadrant of the visual field have been previously measured (Kastner, et al., 1999). This suggests that changes in baseline activity across the regions tested in the present study are plausible.

Recently, a model has been proposed that includes such baseline variations in activity to account for changes in localization performance. This model is an extension of the dynamic neural field model, which was originally developed in order to describe the evolution of spatial coding within the motor (Schöner, Kopecz, & Erlhagen, 1997) and visual systems (Jancke, et al., 1999). The model has since been proposed to account for systematic mislocalization of successively presented targets in the peripheral visual field (Bocianski, Müsseler, & Erlhagen, 2008; Bocianski, et al., 2010). In brief, the model proposes that the first stimulus activates a population of spatially tuned neurons. Across this population the interaction profiles are asymmetrically distributed such that neurons receive the maximum input from other neurons located towards the fovea. This asymmetry leads to a "drift" of population activity, and thus perceived position, over time toward the fovea. Local interactions between populations of neurons representing the first and second stimulus then cause the position coding of the second stimulus to be further skewed toward the fovea. Importantly, the interactions are both local and change from predominantly excitatory to inhibitory over time which means that how the first stimulus influences the perceived position of the second stimulus is both dependent on the distance between the two stimuli and the time between their presentations.

In a follow-up study, Bocianski et al. (2010) show that attention can modulate errors in the same relative localization task. In one condition, participants were informed which side of the display the stimuli would appear (predictable left/right condition). Here, no significant errors in relative localization were found. In contrast, a significant foveal bias was observed when participants were unsure whether a given pair of stimuli would appear to the left or right of fixation on each trial, replicating previous findings (Müsseler, et al., 1999). In a second experiment, the researchers compared the unpredictable (left/right) condition with another in which the stimulus pair could appear to the left or right of fixation and above or below the horizontal meridian. This created four locations that the observers had to attend to, and relative mislocalizations were found to be even greater in this condition. There are obvious similarities between the attentional manipulation used by Bocianski et al. (2010) and the one employed in the present study. While the position of the second stimulus varied slightly compared to the first stimulus (which was always located at 5º, slightly above the horizontal meridian), the general locations of the two stimuli varied from one location in the predictable condition, to two locations in the unpredictable condition, and finally four in the distributed condition. In the current study, much larger ranges of possible target locations were tested within a block of trials. However, across the three attention conditions participants knew that they either had to attend to one, two, or four axes at a time. Similar to the findings of Bocianski et al. (2010), we also found the greatest foveal bias when participants were required to distribute their attention across the largest region of space, and foveal biases were systematically reduced as attention was focused over smaller regions.

To explain this reduction in foveal bias, Bocianski et al. (2010) introduce a tonic surround-suppression input into the model representing a spatially structured change in baseline activity at attended locations. This surround-suppression input both increases activity of neurons responsive to the attended location and suppresses the baseline firing rates of neurons responsive to other locations. One consequence of this change in connections is that errors in the relative position coding of the second stimulus are reduced, consistent with the behavioral findings of Bocianski et al. (2010). However, another consequence is that the introduction of this baseline activity reduces the position drift of the first stimulus (Bocianski, et al., 2010, Figure 7). The introduction of the surround-suppression resting state activity can therefore also accommodate the attentional modulations found in the current study when only one target was presented on each trial. If one assumes that the strength of the baseline activity increases as attention is focused on smaller regions of space, the model outlined above predicts corresponding reductions in foveal biases at attended locations.

2.5.2. Source of the Foveal Bias

While the dynamic neural field model including tonic baseline shifts (Bocianski, et al., 2010) is best able to account for the current findings, there is one aspect of the model that is lacking. This is the source of the foveal bias that was observed across all of the attention conditions and experiments in the present studies. In order to accommodate a foveal bias in the original model, Bocianski et al. (2008) altered the Gaussian weight profiles of the interactions such that they were skewed towards more foveal connections, creating the foveal "drift" of perceived position. While this drift creates the foveal bias observed across many peripheral localization studies, it does not explain why such a drift exists to begin with. In the behavioral literature, several studies have investigated the source of foveal bias. In many tasks of peripheral localization, fixation points are used and it is known that targets can be misperceived toward the locations of landmarks in a display (Hubbard & Ruppel, 2000; Makovski, et al., 2010; Yamada, et al., 2008). While it could be argued that a fixation cross serves as a landmark and foveal biases are the result of memory averaging across the fixation cross and target, research has shown that foveal biases persist when no physical stimulus is present at the point of fixation (Kerzel, 2002; van der Heijden, et al., 1999). It should be noted that maintaining fixation throughout an experiment is not a passive process. Under normal viewing conditions, ones eyes are continuously moving and it has been suggested that attention shifts proceed eye-movements (Hoffman & Subramanian, 1995). Thus, it seems plausible that the source of the original "drift" in the model of Bocianski et al (2008) is due to attention being actively maintained at the point of fixation prior to target onset. This would alter the model somewhat by assuming that tonic baseline shifts are always present and spatially structured, and that variations across tasks determine both the focus of this baseline as well as the spread. For example, when participants know where the target will appear, the focus of attention is moved from fixation prior to target onset. In the present study, participants were required to attend to entire axes in the display. Here, one might assume that the distribution of attention is spread along each tested axis, with the form of attention changing across the three attention conditions. In particular, in the Attend All condition participants needed to distribute their attention across all four axes for optimal performance. If such a distribution leads to focal baseline changes at the point of fixation that dissipated with eccentricity, one should find the strongest foveal bias and drift in position coding. As attention is focused on fewer axes, participants should be able to focus their attention more directly along the axes being tested, thereby reducing attentional focus at the point of fixation. This would serve to essentially flatten the distribution of the baseline function and eliminate the foveal bias. This interpretation is consistent with the results of Tsal and Bareket (Tsal & Bareket, 1999, 2005) who found greater dispersion in estimated locations along the radial line connecting the target to the point of fixation compared to the orthogonal direction. Though this result may appear contradictory at first, if one assumes that the distribution of attention is spread from the point of fixation out toward the cued location, then biases in perceived location due to changes in baseline activity will occur along this line more than in the orthogonal direction. This will result in errors in the perceived distance of the target from fixation and not effect the radial position.

In conclusion, one of the most important functions of vision is that it allows us to act, not only upon objects that may be the focus of attention but also the environments in which we perceive ourselves. Even on the darkest night, attention can be focused in space to help guide us through the environment. The present results demonstrate that the location where we believe items to be can be changed by the very act of attending toward or away from that direction. While objects and other visual cues can change the metric of perceived space, the results presented in these three studies demonstrate that attentional distribution can also modulate location perception, suggesting a dynamic interaction between the form of space, the representation of objects, and attention.

3. The Influence of Involuntary Shifts of Attention on Object Structure

There are many ways in which one can "attend" to an object or region of space. In the previous chapter we examined how changes in the distribution of sustained attention alter perceived location in the visual periphery. Changes in the distribution of attention can be thought of as changing the extent to which attention is spread over a region of space while the focus of attention is maintained at fixation. For example, when taking a hike, one might want to distribute their attention broadly to take in a whole scene or focus his or her attention on a small region of space to examine a flower in detail. However, attention can also move such that the focus of attention is dissociated from the point of fixation (Peterson, Kramer, & Irwin, 2004). Specifically, the rapid onset or offset of objects in an environment can drive the focus of attention involuntarily toward the object's location (Jonides, Long, & Baddeley, 1981; Yantis & Hillstrom, 1994; Yantis & Jonides, 1990). In Chapter 3, we extend our investigation of the effects of attention on the structure of visual space by investigating whether rapid, involuntary shifts in the focus of attention also lead to distortions in visual space.

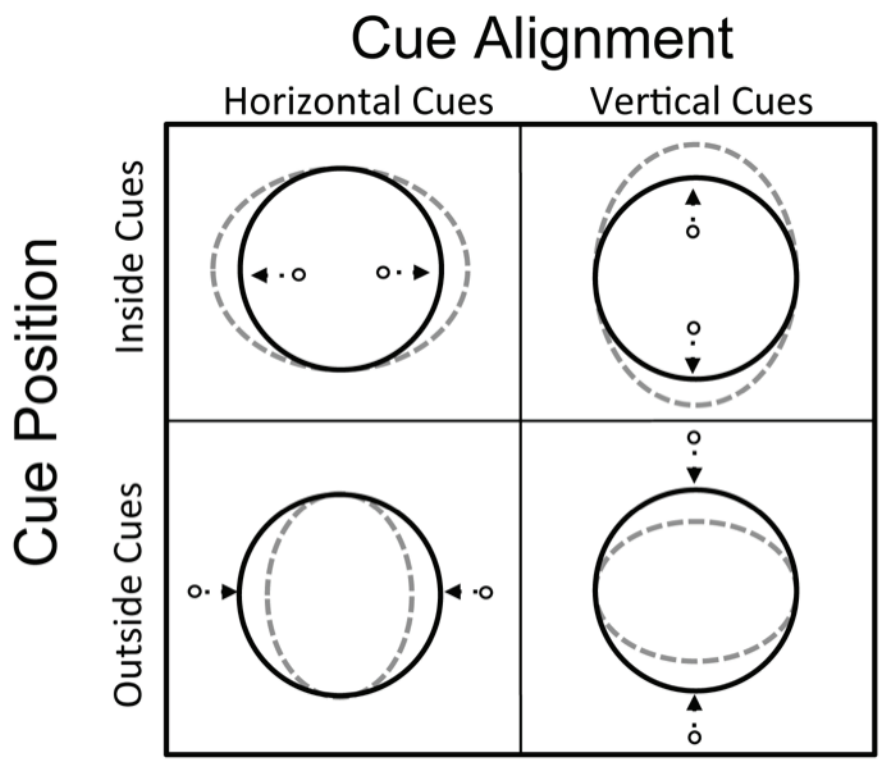

Figure 13. Experimental Predictions. Schematic representation of the predicted distortions if the Attentional Replusion Effect changes perceived shape. The columns represent cue alignment along the horizontal and vertical meridians, while the rows represent the cue positions inside or outside of the oval contour. The small dots represent the cues and the large solid ovals represent the oval presented to participants. The dashed arrows represent the predicted direction of the repulsion away from the cued locations and the dashed oval contours represent the percept. The figure is not drawn to scale.

3.1. Introduction to Rapid Shifts of Attention and Space Perception

Research has shown that changes in the focus or distribution of spatial attention not only alters how quickly observers are able to detect target items in a display (Jonides, 1980; Posner, et al., 1980), but also the perceived location of subsequently presented targets (Adam, et al., 2008; Tsal & Bareket, 1999). For instance, Suzuki and Cavanagh (1997) demonstrated that the perceived offset of two vertically oriented vernier lines (arranged above and below fixation) can be systematically displaced when a pair of circular, non-informative, cues are laterally presented on opposite sides of the two vernier lines prior to their onset. The displacement was also found when a single attentional cue was used. This effect is called the Attentional Repulsion Effect (ARE) because the perceived displacement of the top vernier line relative to the bottom vernier line was found to be in the direction away from the cued locations.

The present study asked a different but complementary question, namely, can involuntary attention alter the perception of an object's shape? To address this question we modified the ARE paradigm by replacing the two vernier lines with a single, large oval contour that varied in height and asked participants to determine whether each oval was wider or taller than a perfect circle. Prior to presenting the oval, two small white dots (cues) were flashed along either the horizontal or vertical meridian, and were located either inside or outside the contour of the subsequently presented oval.

Figure 13 represents the predictions if attention alters the perceived shape of an oval contour and the cues selectively repel the part of the contour closest to the cue locations (i.e. an ARE on *shape perception*). When the cues are along the horizontal meridian and inside the oval this should cause the oval to appear wider than it actually was (dashed line). When the cues are outside the oval along the horizontal meridian the oval should appear taller than it was. Importantly, vertical cues should lead to the opposite perception (i.e. outside cues making the oval look wider while inside cues make the oval look taller).

3.2. Experiment 4: Demonstrating Distortions in Object Shape

In Experiment 4 we assessed whether distortions in perceived shape would be observed that are similar in nature to the distortions in perceived relative location reported in previous studies of the ARE. We modified the paradigm developed by Suzuki and Cavanagh (1997) to test the predictions laid out in Figure 13.

3.2.1. Methods

Participants. Thirteen undergraduates (10 females, mean age: 22.7 ± 4.03 years) participated for course credit. All reported normal or corrected-to-normal vision and no ocular disorders. Glasses, astigmatism, or any indication of ocular disease were criteria for exclusion. One subject was an outlier, showing no sensitivity to physical changes in the height of the ovals (chance performance), and was removed from all analyses. All participants gave informed consent, and the Committee for the Protection of Human Subjects at the University of California, Berkeley, approved the experimental protocol (#2010-04-1159).

Design. A within-subjects design was used for the behavioral paradigm with 40 experimental conditions. There were a total of 15 ovals tested. The ovals had 3 possible

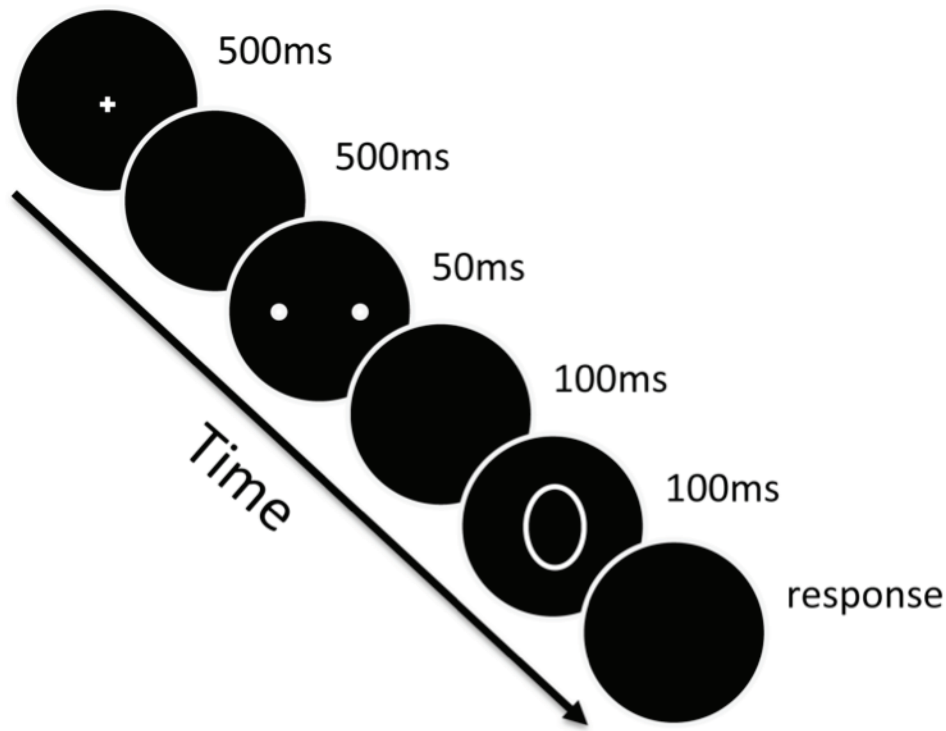

Figure 14. Illustration of a trial in Experiment 4. An exemplary trial that shows the timing for the cue and target presentations. The display was viewed inside a circular aperture (shown as a black circle here). The cue pair and oval are not drawn to scale.

horizontal radii (5º, 11º, and 17º radius). For each horizontal radius there were 5 vertical heights tested. The vertical radii differed from the horizontal radii by 0%, ±5%, or ±10%. There were four cue configurations. The cue pairs were aligned along the horizontal or vertical meridians and were located at 8º or 14º eccentricity. The cues were paired with ovals such that every cue pair was followed by an oval with a horizontal radius that was larger or smaller than the eccentricity of the cues. Thus, the 8º cues could be followed by an oval with a 5º or 11º horizontal radius and the 14º cues were followed by an oval with an 11º or 17º horizontal radius.

Materials and Procedure. Participants sat 25.4 cm from the monitor (ViewSonic G225f, refresh rate = 100Hz). Head position was stabilized with a chin and forehead rest. A large black piece of cardboard with a cut out circular aperture (14.67cm or 30° radius) was centered over the screen to eliminate influences from the lines and angles of the monitor itself. The experiment was run in a dark room. The fixation cross was centered laterally and vertically so that the participant looked straight ahead.

The experiments were controlled with Matlab® software using the Psychophysics Toolbox (Brainard, 1997). Figure 14 shows an example trial sequence. A blue fixation cross (1° in visual angle; 10 cd/m^2) first appeared for 500ms on a black background (0.3 cd/m^2). After a 500ms blank the cues, two white dots (1° diameter; 84 cd/m^2), appeared for 50ms along the horizontal or vertical meridian. The dots were both located at a distance of either 8° or 14° from fixation. After a 100ms blank a blue oval (line thickness: 0.08°; 10 cd/m^2) was presented for 100ms. A Two Alternative Forced Choice task was used. Participants judged whether the oval was wider or taller than a perfect circle by pressing the left or up arrow keys on a keyboard.

Fifteen ovals with three different horizontal radii (5°, 11°, or 17°) were used so that participants could not predict whether the subsequent oval contour would be inside or outside the cued locations. For each radii, five different ovals of varying relative heights were created; the relative heights differed from the widths by 0%, ±5%, or ±10%. Thus, two of the ovals were wider than a perfect circle, two were taller than a perfect circle, and one was a perfect circle. A total of 40 different stimulus combinations were created from the four cues (two cue eccentricities: 8° or 14° and two cue alignments: horizontal or vertical) and fifteen ovals. The ovals were paired with the cues such that the 8° cues could only be followed by one of the ten ovals with a 5° or 11° horizontal radius and the 14° cues could only be followed by one of the ten ovals with an 11° or 17° horizontal radius. Therefore, for any given cue, participants could not predict whether the cues would fall inside or outside the following oval contour. Moreover, as all five oval heights were used, the orientation of cues could not be used to predict whether the following oval would be wider or taller than a perfect circle. The critical ovals were the five with an 11° radius, as these were the only ovals that were paired with all four sets of cues, two sets inside the oval contour (8°) and the other sets outside (14°). All the other ovals were controls to assure no contingency existed between the cues and ovals.

Participants were informed before beginning the experiment that the locations of the cues were not informative of which dimension was longer. All participants completed 10 randomly chosen practice trials before beginning the experiment. Twenty-five repeats of each cue-oval combination were included for a total of 1,000 trials completed over four blocks.

3.2.2. Results and Discussion

For every participant, the percentage of Taller responses was calculated for each condition. These were analyzed in a 2 Cue Alignments (Horizontal/Vertical) x 2 Cue Positions (inside/outside) x 5 Relative Heights (0%, ±5%, and ±10%) Repeated-Measures ANOVA. Greenhouse-Geisser correction was applied when appropriate.

As seen in Figure 15a, participants increasingly responded that the oval was taller as the height of the oval increased, $F(1.84,20.28)=179.41$, $p<0.001$, $\eta^2=0.94$, as would be expected. There was no main effect of Cue Position, $F(1,11)=0.47$, $p=0.51$, $\eta^2=0.04$, or Cue Alignment, $F(1,11)=3.15$, $p=0.10$, $\eta^2=0.23$.

Most importantly, there was a significant Cue Position x Cue Alignment interaction, $F(1,11) = 8.46$, $p = 0.01$, $\eta^2 = 0.44$, and a significant three-way interaction, $F(1.35,14.88)=5.50$, $p=0.03$, $\eta^2 = 0.33$, reflecting the crossover with Cue Position that can be seen in Figure 15a across the two Cue Alignment conditions. The crossover shows the expected change in perceived height of the oval as the cues are moved inside or outside the oval contour. However, the three-way interaction also shows that the effect of cue placement is not apparent when the ovals were the most elongated along either dimension. Instead, the interaction in the means is most obvious when the oval was a true circle (Relative Height = 0%). Repulsion effects in the original study by Suzuki and Cavanagh (1997) were found to be small, on the order of 10' arcmin of visual angle, or 1/6 of a degree. In the present study, each 5% change in the height of the 11° horizontal radius

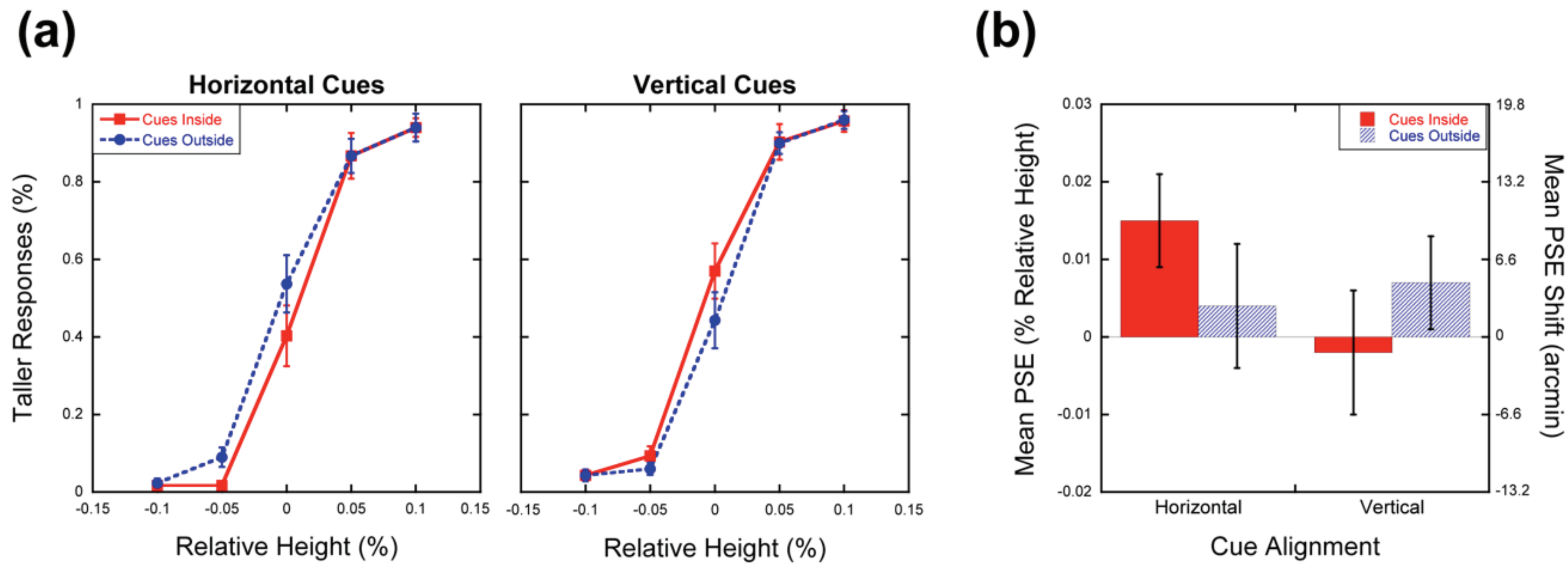

Figure 15. Results from Experiment 4. (a) The mean percentage of Taller Responses for cues presented along the Horizontal and Vertical meridians as a function of the Relative Height of the ovals and Cue Position, for the ovals with a horizontal radius of 11°. Trials in which the cues were presented inside the oval contour are shown as squares and solid lines and trials in which the cues were presented outside the oval contour are shown as circles and dotted lines. (b) Mean estimated points of subjective equality (PSE) as a function of Cue Alignment and Cue Position. The right y-axis shows the PSE in units of arcmin of degrees. Error bars represent ±1 S.E.

ovals corresponds to 0.55°, roughly 3x the average repulsion effect found by Suzuki and Cavanagh (1997). As physical changes in the oval's height are larger than the reported magnitude of the repulsion effect, it is consistent with Suzuki and Cavanagh's findings that the present effects are only seen when the height and width are similar.

To further explore the Cue Position x Cue Alignment interaction, the individual participants' psychometric functions were fit with cumulative Gaussian distribution functions (GraphPad Prism, GraphPad Software, Inc.). This allowed an estimate of the point of subjective equality (PSE), or the relative height of the oval that appeared to be a perfect circle. The data were well fit by cumulative Gaussian distributions (average $R^2 = 0.98$; range = 0.80-1.0). Figure 15b shows the PSE for the two Cue Positions when the cues were aligned along the horizontal and vertical meridians. A Repeated-Measures ANOVA on the estimated PSE shows a significant Cue Alignment x Cue Position interaction, $F(1,11)=5.38$, $p=0.04$, $\eta^2=0.33$. For the horizontally aligned cues, ovals needed to be taller than a perfect circle in order to be seen as a perfect circle. However, a larger shift was observed when the cues were placed inside the oval contour, consistent with the cues inside the circle repelling the contour out and making the oval look wider relative to when the cues were placed outside the oval contour. Consistently, just the opposite effect was found for vertically aligned cues. Here, placing the cues inside the oval contour resulted in a smaller PSE relative to when the cues were placed outside the oval contour suggesting that vertically aligned cues inside the oval contour increased the perceived height of the oval. Thus, the global structure of an object appears to be stretched or squeezed along the dimension parallel to the attentional cues. Experiment 5 further supports this conclusion.

3.3. Experiment 5: The Influence of Cue Timing on Distortions

It is possible that the results of Experiments 4 were due to a complex response bias or some interaction between the contours of the cues and oval that was not due to attentional repulsion. In order to rule these out Experiment 5 presented the ovals either simultaneously with the cue (Simultaneous condition) or before the cues (Post-Cue condition). If the results are due to a response bias, the same crossover found in Experiment 4 should be replicated in both timing conditions. If the results are due to an interaction between the contours of the oval and cues present in the display, then the same crossover should be observed in at least the Simultaneous condition. Conversely, if distortions in perceived shape depend on the cues attracting attention, the effect should require that the cues precede the oval in time, and the results of Experiment 4 should not be replicated here.

3.3.1. Methods

Participants. A new set of twenty-six undergraduates, selected as before, participated in this experiment. There were 16 females and the mean age was 20.73 ±3.94 years. The same exclusion criterion from the previous experiment was applied here.

Materials and Procedure. The stimuli and task was the same as in Experiment 4. Fourteen participants completed the Post-Cue condition. In this condition, each trial started with the fixation cross for 500ms followed by a 500ms blank screen. The oval was then presented for 100ms, followed by a blank screen for 100ms, and then the cues for 50 ms. Twelve participants completed the Simultaneous-Cue condition. On every trial here the fixation cross was shown for

500ms, followed by a blank screen for 500ms, and then both the cues and oval together for 100ms.

3.3.2. Results and Discussion

The percentage of Taller responses was calculated for each participant for each condition. As can be seen in Figure 16a and Figure 17a, for both timing conditions, increasing the physical height of the stimulus led to increases in the percentage of Taller responses (p<0.001 for both). However, in contrast to Experiment 4, the same crossover across the different cue placements was not found. For both timing conditions the three-way interactions were not significant (F<1 for both).

As in Experiment 4, psychometric functions were fit with cumulative Gaussian functions to estimate the PSE. The data were well fit by cumulative Gaussian distributions (average R^2 = 0.98; range: 0.88-1.0). The mean PSE are shown in Figures 16b and 17b. As seen in Figure 16b, for the Post-Cue condition there was no main effect of Cue Position, $F(1,13)=0.33$, $p=0.58$, $\eta^2=0.03$. Cue Alignment influenced perceived shape, with ovals appearing taller when the cues were vertically aligned, $F(1,13)=15.48$, $p=0.002$, $\eta^2=0.54$. More importantly, the interaction between the two factors did not reach significance, $F(1,13)=3.49$, $p=0.09$, $\eta^2=0.21$. While a possible trend was observed, inspection of Figure 16b shows that the effect was in fact in the opposite direction of that seen in Experiment 4. The main effect of Cue Alignment is indicative of a response bias where participants used the alignment of the cues to guide responses for the circle condition. More importantly, the lack of a significant interaction and the fact that the pattern of the means was in the opposite direction, suggesting a possible attraction effect, demonstrates that a response bias cannot explain the results of Experiment 4.

The same analyses were performed on the means in the Simultaneous condition (Figure 17b). There was a main effect of Cue Position, $F(1,11)=5.19$, $p=0.04$, $\eta^2=0.32$, with ovals seen as relatively taller when the cues were placed inside the oval contour. The PSE also showed an elongation of the ovals along the dimension of the cues, $F(1,11)=19.46$, $p=0.001$, $\eta^2=0.64$. More importantly, there was no interaction between the two factors, F<1. These findings demonstrate that contextual interactions between the cue and oval cannot explain the repulsion of the oval contour found in Experiment 4.

Can the lack of a replication in Experiment 5 be explained by the recruitment of different participants? To address this question a 2 Cue Alignment x 2 Cue Position x 3 Timing Condition mixed-design ANOVA was run on the mean PSE estimates with Timing as a between-subjects factor. There was no difference in the overall means across the three Timing conditions (F<1). There was a Timing x Cue Alignment interaction, $F(2,35)=6.85$, $p=0.003$, $\eta^2=0.28$, driven by the large response bias found in the Simultaneous-Cue condition that was not observed in Experiment 4. There was no Timing x Cue Position interaction, $F(2,35)=1.91$, $p=0.16$, $\eta^2=0.10$. Importantly, there was a three-way interaction, $F(2,35)=5.12$, $p=0.01$, $\eta^2=0.23$, showing that the relative changes in responses when the cues were placed inside and outside the oval contour across the two Cue Alignment conditions varied significantly depending on the presentation timing of the ovals and cues. This result demonstrates that differences in response variability on the part of participants cannot explain why the interactions of interest in Experiment 4 were not observed in Experiment 5 as such an increase would eliminate this three-way interaction given the lack of a significant difference in the overall means across the three Timing conditions.

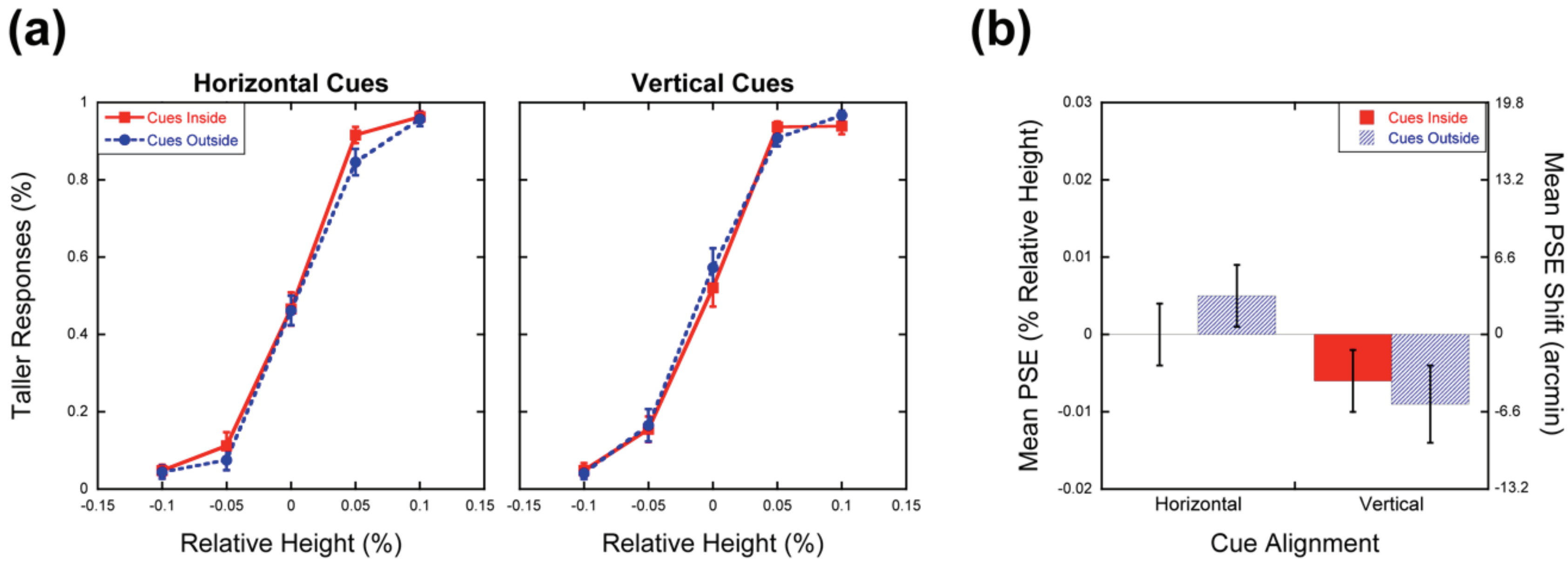

Figure 16. Experiment 5: Post-Cue Condition. (a) The mean percentage of Taller Responses for cues presented along the Horizontal and Vertical meridians as a function of the Relative Height of the ovals and Cue Position, for the ovals with a horizontal radius of 11°. The same formatting from Figure 15 is used here. (b) Mean estimated points of subjective equality (PSE) as a function of Cue Alignment and Cue Position. The right y-axis shows the PSE in units of arcmin of degrees. Error bars represent ±1 S.E.

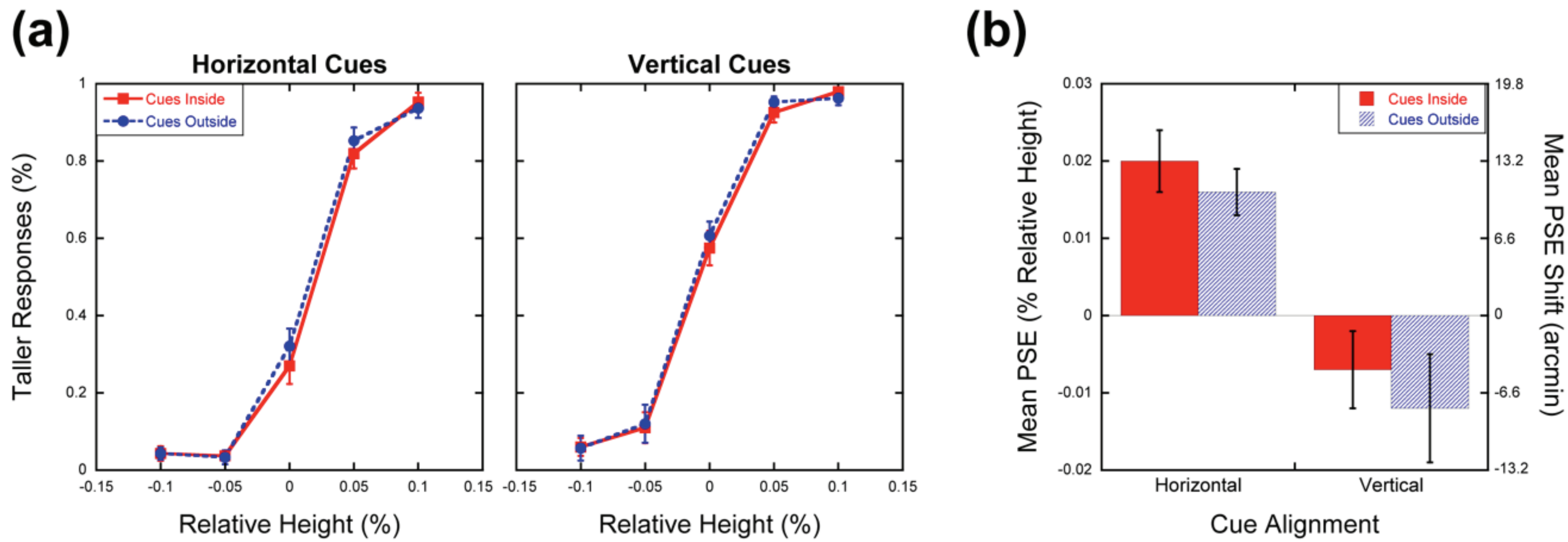

Figure 17. Experiment 5: Simultaneous Condition. (a) The mean percentage of Taller Responses for cues presented along the Horizontal and Vertical meridians as a function of the Relative Height of the ovals and Cue Position, for the ovals with a horizontal radius of 11°. The same formatting from Figure 15 is used here. (b) Mean estimated points of subjective equality (PSE) as a function of Cue Alignment and Cue Position. The right y-axis shows the PSE in units of arcmin of degrees. Error bars represent ±1 S.E.

A final concern is whether the results of Experiment 4 reflect a figural aftereffect rather than a distortion due to shifts of attention. While Experiment 4 showed repulsions of the oval contours from the cued locations, Experiment 5 showed something similar to an assimilation effect with simultaneous presentation: the ovals were elongated in the dimension consistent with the cues. While this can be interpreted as a response bias on the part of participants, research on Delboeuf concentric circles shows contrast effects when an inducing circle is shown prior to the target circle and assimilation effects when it is shown simultaneously (Sagara & Oyama, 1957). However, this effect cannot explain the current results. First, with the simultaneous presentation no interaction was found and an assimilation account still predicts differential effects on the shape of the ovals depending on whether the cues were placed inside or outside the oval contour. Second, research (Cooper & Weintraub, 1970) has shown consistent contrast effects with simultaneous presentation when four non-concentric circles or quarter circle-arcs are used as inducers. These stimuli are more consistent with the dots used in the present study. Yet no interaction across the two cue positions was found with the simultaneous presentations.

Another effect, the shape-contrast effect (Suzuki & Cavanagh, 1998), can be ruled out based on the current results. In the shape-contrast effect a line presented prior to an oval distorts the perceived shape of the oval such that it is seen as elongated in the direction perpendicular to the line. Assuming that the two cue dots could represent the endpoints of a line, at first the results appear similar. However, Suzuki and Cavanagh found that the ovals were always repelled in the perpendicular direction regardless of whether the line was longer or shorter than the diameter of the circle. As these conditions would correspond to the outside and inside cue conditions, the shape-contrast effect cannot explain why the ovals in Experiment 4 appeared elongated along the dimension of the cues when the cues were placed inside the oval contour.

3.4. Experiment 6: Dissociating Figural Aftereffects From Shifts of Attention

As there are different types of figural aftereffects, a final experiment was conducted that puts the influence of adapting cues in conflict with the brief cues previously used. In this experiment, we presented two pairs of cues on each trial at the same eccentricity, one set along each meridian. As the magnitude of aftereffects increase with the duration of the adapting stimulus, we presented one pair of cues for a long duration (1.4sec) and then both pairs for 50ms (see Figure 18a). If the results of Experiment 4 are due to a figural aftereffect, the results should show a repulsion effect away from the locations of the long adapting cues. On the other hand, if the distortion is due to rapid shifts of attention to the brief cues, the same pattern of errors should be observed.

3.4.1. Methods

Participants. Eleven undergraduates and one author (F.C.F), selected as before, participated in this experiment. There were 11 females and the mean age was 21.1 ± 3.73 years. The same exclusion criterion from the previous experiments applied.

Materials and Procedure. The task was the same as Experiment 4 with the following exceptions (Figure 18a). Only the perfect circles with 5°, 11°, and 17° radii were presented. The same cue locations were used. The trial structure was changed such that after presentation of the fixation cross, a pair of adapting cues was presented for 1.4sec. Both the adapting cues and the

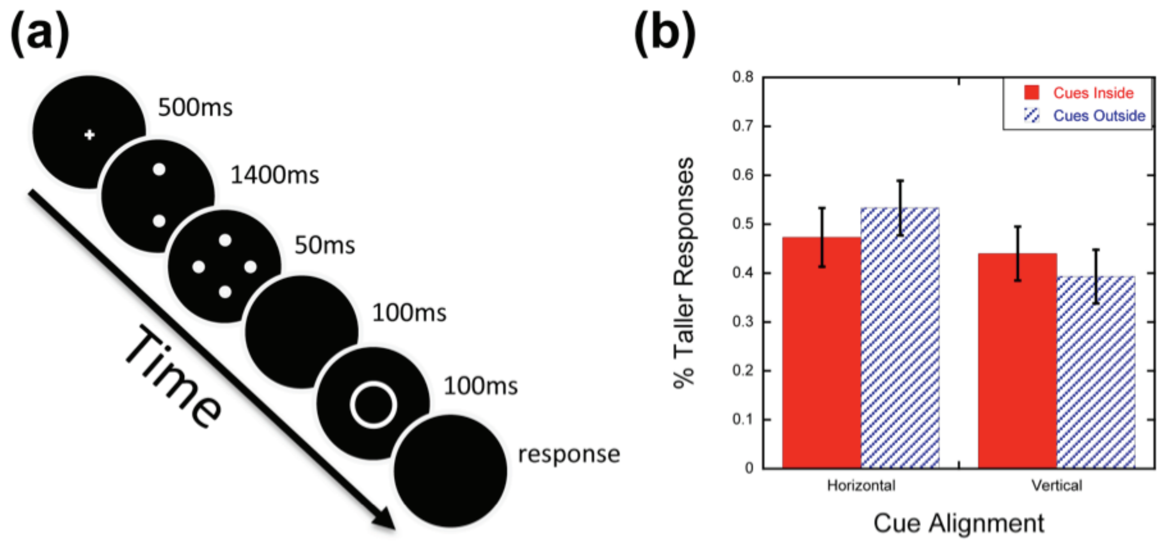

Figure 18. Trial Sequence and Results from Experiment 6. (a) An example trial sequence showing the timing of the long adapting cues (vertical) and the brief cues (horizontal) presented before the target circle. The positions of the cues relative to the circle contour (inside vs. outside) were the same on every trial. Cues were always presented on the opposite meridians. (b) The mean percentage of Taller Responses for the 11° radius circle contours as a function of Cue Alignment and Cue Position. Cue Alignment is defined according to the position of the brief (50ms) cues. Error bars represent ±1 S.E.

corresponding pair of cues along the opposite meridian were then presented for 50ms. After a 100ms blank, the target oval was presented for 100ms. Both the horizontally and vertically aligned cues were presented at the 8° or 14° cue locations so cue positions (inside/outside) were the same. The circles were paired with the cues as before, such that the 8° cues were followed by the 5° or 11° circles and the 14° cues were followed by the 11° or 17° circles. This created eight conditions. Each condition was repeated 25 times.

3.4.2. Results and Discussion

As before, results are considered for the circle with an 11º radius. Figure 18b shows the mean percentage of Taller responses when the *brief* cues were aligned along the horizontal and vertical meridians. As seen in Figure 18b, the introduction of long adapting cues along the opposite meridian did not eliminate the repulsion effect observed in Experiment 4. Results from a 2(Cue Alignment) x 2(Cue Position) Repeated-Measures ANOVA show a significant Cue Alignment x Cue Position interaction in the same direction found in Experiment 4, $F(1,11)=4.82$, $p=0.05$, $\eta^2=0.31$. There was no main effect of Cue Position or Cue Alignment ($ps \geq 0.31$). Had the repulsion of the oval contours in Experiment 4 been due to rapid adaptation to the cues in the absence of any attention effect, the interaction should have been eliminated, if not reversed, in this experiment. The fact that the responses show a repulsion away from the locations of the brief cues, and thus toward the long adapting cues, supports the hypothesis that the capture of attention by brief cues can distort the perceived shape of subsequently presented targets.

As seen in Figure 18b, the repulsion of the contours away from the brief cues was attenuated relative to Experiment 4. This finding suggests that the long adapting cues did influence the perception of the circles by reducing the repulsion from the brief cues. While it is beyond the scope of the current paper to untangle the individual contributions of the long and brief cues, it should be noted that adaptation and attention effects are not mutually exclusive phenomenon. Attentional modulations of figural aftereffects have been documented (Yeh, Chen, De Valois, & De Valois, 1996). However, the present results suggest that rapid shifts of attention dominate perception in the present paradigm.

3.5. General Discussion of Experiments 4-6

The present findings demonstrate that it is not just the location of objects that can be distorted by rapid changes in spatial attention, but also the shape of objects themselves. In Experiment 4 we found that the placement of non-informative cues followed by an oval contour alters the oval's perceived shape. Experiment 5 demonstrates that this effect depends on temporal asynchrony between the cues and oval. In order for part of the oval contour to be repelled away from the cued location, the cues must precede the ovals. The last experiment demonstrates that this effect cannot be solely explained by adaptation to the cued location. Collectively, these findings support an account based on changes in attentional orienting induced by the brief cues and their relative position to the target.

How could such involuntary cues lead to a repulsion of the oval contours? Suzuki and Cavanagh (1997) proposed that the orienting of attention toward the cue onsets leads to changes in spatial coding by receptive fields (RF) around the cued locations. Surround suppression, RF recruitment, or RF shrinking were suggested as possible mechanisms that could lead to shifts in the coded location of the vernier lines away from the cues. These are all viable possibilities as changes in neuronal spatial response profiles have been documented following manipulations of focal attention (Connor, Preddie, Gallant, & Van Essen, 1997; Moran & Desimone, 1985).

As noted by Pratt and Turke-Browne (2003), these mechanism would most likely be restricted to changes in neural processing in early visual cortex, where retinotopy is most evident. Changes in the initial position coding within a retinotopic map can be thought of as altering the structure of the underlying space in which objects exist, as the coding of position across a space provides the information that is used to determine both size and scale (i.e. it defines the metric of a space). Localized errors in position coding will therefore cause distortions in a spatial metric. As a result, such errors would be expected to not only alter the perceived relative locations of multiple objects presented simultaneously, but also the overall structure of a single two-dimensional object in neighboring regions of that space.

While the physiological mechanisms underlying the attentional repulsion effect are still open to debate, the present results demonstrate that the effect of rapid changes in spatial attention are not limited to errors in perceived location. Changes in the distribution of spatial attention can also impact the perceived shape of objects.

4. The Role of Visual Boundaries on Spatial Localization

In the previous two chapters we investigated how changes in attention, due to either changes in the distribution of sustained attention or involuntary shifts in the focus of attention, alter visual space. However, attention is just one of many factors that influence how we perceive the world. In the next two chapters we investigate the role that visual boundaries play in space perception. As noted by Indow (2004), visual space is closed, meaning that in all landscapes and environments, there exist boundaries that limit how much or how far we can see. These can include boundaries produced by physical objects or limitations imposed by the resolving power of the visual system. For example, when viewing a flat plane, the horizon represents the farthest distance that can be resolved. While conceptually we can understand the concept of an open or infinite space, limits in visual-processing capability mean that we cannot perceive anything as being infinite. Another type of visual boundary is imposed by the quantity of information that can be processed within a single glance. When an observer's eyes are fixed, the far edges of the visual field create a boundary that defines the region of space that can be perceived at any given point in time. This region is often referred to as the field of view or visual field of an observer. The research in Chapter 4 focuses on the question of the role that visual field boundaries play in determining where we perceive objects across the visual field.

4.1. Introduction to Spatial Localization in the Peripheral Visual Field

Without the ability to localize objects in the environment, it would be nearly impossible to perform important functions in everyday life, including obstacle avoidance, wayfinding, or the development of spatial representations to guide behavior. While a significant amount of work has been conducted on localization in depth perception (Cutting & Vishton, 1995; Fortenbaugh, Hicks, Hao, & Turano, 2007; Gibson, 1950; He, et al., 2004; Luneburg, 1950; Ooi, Wu, & He, 2001, 2006; Philbeck, Loomis, & Beall, 1997; Sinai, Ooi, & He, 1998) and localization of moving targets (Hubbard, 2005; Kerzel & Gegenfurtner, 2004; Thornton, 2002), far less is known about the factors that influence how individuals localize stationary objects across the visual field. Visual perception begins with 2D representations of space, and the 3D world in which we live arises only after a significant amount of processing (Palmer, 1999). It is therefore of great importance to understand the principles that guide location perception as a function of eccentricity. Moreover, visual field deficits, such as those occurring from retinal degeneration and cortical damage following brain trauma, affect entire regions of the visual field, not just locations at specific depths. A better understanding of intrinsic biases in the perception of locations across the visual field and the factors that influence these biases in normal vision will therefore elucidate how visual perception changes when parts, but not all, of the visual field are lost (e.g. Temme, et al., 1985; Turano, 1991; Wittich, Faubert, Watanabe, Kapusta, & Overbury, 2011).

4.1.1. Foveal and Peripheral Biases in Peripheral Localization

One of the initial studies in this area (Mateeff & Gourevich, 1983) found that participants display a foveal bias when estimating locations of peripheral stationary targets, with perceived locations being increasingly displaced towards the fovea as the true target eccentricity increases. Since then, numerous studies have replicated the finding of a foveal bias (Adam, et al., 2008;

Hubbard & Ruppel, 2000; Kerzel, 2002; Müsseler & Van der Heijden, 2004; Müsseler, et al., 1999; Rose & Halpern, 1992; van der Heijden, et al., 1999), including the findings from Chapter 2. Notably, the studies reporting a foveal localization bias used either closed-loop pointing responses, such as moving a mouse cursor to the perceived target location (Adam, et al., 2008; Hubbard & Ruppel, 2000), or perceptual responses, as classified by Uddin (2006): verbal report of perceived target location, such as that used in Experiments 1-3, or key-presses indicating the perceived relative positions of targets (Kerzel, 2002). However, other studies (Bock, 1993; Bruno & Morrone, 2007; Enright, 1995) employing open-loop pointing movements toward perceived locations of stationary targets (where visual feedback regarding the position of the arm is not available) have found evidence for a peripheral bias, with targets being mislocalized away from the fovea.

One explanation that has been proposed to account for the discrepancy between studies reporting a foveal bias and those reporting a peripheral bias is the manner in which participants respond (Bruno & Morrone, 2007; Uddin, 2006). In particular, it has been suggested that open-loop motor responses (e.g., pointing without visual feedback) are more likely to show a peripheral bias, while both closed-loop motor responses (such as moving a mouse cursor on a computer monitor) and perceptual responses (such as verbal reports) are more likely to result in foveal biases. This account suggests that peripheral biases may result from errors in the motor system or in the transformation of spatial information from a retinotopic reference frame to an egocentric arm- or hand-based motor reference frame.

Of special interest to the current study are the results of Temme et al. (1985), in which a peripheral bias was found, but the response mode does not fit well within the open-loop motor explanation. In this study, a Goldmann perimeter[2] was used to present a target light at 10° intervals between the central visual field and the edge of the visual field, along the cardinal and oblique meridia. Participants reported perceived target location by drawing a hash mark along a line printed on a sheet of paper, where the center of the line corresponded to the point of fixation and the edges corresponded to the perceived visual field edges along the meridian that was being tested. In this study, participants overestimated target eccentricity at all locations, and errors were largest in the near periphery and decreased for target locations closer to the edges of the visual field.

Although the response mode used in the Temme et al. (1985) study was motor-based, it was not an open-loop pointing task. Participants first needed to assess the perceived location of the target on a scale bounded by the point of fixation on one end and the perceived edge of their visual field on the other. This scale was then transformed to match the line on the response sheets. The fact that peripheral biases were found in this study suggests that such biases cannot be attributed solely to errors in the motor system.

4.1.2. Resolving Discrepancies: The Influence of Visual Boundaries.

The present study investigates an alternative explanation for foveal and peripheral biases in the localization of stationary targets in the visual periphery. In previous studies reporting a peripheral bias, strong external visual borders (such as the edges of a computer monitor) were

[2] A Goldmann perimeter (Figure 19) is a self-illuminated half-dome with a uniform white background and is used for kinetic perimetry.

not present (Bock, 1993; Enright, 1995; Temme, et al., 1985). In contrast, the majority of studies that found a foveal bias either presented the stimuli within a space defined by the edges of a computer monitor (Adam, et al., 2008; Bocianski, et al., 2008; Kerzel, 2002; Tsal & Bareket, 2005; Uddin, et al., 2005a) or obtained distance judgments relative to a visible reference line (Mateeff & Gourevich, 1983). It has previously been suggested that when target locations can be encoded in either an extrinsic or intrinsic reference frame, extrinsic reference frames defined by external visual cues take precedence (Lemay & Stelmach, 2005; Sheth & Shimojo, 2004). In order to explain peripheral and foveal biases, it is therefore important to consider not only the type of reference frame used but also the metrics (i.e., distance functions) within these reference frames that define coordinate systems for localizing stimuli.

Thus, another way to interpret the results of Temme et al. (1985) is that the borders of the visual field provide a natural boundary with which to define a metric of visual space within an egocentric reference frame. This would be similar to the use of external visual boundaries to define relative positions in extrinsic (allocentric) reference frames. However, for the same target locations, there may be different metrics associated with intrinsic versus external visual field boundaries. In three experiments, we tested the hypothesis that scaling location judgments relative to one's perceived visual field extent leads to an expansion in perceived eccentricity for stationary targets in perifoveal and peripheral visual field locations, while the introduction of external visual boundaries modifies the scaling and causes a switch from peripheral to foveal bias. Moreover, we show that the type of border used to make judgments modulates the scaling of space across eccentricity across multiple response types.

4.2. Experiment 7: Border Type Alters Localization Bias and Spatial Scaling

For this experiment we sought to first replicate the findings of Temme et al. (1985), as the methodology of this study differs significantly from that typically used in spatial localization studies. An additional motivation for Experiment 7 was to determine whether Temme et al.'s (1985) results would be replicated using the same design, given that no other studies in the peripheral localization literature have used a similar paper-and-pencil method. We also sought to extend the findings of Temme et al. (1985) by quantifying the scaling of locations along each axis in order to test for systematic differences in the metric across axes, depending on the natural visual boundaries of the face.

4.2.1. Methods

Participants. Six participants (four female, mean age: 21.7 ± 2.6 years) participated in this experiment. All participants had 20/20 visual acuity, either without any optical correction or with optical correction by contact lenses. Participants were excluded if they wore eyeglasses, as these can artificially restrict the visual field along the horizontal axis (Steel, Mackie, & Walsh, 1996). Eye disease of any kind was also an exclusion criterion. All participants gave informed consent, and the Committee for the Protection of Human Subjects at the University of California, Berkeley, approved the experimental protocol (#2010-04-1159).

Materials and Procedure. Following the procedure of Temme et al. (1985), a Haag-Streit Goldmann projection perimeter (Figure 19) was used to obtain an initial measurement of the full monocular visual field extent for each participant using standard clinical procedures. This

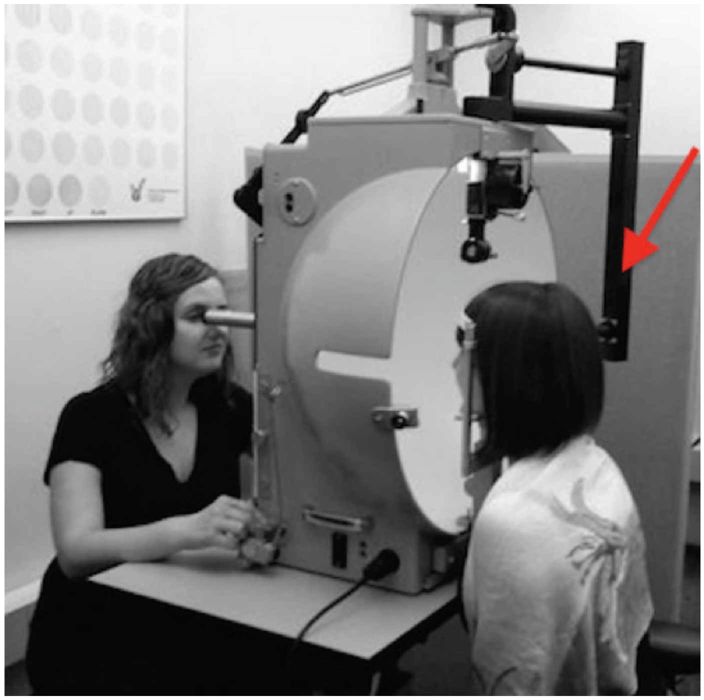

Figure 19. Photograph of the Goldmann perimeter. The participant is seated on the right, facing into the dome, and the experimenter is seated on the left. The experimenter controls the position of the target light by moving the projector (indicated by red arrow) via a bar with their left hand. This bar has a marker on the experimenter's side that indicates the target light's location on a chart in polar coordinates. The target light is presented by pressing a lever with the right hand. Fixation is monitored through a telescope.

was performed using the standard III4e test target (0.44° test spot at a viewing distance of 30 cm; 318 cd/m^2 on a background luminance of 10 cd/m^2). As in Temme et al. (1985), only the right eye was tested, while the left eye was occluded. Participants maintained fixation on a dot located in the opening of the telescope at the center of the half dome while the experimenter projected the target light in the far periphery and then slowly moved it toward the fovea. Participants pressed a button that elicited a tone as soon as they detected the light in the periphery. Upon hearing the tone, the experimenter, situated on the other side of the perimeter, marked the location of the target dot on a chart. After determining the participant's visual field extent, the experimenter briefly flashed the target at the boundary location along each of the four axes to remind participants of the locations of the edges of their visual field. Given that naïve observers participated in the experiments in this paper, this procedure assured that all participants were familiar with the concept of visual field extent and were aware of the boundaries of their monocular visual field.

The Goldmann perimeter was then used to present targets at various locations. The III4e target was presented at 10° intervals, from 10º eccentricity to the edge of the participant's visual field, along the four cardinal axes. Different pre-generated random sequences were used for each participant to control target presentation along the chosen meridian, with each location being tested five times. As target presentation times are not automated in Goldmann perimeters, the experimenter manually controlled target locations and presentation times (see Figure 19). The same experimenter conducted all testing. Prior to testing participants, 200 measurements of presentation time were recorded, and the average presentation time was 176.8 ms (SD = 25.5 ms). Throughout testing, participants maintained fixation at the center of the perimeter, where a small telescope was located that allowed the experimenter, seated on the other side of the dome, to view the participant's eye and to ensure that fixation was maintained. Prior to each trial the experimenter adjusted the projector arm to the correct position to present the target for that trial. Then the experimenter verbally indicated to the participant that the next trial was about to begin, and once the participant established fixation, the target was then briefly presented. Eye position was continually monitored throughout target presentation by the experimenter, and any trial in which fixation was not maintained was repeated.

Participants indicated their response on a sheet of paper (20.3 x 7.6 cm) that was placed on a table on the side corresponding to the participant's preferred hand. A black line 180 mm in length was centered on this paper, with a 5 mm hash mark bisecting the line. Following target presentation, participants indicated perceived target location by drawing a line on the response sheet. They were told that the central hash mark on the response sheet corresponded to the fixation point in the perimeter and that the ends of the line corresponded to the perceived edges of their visual field along the meridian being tested. When generating their response, participants were instructed to sit back from the perimeter chin rest and to turn towards the side table to mark the response sheet. After each response, participants were realigned in the perimeter before continuing to the next trial.

Testing was conducted in two one-hour sessions on different days, with either the horizontal or vertical meridian being tested on a given day. Testing of the horizontal and vertical meridian was separated in order to follow the methodology of Temme et al. (1985) as well as for testing convenience. In each session, the orientation of the response sheets was adjusted to align with the meridian being tested. For horizontal meridian testing, sheets were oriented such that the response line was also horizontally oriented, and the response line was vertically oriented when the vertical meridian was tested. Testing order was counterbalanced across participants.

4.2.2. Results

Localization Errors. The mean measured monocular visual extents of the participants' right eyes were: temporal axis = 89º ± 3º, nasal axis = 57º ± 3º, inferior axis = 70º ± 3º, and superior axis = 48º ± 6º. We performed the same data analyses as Temme et al. (1985). First, the distance of the response line from the central hash mark was measured in millimeters. This value was converted to percentage of the line length, representing the estimated percentage of visual field extent. True target position was expressed as percentage of visual field extent by dividing the target eccentricity by the measured visual field extent for the axis being tested, as visual field extents varied across participants. Figure 20 shows the average errors in units of percentage of visual field extent as a function of target eccentricity in degrees for the vertical and horizontal meridians. Errors were defined as the estimated percentage of visual field extent minus the true percentage of visual field extent. Thus, positive values indicate overestimation, or peripheral bias, while negative values indicate underestimation, or foveal bias.

A 4 (Axis, upper and lower vertical meridians, nasal and temporal horizontal meridians) x 5 (Eccentricity) repeated measures ANOVA was used to analyze the error scores for the five most central eccentricities for each of the four axes. These eccentricities were chosen because they were represented on all axes. There was no main effect of Axis ($F(3,6) = 1.25$, $p = 0.37$) or

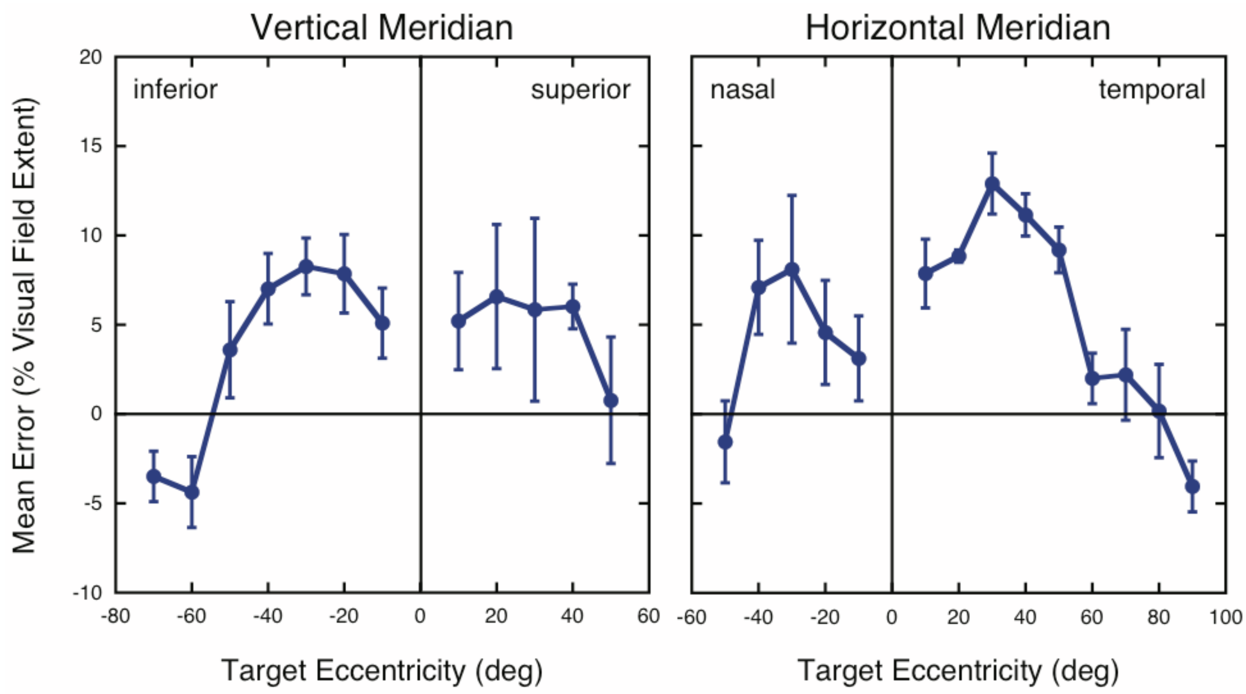

Figure 20. Experiment 7 Localization Errors. Mean errors in percent of visual field extent for the vertical and horizontal meridians as a function of target eccentricity. Error bars represent S.E.M. Solid horizontal lines at zero represent expected performance if no distortion exists.

Axis x Eccentricity interaction ($F(12,24) = 0.65$, $p = 0.78$). However, the main effect of Eccentricity was significant ($F(4,8) = 6.66$, $p = 0.012$). Trend analysis of the Eccentricity factor indicated a significant quadratic trend ($F(1,2) = 33.77$, $p = 0.028$), and the linear and cubic trends were not significant ($p > 0.23$ for both). Figure 20 shows that the quadratic trend is characterized by an inverted U-shaped function, with errors showing maximal peripheral bias at approximately 20°-30° eccentricity.

Spatial Uncertainty In Perceived Location. As visual acuity and contrast sensitivity are known to decrease substantially in the periphery (Low, 1951; Randall, Brown, & Sloan, 1966; To, Regan, Wood, & Mollon, 2011), it is possible that target localization errors may reflect increased spatial uncertainty in the far periphery. We estimated spatial uncertainty by calculating standard deviations of the five repeats at each target location. Figure 21 shows the mean standard deviations of the errors as a function of target eccentricity along the four axes tested. As with the magnitude errors, a 4 (Axis) x 5 (Eccentricity) repeated measures ANOVA was conducted on the standard deviations of the errors for the five most foveal eccentricities tested. No significant main effects or interaction terms were found ($F < 1$ for all).

Magnitude Scaling. As visual field extents vary across axes and across individuals, we normalized both target eccentricity and participants' responses to assess the scaling of localization responses independent of the absolute size of the visual field. Following Temme et al. (1985), the farthest point tested along each axis for each participant was considered to be 100% target eccentricity, and all other visual field locations were normalized relative to this

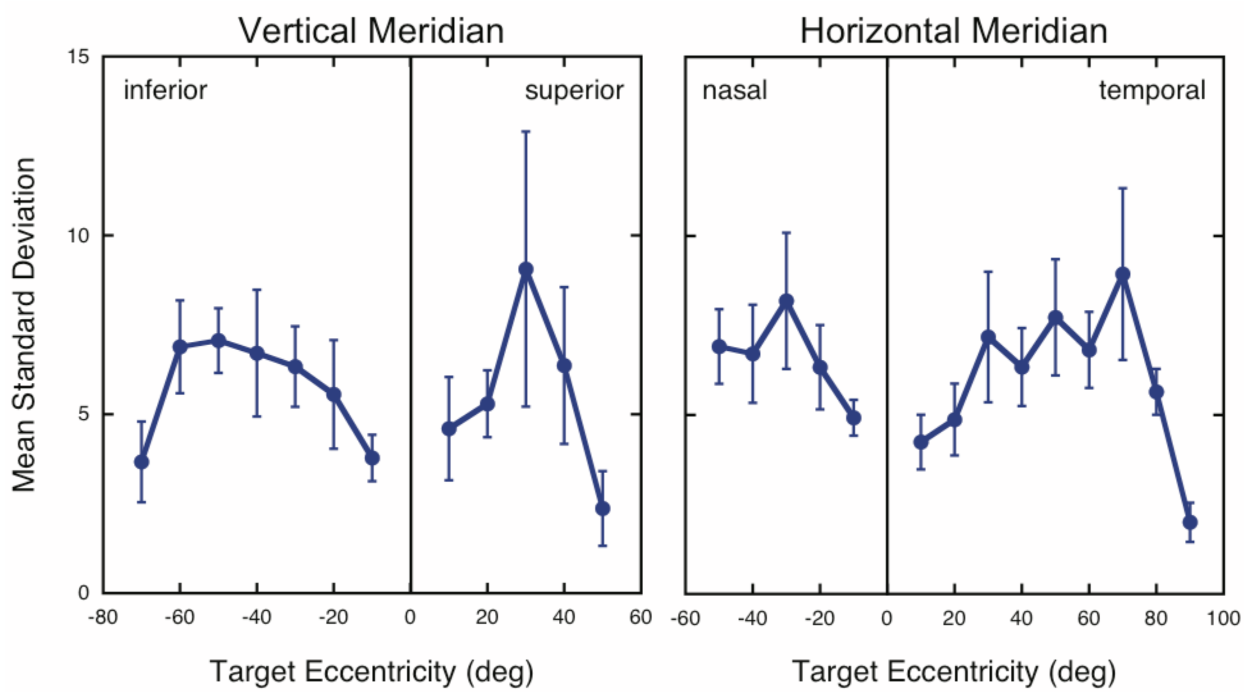

Figure 21. Experiment 7 Spatial Uncertainty. Mean standard deviations of the errors in units of percent of visual field extent for vertical and horizontal meridians as a function of target eccentricity. Error bars represent S.E.M.

eccentricity. We also normalized responses by computing the average response to the most peripheral target tested for each axis and each participant and defining this average response as 100% maximum. Average responses to all other target eccentricities were then scaled relative to this maximum response for each participant and axis. This normalization of both the maximum eccentricity tested and the maximum response was used to examine the linearity of scaling of responses.

Figure 22 shows the means of the percentage of maximum response as a function of the percentage of maximum eccentricity for the vertical and horizontal meridians, respectively, for each participant. If participants accurately scaled target locations relative to a fixed maximal visual field size, then all the points would fall on the black line that indicates a linear relationship between perceived and actual target eccentricity. As is evident in Figure 22, the data points from the six observers are primarily above the line, indicating an overestimation of perceived eccentricity beyond that due to a factor that is constant across the visual field, consistent with a nonlinear peripheral bias for targets presented in the peripheral visual field.

While the normalization procedure shown in Figure 22 provides evidence of nonlinear scaling that is consistent with the type of errors reported by Temme et al. (see Figure 8, Temme, et al., 1985), this approach cannot quantify the underlying metric. To do this, we used a hierarchical modeling scheme to fit a two-parameter power function relating the non-normalized magnitude estimate to the target eccentricity for each trial (with target eccentricity expressed in units of percent of participant's visual field extent along the axis tested). A predefined origin (the

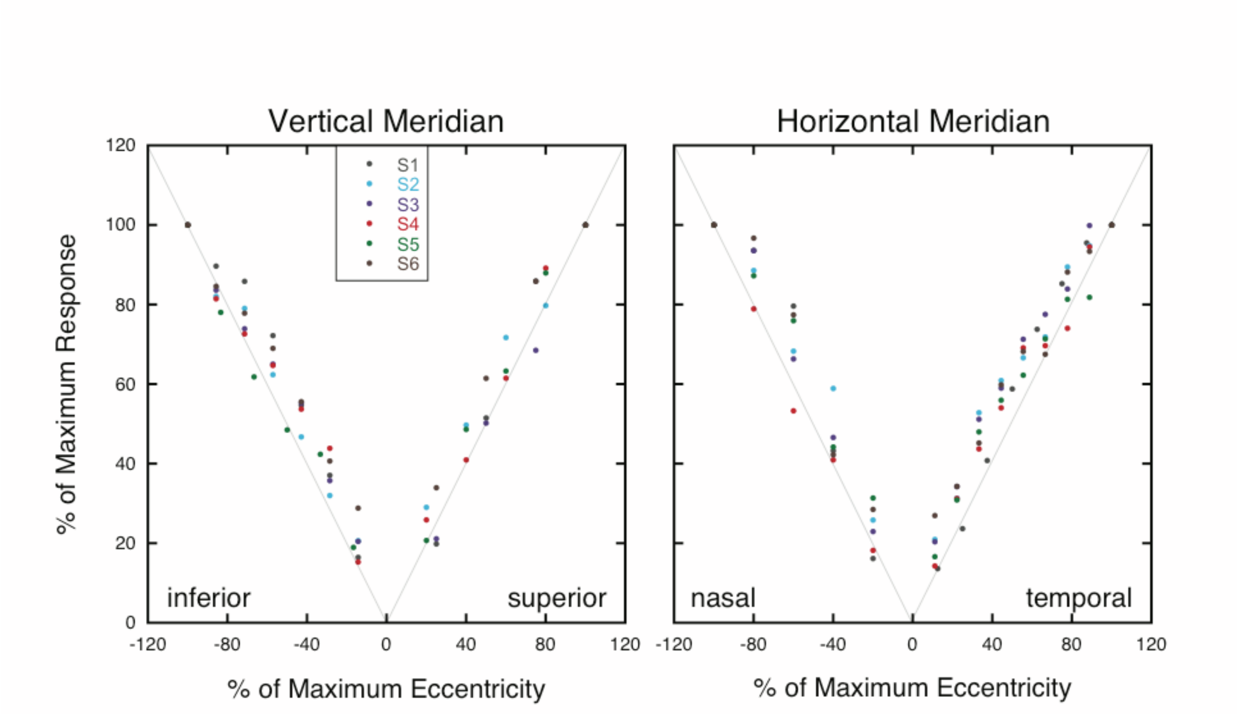

Figure 22. Experiment 7 Normalized Magnitude Estimates. y-axis: mean magnitude estimates for each participant, normalized by the mean maximum magnitude estimate reported by that participant for each of the four cardinal axes. x-axis: percent of the maximum target eccentricity tested along each axis. Solid lines show expected performance if scaling of responses along each axis was linear and unbiased.

fixation dot located inside the telescope at the center of the dome) was present on every trial, eliminating the need for a constant parameter in the model. For every participant, two power functions (Equation 2) were fit to the raw magnitude estimates for all eccentricities tested, separately for each of the four axes.

$$J = \lambda D^{\alpha} \tag{2}$$

In this equation, J = estimated target magnitude; D = actual target magnitude; λ = slope parameter that represents a global scaling factor that compresses or expands all values by a constant amount proportional to the actual target magnitude; α = exponent parameter that quantifies the linearity of the function. An α value of 1 indicates a linear relationship between magnitude estimate and target location, while deviation from a value of 1 indicates that estimates do not scale linearly across eccentricity. For every participant and axis tested (6 participants and 4 axes = 24 combinations), two models were fit, one in which both the λ and α parameters were free to vary and one in which the α parameter was fixed at a value of 1 (GraphPad Prism, San Diego, CA). The increase in the amount of variance explained by the two-parameter compared to the null one-parameter model was quantified with an F-ratio, taking into account differences in degrees of freedom in the two models (Motulsky & Christopoulos, 2004). The two-parameter

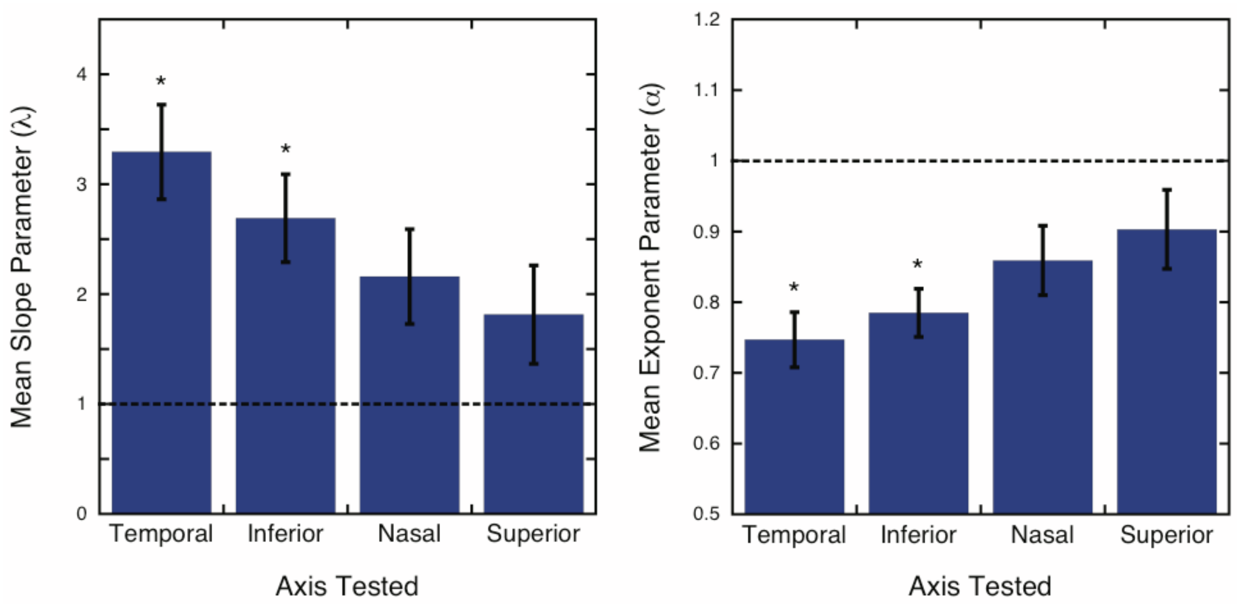

Figure 23. Experiment 7 Power Function Parameters. Mean estimated slope and exponent parameters as a function of axis tested, obtained from fitting individual participant magnitude estimates with the two-parameter function $J=\lambda D^{\alpha}$. Error bars represent S.E.M. Dotted lines at one represent expected performance if perceived and actual eccentricities were identical across tested locations. Asterisks indicate mean value is significantly different from 1, following correction for multiple comparisons.

model was determined to provide a significantly better fit than the null one-parameter model for a given participant/axis combination when the F-ratio had a corresponding $p \leq 0.05$. For the one-parameter model, the average percent variance accounted for was 88% (range: 80 to 95 across participant/axis combinations), while the two-parameter model accounted for an average percent variance of 92% (range: 82 to 96 across participant/axis combinations). Across the four axes for each of the six participants, the two-parameter model provided a significantly better fit than the one-parameter model for 15 out of 24 (63%) participant/axis combinations. Moreover, 5 out of 6 (83%) participants showed significantly better fits for the two-parameter model along the temporal and inferior axes. Given these findings, estimates from the two-parameter model were used in further analyses.

Figure 23 shows the mean slope and exponent parameters for each of the four cardinal axes. If estimated and actual target eccentricity were identical, both of these parameters would have a value of 1. Two one-way repeated measures ANOVAs were conducted on the parameter estimates. There was a trend in the main effect of Axis for the slope parameter ($F(3,15) = 3.10$, $p = 0.06$) and a significant main effect of Axis for the exponent parameter ($F(3,15) = 3.24$, $p = 0.05$). One-sample t-tests were used to determine whether the slope and exponent parameters for the four axes differed significantly from a hypothetical mean of 1 (Sidak-Bonferonni correction for multiple comparisons, $\alpha_{S\text{-}B} = 0.013$). For both the slope and exponent estimates, only the inferior and temporal axes were significantly different than 1, with mean slopes greater than 1 and mean exponents less than 1 (mean slope: temporal = 3.29, $p = 0.003$; inferior = 2.69, $p =$

0.008; nasal = 2.16, p = 0.043; superior = 1.81, p = 0.129) (mean exponent: temporal = 0.75, p = 0.001; inferior = 0.78, p = 0.001; nasal = 0.86, p = 0.034; superior = 0.90, p = 0.144). These results demonstrate that the degree of peripheral bias was least prominent along the superior and nasal axes and largest along the temporal and inferior axes, both of which show significant deviations from a linear scaling.

4.2.3. Discussion

Replicating Temme et al. (1985), we found an overall peripheral bias for both directions of horizontal as well as vertical dimensions. However, the magnitude of the errors was not constant across eccentricity. Trend analyses showed a significant inverted-U shaped function, with errors peaking at 20°-30° eccentricity. Moreover, there were differences in scaling across the four axes, as evident by the main effect of axis for the exponent parameters and differences in linearity across the axes, as demonstrated by the one-sample t-tests. Results from these analyses show that the degree of peripheral bias was most prominent along the temporal axis, followed by the inferior axis, then nasal and superior axes.

These findings extend those of Temme et al. (1985) in that they more fully characterize the type of scaling used in estimating target location. This was accomplished by fitting power functions to the mean estimated eccentricities for each participant along the four cardinal axes. Unlike the linear regression analyses employed by Temme et al. (1985), the power functions used to fit the data here had two free parameters: a slope parameter, reflecting a global scaling factor, and an exponent parameter, quantifying the linearity of the scaling. Power functions with an exponent value that was not fixed at 1 accounted for the scaling across eccentricity better than linear fits, indicating that in general, participants did not use a linear metric in scaling responses across the visual field.

Importantly, the results further show that the type of scaling varied across the axis tested. Neither the slope nor the exponent parameters were significantly different from 1 along the superior and nasal axes, suggesting that the degree of peripheral bias is relatively stable across eccentricity for these two axes and indicating a linear scaling metric for these axes. For the inferior and temporal axes, a nonlinear metric was observed, with slope parameters significantly greater than 1 and exponent parameters significantly less than 1.

The slope and exponent parameters showed opposing patterns across the four axes (Figure 23). These parameters capture the degree to which the magnitude of peripheral biases varied across eccentricity for the four axes. In particular, the largest slopes are found for the temporal axis, which also exhibited the greatest overestimations in perceived location. However, as seen in Figure 20, peripheral biases peaked in the mid-periphery and were absent in the far periphery. This nonlinearity in peripheral bias as a function of eccentricity results in the exponent parameter having a value less than 1. In contrast, the magnitude of the peripheral bias was relatively smaller and more consistent across eccentricity for the superior axis, resulting in a smaller slope parameter and a larger exponent parameter, both of which were not significantly different than a value of 1. Collectively, then, the results support the existence of two distinct scaling functions across the four axes[3].

[3] While differences in perception between the left and right hemispheres have been reported for a variety of dimensions (Charles, Sahraie, & McGeorge, 2007; Toba, Cavanagh, & Bartolomeo, 2011), hemispheric

Reduced eccentricity overestimation in the superior and nasal visual field may be due to visual field borders arising from facial anatomical constraints. In particular, the superior and nasal fields are bounded by the upper brow and nose (external borders), while the temporal and inferior fields are typically not constrained by facial features. Thus, the visual field boundaries along these axes are intrinsic. One possibility is that the presence of these facial boundaries reduces uncertainty in the location of the edge of the visual field, leading to reduced peripheral bias and a linear scaling metric. However, analysis of the standard deviations argues against this interpretation. As seen in Figure 21, standard deviations were comparable in size across the four axes. For all axes but the nasal axis, the smallest standard deviations are associated with the most peripheral targets, demonstrating that participants showed the least spatial uncertainty for target locations near their visual field extents. Moreover, the nasal axis contains the strongest external visual border (the nose), yet standard deviations remain high for this axis for the most peripheral eccentricities tested. Finally, if the absence of external visual field boundaries led to greater uncertainty in target positions along the inferior and temporal axes, standard deviations should have been larger for more eccentric locations along these axes, but this was not the case.

An additional argument against an uncertainty-based explanation of our results is based on the magnitude of the localization errors. Had participants been more uncertain of target locations along the inferior and temporal axes, there should have been greater variability in responses in both directions (overestimations and underestimations), resulting in a reduction in the mean bias for these axes. In contrast, larger peripheral biases were observed along these axes than the superior and nasal axes. These results therefore suggest that differences in spatial uncertainty across the four axes tested cannot explain the differences in scaling.

Results from the normalization procedure (Figure 22) also argue against systematic differences in mislocalization of visual field extent driving the peripheral bias that we observed across all axes. Here, for each participant and each axis, all responses were scaled relative to the maximum response, and target eccentricities were scaled relative to the maximum eccentricity tested. If participants underestimated the extent of their visual field along the inferior and temporal axes due to decreased visibility of intrinsic visual field boundaries, our normalization procedure would correct for this. As is evident in Figure 22, even if participants had underestimated their visual field extent, scaling was still nonlinear and/or showed additional peripheral bias in estimated locations across the range of eccentricities tested (i.e., estimated magnitudes were predominantly above the line that represents a linear scaling of perceived eccentricity relative to the maximum eccentricity tested). This rules out an explanation of peripheral localization bias based on inward shifts of the perceived visual field boundary.

Our findings support an interpretation in which peripheral biases and nonlinear scaling metrics are evident when localization occurs in spaces without clearly visible boundaries (i.e., when scaling is made relative to intrinsic visual field boundaries). In these cases, participants must localize targets within a retinotopic, egocentric reference frame. Indeed, the absence of clear external boundaries distinguishes previous studies on peripheral localization that reported peripheral biases (Bock, 1993; Enright, 1995; Temme, et al., 1985) from those that have found

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specialization cannot explain all of our findings. In particular, hemispheric specialization predicts differences in localization solely between the left and right sides of a display and not between the upper and lower vertical meridians. In contrast, in the present study, we found one type of scaling for the temporal (right) and inferior axes and a different type of scaling for the nasal (left) and superior axes.

foveal biases (Hubbard & Ruppel, 2000; Kerzel, 2002; Mateeff & Gourevich, 1983). The presence or absence of external visual boundaries also accounts for the different localization biases found across the four axes tested in the present study. However, the unique paper-and-pencil response type used in the present study and Temme et al. (1985) may also have influenced participants' magnitude estimates. We therefore conducted Experiment 8, in which verbal responses were used to indicate perceived target location.

4.3. Experiment 8: Demonstrating Peripheral Biases with Verbal Response

The goal of Experiment 8 was to demonstrate that similar peripheral biases are observed when participants are required to make verbal judgments of perceived target locations under similar experimental conditions. We also added a binocular condition that eliminated the border of the nose that was present in the monocular target presentation in Experiment 7. We hypothesized that in the monocular (right eye) condition, response scaling along the nasal (left) axis should be linear (as we found in Experiment 7), but that in the binocular condition, removal of the external visual boundary of the nose should result in nonlinear scaling along the left axis (as we found for monocular presentation along the temporal (right) axis in Experiment 7).

4.3.1. Methods

Participants. Twelve healthy undergraduates (9 females; mean age: 21.3 ± 3.9 years) who had not participated in the previous experiment participated in this experiment for course credit. The same exclusion criteria as in Experiment 7 were used.

Materials and Procedure. As in Experiment 7, a Goldmann perimeter was used to measure the visual field extent of all participants and to present visual targets, and the same III4e target dot was used for both boundary determination and testing. For the binocular viewing condition, head position was adjusted so that patients could comfortably view the fixation dot in the center of the perimeter. Eye position was monitored via the telescope in the center of the perimeter, which provided a view of the right eye.

For both monocular and binocular conditions, targets were presented at 10º intervals from 10º eccentricity to the edge of the participant's visual field along the four cardinal axes, with trials containing target locations along the horizontal and vertical meridians intermixed within each viewing condition block. All locations were tested five times during a block, and a separate random testing sequence was generated prior to testing for each participant. On each trial, participants generated a verbal magnitude estimate of the target's location. The estimate ranged between 0 and 100, where 0 corresponded to the point of fixation and 100 corresponded to the edge of the participant's perceived visual field extent. Thus, the magnitude estimates mirrored the manual response in Experiment 7, where the center hash mark corresponded to the point of fixation and the edge of the line corresponded to the edge of the perceived visual field extent. Any trial in which fixation was not maintained was repeated. All participants completed five practice trials before beginning the experiment, and block order (monocular vs. binocular) was counterbalanced across participants.

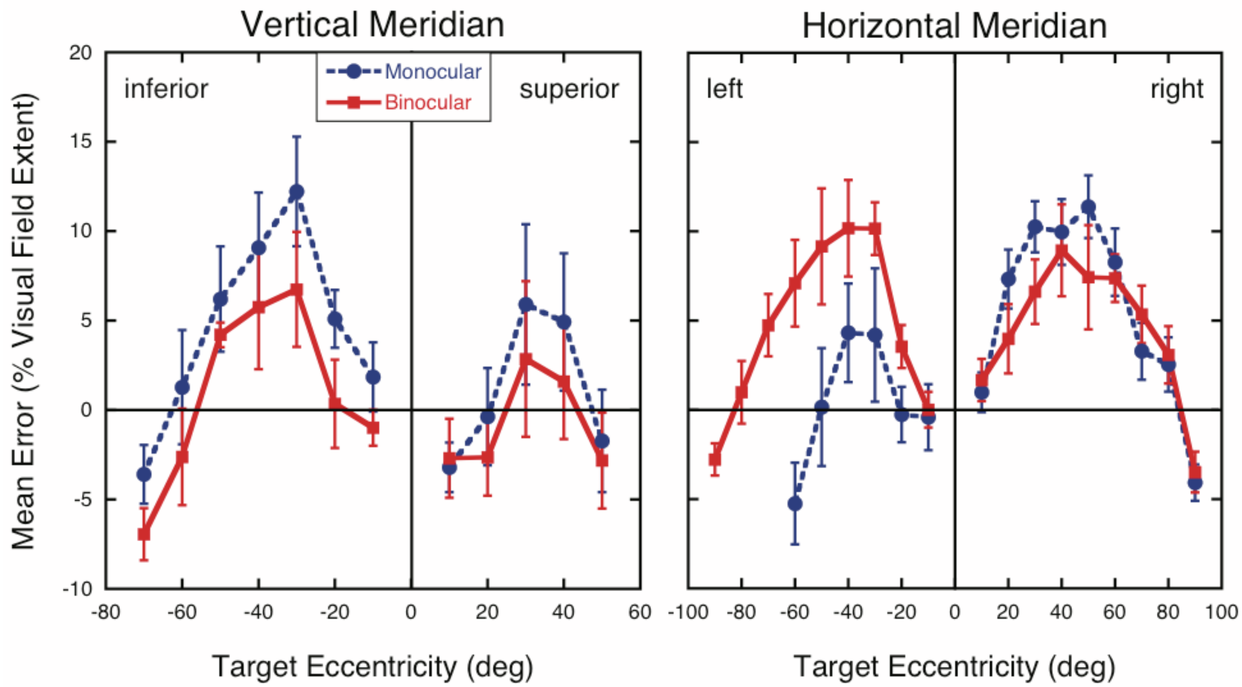

Figure 24. Experiment 8 Localization Errors. Mean errors in percent of visual field extent for vertical and horizontal meridians as a function of viewing condition and target eccentricity. Error bars represent S.E.M. Solid horizontal lines at zero represent expected performance if no distortion exists.

4.3.2. Results

Localization Errors. The mean measured visual extents of the participants' right eyes were: temporal axis = 90º ± 2º, nasal axis = 61º ± 3º, inferior axis = 71º ± 4º, superior axis = 49º ± 8º. The mean visual extents of the binocular visual fields were: right axis = 90º ± 2º, left axis = 89º ± 4º, inferior axis = 71º ± 4º, superior axis = 51º ± 7º. As in Experiment 7, each target eccentricity was converted to percentage of visual field extent, and errors in magnitude estimates were then calculated by subtracting this percentage from the verbal magnitude estimates. Figure 24 shows the mean errors in percent visual field extent as a function of target eccentricity and viewing condition (monocular or binocular) for the vertical and horizontal meridians. For the monocular viewing condition, the results mirror the pattern in Experiment 7: there was a peripheral localization bias, particularly along the temporal (right) and inferior axes. The peripheral bias was much smaller along the nasal (left) axis. In contrast, binocular viewing produced large peripheral biases along the left axis that were similar in magnitude and eccentricity profile to those observed along the right axis. Errors were similar for monocular and binocular viewing along the superior and inferior axes.

A 2 (Viewing Condition) x 4 (Axis) x 5 (Eccentricity) repeated measures ANOVA was conducted on localization errors for the five most central eccentricities, using Greenhouse-Geisser corrections when Mauchly's Test of Sphericity indicated that the assumption of sphericity was not met. As in Experiment 7, these five eccentricities were chosen because they were represented on all axes. There were significant main effects of Eccentricity (F(1.37,10.93)

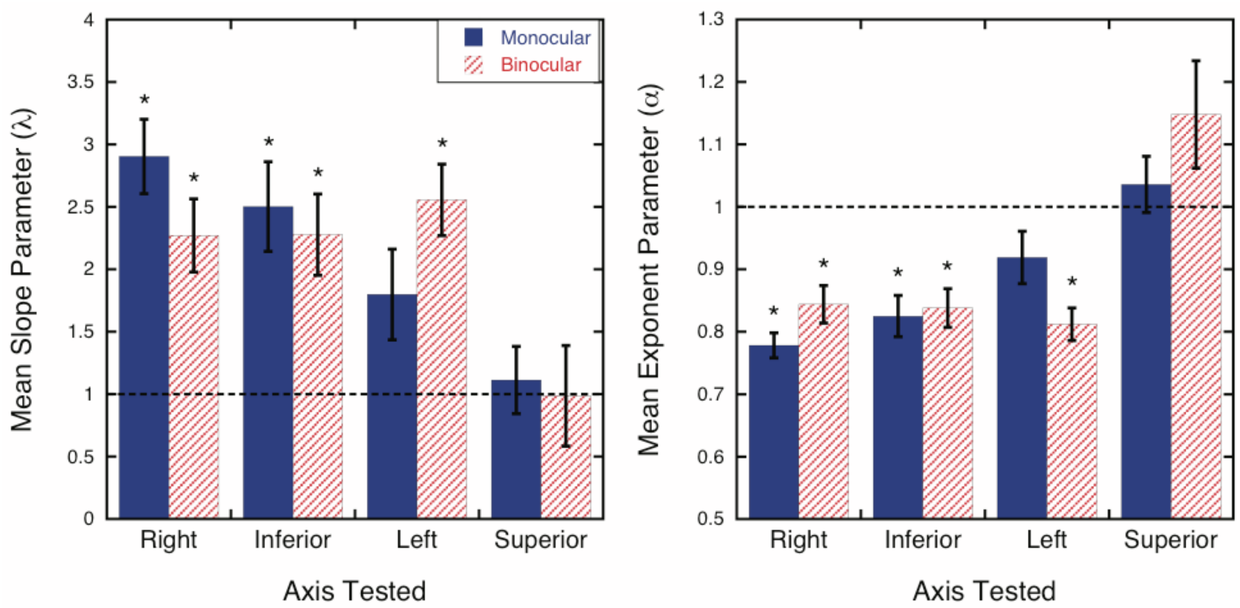

Figure 25. Experiment 8 Power Function Parameters. Mean estimated slope and exponent parameters as a function of viewing condition and axis tested, obtained from fitting individual magnitude estimates with the two-parameter function $J=\lambda D^{\alpha}$. Error bars represent S.E.M. Dotted lines represent expected performance if the mapping is undistorted and Euclidean. Asterisks indicate mean value is significantly different from 1, following correction for multiple comparisons.

= 8.23, p = 0.01) and Axis ($F(3,24)$ = 7.49, p = 0.001). The main effect of Viewing Condition was not significant ($F(1,8)$ = 0.002, p = 0.97), but the Viewing Condition x Axis interaction was significant ($F(3,24)$ = 3.06, p = 0.05), as was the Axis x Eccentricity interaction ($F(12,96)$ = 2.10, p = 0.02). The Viewing Condition x Eccentricity interaction was not significant ($F(4,32)$ = 0.17, p =0.95), nor was the three-way interaction ($F(12,96)$ = 1.25, p = 0.26). Trend analysis of the Eccentricity factor indicated a significant quadratic trend ($F(1,8)$ = 35.64, $p < 0.001$), and the linear and cubic trends did not reach significant levels (linear: p = 0.07, quadratic: p = 0.08). As in Experiment 7, the quadratic trend as a function of eccentricity is characterized by an inverted U-shaped function (Figure 24).

Magnitude Scaling. The same hierarchical modeling scheme described in Experiment 7 was used to fit the function relating magnitude estimates to actual target locations, expressed in terms of percent of visual field extent. Both one-parameter (exponent fixed at α=1) and two-parameter (exponent was free parameter) functions were tested. The one-parameter model accounted for 90% of average variance (range: 70 to 98), and the two-parameter model accounted for 93% of average variance (range: 82 to 98). Overall, the two-parameter model provided a significantly better fit for 53 of the 96 (55%) combinations of participant (12 subjects), axis (4), and viewing condition (monocular and binocular). Specifically, results showed that the two-parameter model provided a significantly better fit than the null model for all 12 participants in the monocular viewing condition along the temporal axis and a significantly better fit for 10 out of 12 (83%) participants for both the left and right axes in the binocular viewing condition. Thus, estimates from this model were used in subsequent analyses.

Figure 25 shows the mean slope and exponent parameters for each of the four cardinal axes under monocular and binocular viewing conditions. A 2 (Viewing Condition) x 4 (Axis) repeated measures ANOVA indicated that the slopes differed across the four axes ($F(3,33) = 11.46$, $p < 0.001$). While the main effect of Viewing Condition was not significant ($F(1,11) = 0.05$, $p = 0.83$), there was a significant Viewing Condition x Axis interaction ($F(3,33) = 3.16$, $p = 0.04$). One-sample t-tests were used to determine whether the slope parameters across the eight conditions differed significantly from a hypothetical mean of 1 using the Sidak-Bonferonni correction for multiple comparisons ($\alpha_{S\text{-}B} = 0.006$). For binocular viewing, all axes except the superior axis had mean slopes significantly greater than one (right = 2.27, $p = 0.001$; inferior = 2.28, $p = 0.002$; left = 2.56, $p < 0.001$; superior = 0.99, $p = 0.97$). Like binocular viewing, monocular viewing resulted in mean slopes significantly greater than one for the right and inferior axes but not for the superior axis (right/temporal = 2.91, $p < 0.001$; inferior = 2.50, $p = 0.002$; superior = 1.11, $p = 0.68$). In contrast, the mean slope for the left axis was not significantly different than 1 for monocular viewing (left/nasal = 1.79, $p = 0.050$), demonstrating a difference between monocular and binocular viewing in the scaling of estimates along this axis.

The same pattern was obtained for the estimated exponent parameters. A 2 (Viewing Condition) x 4 (Axis) repeated measures ANOVA, using Greenhouse-Geisser corrections when appropriate, showed a main effect of Axis ($F(3,33) = 23.20$, $p < 0.001$). The main effect of Viewing Condition was not significant ($F(1,11) = 0.36$, $p = 0.56$), but the Viewing Condition x Axis interaction was significant ($F(1.66,18.24) = 3.97$, $p = 0.04$). One-sample t-tests were again used to determine whether the exponent parameters across the eight conditions differed significantly from a hypothetical mean of 1 using the Sidak-Bonferonni correction for multiple comparisons ($\alpha_{S\text{-}B} = 0.006$). In the binocular viewing condition, all axes except for the superior axis had mean exponent values that were significantly less than 1 (right = 0.84, $p < 0.001$; inferior = 0.84, $p < 0.001$; left = 0.81, $p < 0.001$; superior = 1.15, $p = 0.112$). In the monocular condition, the mean exponent along the left axis was not significantly different than 1 (0.92, $p = 0.082$), further supporting a difference between monocular and binocular viewing in the scaling of estimates along this axis. Mean exponent values for monocular viewing of the other axes were similar to those obtained from binocular viewing (right/temporal = 0.78, $p < 0.001$; inferior = 0.82, $p < 0.001$; superior = 1.04, $p = 0.438$).

4.3.3. Discussion

The results of Experiment 8 replicate the peripheral localization bias found in Experiment 7 and, together with the results of Experiment 7, show that for monocular viewing, verbal and motor responses produce the same qualitative pattern of results. Our finding of peripheral bias using verbal magnitude responses is inconsistent with the theory that peripheral biases are found primarily with open-loop motor responses, while closed-loop motor responses and perceptual responses are associated with foveal biases (Uddin, 2006). Rather, our results demonstrate that peripheral biases can also be observed using perceptual tasks such as verbal report and are therefore likely to reflect perceptual distortions. However, some aspects of our data are consistent with an additional peripheral bias introduced by motor, relative to verbal, responses. Peripheral biases tended to be smaller overall in Experiment 8 compared to Experiment 7. Also, peripheral biases were found in Experiment 7 for both the 10º and 20º target locations across all four axes, particularly along the temporal (right) axis, while in Experiment 8, there was little, if any, bias in estimating targets at these locations (compare Figures 20 and 24). This difference suggests that peripheral biases may be more difficult to detect in computer-based localization tasks, which predominantly test locations less than 20º eccentricity. The larger peripheral biases observed in Experiment 7 compared to Experiment 8 at these eccentricities are also consistent with previous reports that the use of a verbal response eliminated the peripheral bias that was observed with pointing responses for targets located in the central 30º (Bruno & Morrone, 2007).

Despite smaller peripheral biases for the nearest eccentricities in Experiment 8, the overall pattern of errors in the monocular viewing condition across the four axes tested matches that found in Experiment 7. Specifically, responses along all four axes showed an overall peripheral bias with monocular viewing. When the raw magnitude estimates were fit with power functions, results showed significant deviations from a value of 1 in the exponent and slope parameters of the right/temporal axis and the inferior axis, similar to those found in Experiment 7. Also, estimates along the superior and left/nasal axes showed essentially a Euclidean mapping of space, with both exponent and slope parameters not significantly different from 1.

However, scaling was different for monocular and binocular viewing along the left axis, while biases were consistent across the two viewing conditions for the other three axes. For the left axis, the mean magnitude of errors with binocular viewing was similar in size to that found along the right axis in both viewing conditions. This finding supports the prediction that the nose provides an external boundary that changes the scaling of visual space. An external boundary could allow participants to make judgments about perceived location in an allocentric reference frame, where space is defined by the boundaries of the external borders. The absence of an external border would then force participants to make judgments relative to the intrinsic border defined by the edge of their visual field and to use an egocentric reference frame that is bounded by the edges of the visual field (i.e., a retinotopic reference frame).

However, there is a potential confound, as the region in which targets were presented along the left axis consisted solely of the nasal visual field for the right eye in the monocular viewing condition, while targets were presented in the nasal visual field of the right eye *and* the temporal visual field of the left eye in the binocular viewing condition. It is therefore possible that differences in spatial processing between the nasal and temporal visual fields (Curcio & Allen, 1990; Fahle & Schmid, 1988; Paradiso & Carney, 1988) could underlie some of the difference between monocular and binocular viewing in scaling along the left axis that we observed in Experiment 8. To address this possibility, we conducted Experiment 9, in which participants completed the same monocular and binocular tasks as in Experiment 8 in the presence of a constant external border consisting of an aperture edge placed in the Goldmann perimeter.

4.4. Experiment 9: External Borders Introduce Foveal Bias

4.4.1. Methods

Participants. Twelve undergraduates (9 females; mean age: 20.3 ± 3.2 years) who had not participated in the previous two experiments participated in this experiment for course credit. The same exclusion criteria from Experiment 7 were used.

Materials and Procedure. Determination of visual field boundaries and stimulus presentation procedures were the same as in Experiment 8, with the addition of a ring-shaped aperture placed inside the Goldmann perimeter with an inner radius of 30° eccentricity. This aperture size was chosen to ensure that the inner edge of the aperture would be visible along all axes for all participants, given that upper visual field extents can be as small as 40º in some participants. Due to the curvature of the dome, the aperture was created by carefully layering 1.3 x 5.1 cm strips of black paper around the dome. Strips were adhered such that the longer dimension was aligned in the radial direction. The first strips were adhered to the cardinal axes, with the longer dimension horizontally oriented for the left/right edges and vertically oriented for the upper/lower edges, as these were the axes along which the targets were presented. The rest of the aperture was then constructed by adhering additional strips of the same size that partially overlapped one another, one strip at a time, to create a continuous curved inner border without any visible boundaries between the strips. The use of multiple thin strips allowed for the creation of a ring-shaped aperture (15° thick) to be formed to the curvature of the dome.

For all participants and in both viewing conditions, the target was presented at seven eccentricities within the aperture, along each of the four cardinal axes. The eccentricities were 4°, 8°, 12°, 16°, 20°, 24°, and 28° of visual angle. Using the same method as Experiment 8, participants generated a verbal magnitude estimate of the target's location on every trial. The estimate ranged between 0 and 100, where 0 corresponded to the point of fixation, and 100 corresponded to the inner edge of the aperture. Each of the 28 target locations was tested 5 times. Different random sequences of target location along all four axes were generated prior to testing for each participant and for each of the two viewing conditions. Trials with target locations along the four axes were intermixed within each block. Before each block, participants completed five practice trials at randomly chosen target locations. As in Experiment 8, monocular and binocular viewing conditions were tested in separate blocks, and block order was counterbalanced across participants.

4.4.2. Results

Localization Errors. The mean measured visual extents of the participants' right eyes were: temporal axis = 88º ± 4º, nasal axis = 55º ± 7º, inferior axis = 69º ± 5º, superior axis = 50º ± 8º. The mean visual extents of the binocular visual fields were: right axis = 86º ± 4º, left axis = 86º ± 4º, inferior axis = 70º ± 6º, superior axis = 50º ± 11º. As participants judged target locations relative to the aperture edge, each target eccentricity was converted to percentage of distance between central fixation and the aperture edge. Errors in magnitude estimates were then calculated by subtracting the true target location (in units of percentage of aperture extent) from the corresponding magnitude estimates. Figure 26 shows the mean errors in percent of aperture extent as a function of target eccentricity and viewing condition for the vertical and horizontal meridians. Across all axes and both viewing conditions, participants showed a foveal bias. That is, participants tended to underestimate target eccentricity, and the magnitude of this underestimation was proportional to target eccentricity.

A 2 (Viewing Condition) x 4 (Axis) x 7 (Eccentricity) repeated measures ANOVA was conducted on mean localization errors, using Greenhouse-Geisser corrections when appropriate. There was a main effect of Viewing Condition ($F(1,11) = 5.08$, $p = 0.05$), with a larger foveal bias in the monocular compared to the binocular viewing condition. There were also main effects of Axis ($F(3,33) = 5.83$, $p = 0.003$) and Eccentricity ($F(1.47,16.16) = 3.92$, $p = 0.05$), with larger foveal biases at more peripheral eccentricities. The Axis x Eccentricity interaction was significant ($F(18,198) = 3.18$, $p < 0.001$), as was the Viewing Condition x Eccentricity

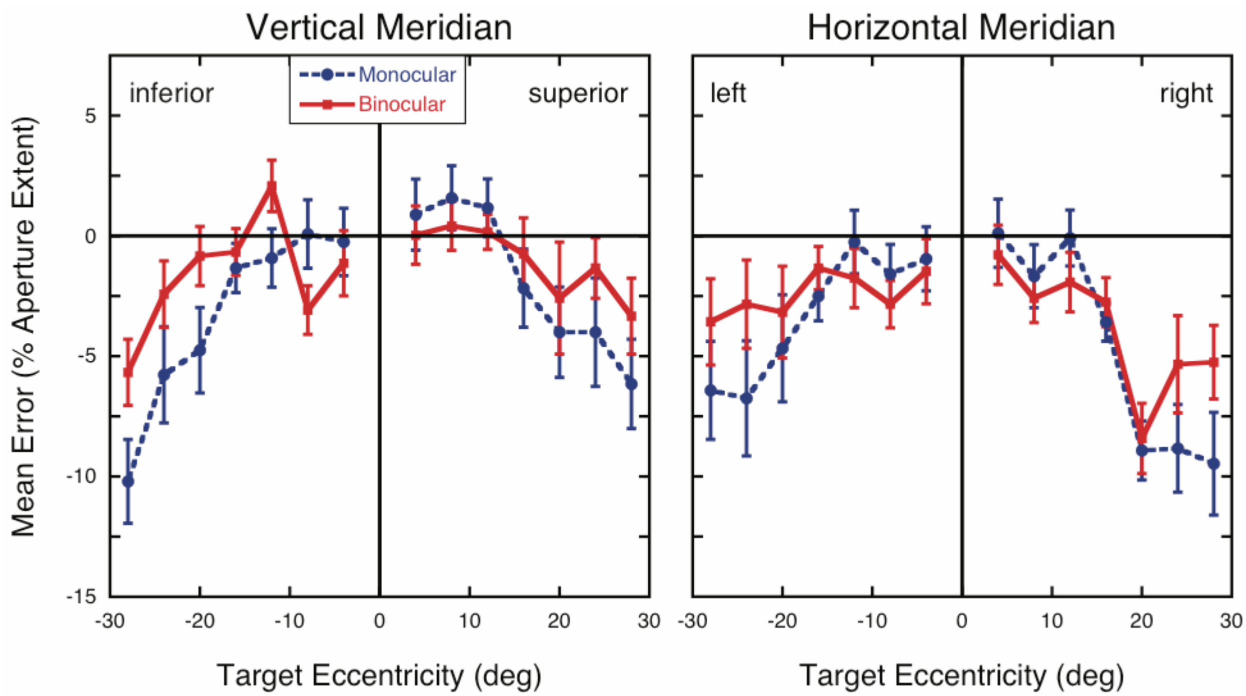

Figure 26. Experiment 9 Localization Errors. Mean errors in percent of aperture extent for the vertical and horizontal meridians as a function of viewing condition and target eccentricity. Error bars represent S.E.M. The solid horizontal lines at zero represent expected performance if no distortion exists.

interaction ($F(2.03,22.37) = 9.67$, $p = 0.001$). In contrast to Experiment 8, localization error differences across the two viewing conditions did not differ across the four axes tested, as indicated by the lack of either a significant Axis x Viewing Condition interaction ($F(3,33) = 1.20$, $p = 0.32$) or a significant three-way interaction ($F(18,198) = 1.33$, $p = 0.17$). A trend analysis of the Eccentricity factor showed no significant trends, though the linear trend approached significance (linear: $p = 0.06$, quadratic: $p = 0.13$, cubic: $p = 0.39$).

Magnitude Scaling. The same hierarchical fitting procedure described in Experiment 7 was used here. The one-parameter model accounted for 92% of average variance (range: 55 to 98), and the two-parameter model accounted for 94% of average variance (range: 81 to 99). Overall, the two-parameter model provided a significantly better fit for only 40 of 96 (42%) cases. Moreover, for each axis and viewing condition individually, there was no clear bias toward one model providing a better fit across participants. As a result, subsequent analyses were conducted on the estimated slope parameters from the one-parameter (linear) model[4].

Figure 27 shows the mean slope parameters for each of the four axes across the two viewing conditions. A 2 (Viewing Condition) x 4 (Axis) repeated measures ANOVA showed a main effect of Viewing Condition ($F(1,11) = 10.46$, $p = 0.008$), with monocular viewing having

[4] Analyses were also conducted on the model fits for the two-parameter model. Results showed that the estimated exponent parameters for all four axes across both viewing conditions failed to differ from a value of 1, confirming that selection of the one-parameter linear model is appropriate for this experiment.

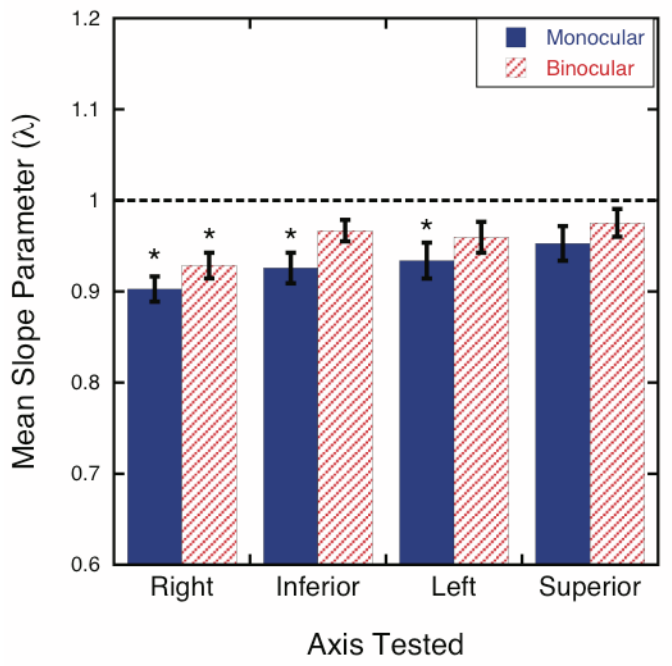

Figure 27. Experiment 9 Slope Parameters. Mean estimated slope parameters as a function of viewing condition and axis tested, obtained from fitting individual magnitude estimates with the one-parameter function J=λD. Error bars represent S.E.M. The dotted line at one represents expected performance if the mapping is undistorted and Euclidean. Asterisks indicate mean value is significantly different from 1, following correction for multiple comparisons.

lower slopes for all axes. There was also a main effect of Axis ($F(3,33) = 6.01$, $p = 0.002$), but the Axis x Viewing Condition interaction was not significant ($F(3,33) = 1.24$, $p = 0.31$). Post-hoc comparisons, corrected for multiple comparisons, indicate that the main effect of Axis was driven by smaller slope estimates along the right compared to the superior axis (Sidak-adjusted value: $p = 0.05$). All other pairwise comparisons between the four axes failed to reach significance (all p values > 0.07). One-sample t-tests were used to determine whether the slope parameters across the eight conditions differed significantly from a hypothetical mean of 1 using the Sidak-Bonferonni correction for multiple comparisons ($\alpha_{S\text{-}B} = 0.006$). For binocular viewing, mean slope estimates were significantly less than 1 only along the right axis (0.93, $p < 0.001$; other axes > 0.96, $p \geq 0.17$), while for monocular viewing, slopes were significantly less than 1 along all axes except for the superior axis (0.95, $p = 0.03$; other axes < 0.93, $p \leq 0.006$).

4.4.3. Discussion

The results of this experiment indicate that in the presence of clear external visual field boundaries provided by an aperture edge, strong foveal biases and linear scaling of judgments as a function of eccentricity are present across all four cardinal axes. These findings provide further support that external borders aid in establishing a linear spatial metric that counters inherent peripheral biases in perceived location that occur when no boundaries are present. Interestingly, the slope estimates in the present experiment are similar to those found in Experiment 1 of

Chapter 2 where participants judged target locations at the same eccentricities along the four cardinal axes relative to an aperture edge located at 30°, although the targets were presented on a computer monitor (see Figure 2). Unlike the results from Experiments 7 and 8 in which there was no aperture present, Experiment 9 revealed foveal biases that increase with eccentricity. The different pattern of errors across eccentricity due to the introduction of external boundaries and the switch from a peripheral to a foveal bias suggests that external boundaries such as the edge of an aperture or the edges of a computer monitor are a distinct class of boundaries from those created by the edges of the visual field.

In Experiment 8, patterns of localization bias and scaling were quite different for monocular and binocular viewing of targets along the left/nasal axis. In contrast, this distinction between monocular and binocular viewing was not evident in Experiment 9, where greater foveal biases (for large eccentricities) and smaller slope estimates were observed in the monocular viewing condition than the binocular viewing condition across all four axes. These results suggest that inherent differences in spatial processing between nasal and temporal visual fields cannot explain the scaling differences between monocular (right eye) and binocular viewing along the left axis that were observed in Experiment 8.

The foveal biases observed in Experiment 9 also rule out the use of the Goldmann perimeter as the cause of the peripheral biases observed in Experiments 7 and 8. Previous studies of peripheral localization have used computer monitors (Adam, et al., 1993; Bocianski, et al., 2008; Bruno & Morrone, 2007; Kerzel, 2002; Sheth & Shimojo, 2004; Tsal & Bareket, 2005; van der Heijden, et al., 1999), arrays of LEDs (Carrozzo, Stratta, McIntyre, & Lacquaniti, 2002; Enright, 1995; Lewald & Ehrenstein, 2000; Mateeff & Gourevich, 1983), and stereoscopic displays (Bock, 1993) for stimulus presentation. To our knowledge, only two studies have used a dome-shaped perimeter to conduct visual spatial localization experiments (Temme, et al., 1985 and the present study). If the Goldmann perimeter had unique properties that led to peripheral biases (for example, the type of target light or the half-dome environment that eliminates any spatial cues from the surrounding testing room), this bias should have been evident in all three of our experiments. The fact that strong foveal biases were observed in Experiment 9 therefore supports the notion that it is the presence or absence of external visual field boundaries, not the Goldmann perimeter itself, which determines the type and magnitude of localization biases.

4.5. General Discussion of Experiments 7-9

We have found that borders that define visual space modulate biases in judging target location for stationary targets presented along the cardinal axes. Specifically, Experiment 7 showed that monocular target localization, as assessed with paper-and-pencil responses, exhibits a peripheral bias (replicating Temme, et al., 1985). Nonlinear regression analyses demonstrated that the spatial scaling along the temporal and inferior axes was different than scaling along the nasal and superior axes. The existence of external facial boundaries in the visual field accounts for these differences: for monocular viewing, the nasal axis (nose) and superior axis (brow) have visibly prominent boundaries, and these are the axes exhibiting linear scaling of target location. In contrast, scaling was nonlinear along the temporal and inferior axes where intrinsic visual field boundaries were present. Thus, these results provide evidence that external visual boundaries change not only the reference frame in which localization occurs (as suggested by Sheth & Shimojo, 2004) but also the spatial metric within the reference frame.

In Experiment 8, we tested whether the same localization biases observed with paper-and-pencil responses in Experiment 7 were evident when participants responded with a verbal magnitude estimate. For monocular viewing, the results replicated the findings of Experiment 7: peripheral biases for all four axes, linear scaling for nasal and superior axes, and nonlinear scaling for temporal and inferior axes. Thus, the patterns of localization bias and scaling are independent of response mode, at least with respect to the two response modes utilized in this study. However, it is possible that other response modes would produce a different pattern of localization errors. Importantly, our finding of peripheral bias when using a verbal magnitude estimate and the similarity in the pattern of errors across Experiments 7 and 8 demonstrate that peripheral biases are not limited to open-loop pointing responses, as has previously been suggested (Uddin, 2006).

Experiment 8 also contained a binocular viewing condition to eliminate the nose as an external visual field boundary, and this produced a significant increase in the magnitude of peripheral bias along the left axis, compared to monocular viewing, as well as a change in scaling from a linear to a nonlinear metric. Experiment 9 provides further support for the role of external visual boundaries in the scaling of visual space. Here, the presence of a strong external border (an aperture edge) caused a consistent foveal bias and linear scaling of visual space across all four axes in both monocular and binocular viewing conditions.

Theories of location perception for stationary targets have predominately focused on the effects of eye movements and attention on the accuracy of responses (Adam, et al., 2008; Adam, et al., 1993; Tsal & Shalev, 1996; Uddin, 2006). Adam et al. proposed a two-process model for localization of stationary targets (Adam, et al., 1993; Adam, Paas, Ekering, & Loon, 1995), in which the movement of attention toward targets provides coarse location information that is further refined with eye movements that are made toward the target. One limitation of the two-process model is that it fails to predict whether a foveal or peripheral bias should occur in a given task, as the model focuses on absolute accuracy rather than bias. One proposal to account for biases is that the dissociation between the point of fixation and the locus of covert attention determines the direction of biases in spatial localization tasks, at least using perceptual reports (Uddin, 2006; Uddin, et al., 2005a; Uddin, Kawabe, & Nakamizo, 2005b). According to this model, when fixation is maintained centrally and a peripheral target is presented, attention is focused at the point of fixation, resulting in a foveal bias in perceived location. However, to the extent that attention is also drawn to objects at more eccentric locations than the target, perceived target location will be determined by the degree of allocation of attention to the relative locations of the fixation point and distracter object, leading to a possible peripheral bias. While the results of Chapter 2 and other studies have shown that attention can modulate localization errors of stationary targets (Adam, et al., 2008; Bocianski, et al., 2010; Tsal & Bareket, 2005; Yamada, et al., 2008), attentional weighting cannot explain the influence of visual field boundaries on either the scaling or type of biases that we have observed in the present study, as the degree to which borders were attended presumably did not vary across the axes tested. In addition, the attentional demands and task were identical in Experiments 8 and 9, but the direction of localization bias was different in these two experiments.

When attention is drawn to landmarks at a greater eccentricity than the target, estimates of target location can be peripherally displaced towards the landmark location (Uddin, et al., 2005a; Yamada, et al., 2008). In the present study, participants were required to allocate attention to both the fixation point and either the edges of the visual field (Experiments 7 and 8) or the inner edge of the aperture (Experiment 9) in order to determine the relative position of targets along the length of an axis. This is due to the nature of the tasks, both of which required participants to first assess the length of the tested axis and then to generate a magnitude estimate based on the perceived distance of the targets from fixation relative to the perceived length of the axis. However, it seems unlikely that the edges of the visual field or the aperture influenced responses in the same way as the landmark/distracter objects used in previous studies (Kerzel, 2002; Sheth & Shimojo, 2004; Uddin, et al., 2005a). First, the aperture in Experiment 9 provided the most salient edge, while the least salient edge was provided by the temporal and inferior visual fields in Experiments 7 and 8. However, the former condition produced the largest foveal bias, and the latter conditions resulted in the largest peripheral biases. Second, the effect of landmarks diminishes with distance from the target location (Uddin, et al., 2005a). However, the largest foveal biases we observed were for the most peripheral target locations closest to the edge of the aperture (Experiment 9), while peripheral biases diminished or switched to foveal biases as target location approached the edge of the visual field in Experiments 7 and 8.

An alternative account of our findings is that different reference frames can be used to assess the location of a single stationary target depending on task demands and that the type of reference frame used can lead to variations in perceived location (Sheth & Shimojo, 2004; Uddin, 2006). The idea that multiple, hierarchical reference frames can coexist and have differing consequences for spatial localization is well established (Bridgeman, 1999; Bridgeman, et al., 1997; Lemay & Stelmach, 2005; Paillard, 1991; Robertson, 2004). In a peripheral localization task, observers rely more on extrinsic than intrinsic reference frames to determine target location, even when this information is unreliable (Sheth & Shimojo, 2004). In our Experiments 7 and 8, the axes varied in the type of visual field border. One account of our results is that an egocentric reference frame is used to make location judgments relative to intrinsic visual boundaries (producing peripheral localization biases), while external visual boundaries, provided either by visible facial features or a physical aperture, results in the use of an allocentric reference frame.

Our measurements of spatial scaling also support the association of intrinsic visual boundaries with an egocentric reference frame and of external boundaries with an allocentric reference frame. In this framework, target location is initially encoded within a retinotopic (egocentric) reference frame. Peripheral biases and non-linear scaling are consistent with known distortions in the representation of the visual field in retinotopically-organized visual areas that contain an over-representation of the central visual field (Horton & Hoyt, 1991). The introduction of external boundaries may allow for a linearization of space across eccentricity and ultimately a switch from a peripheral to a foveal bias, depending on the degree to which boundaries enclose a region that is separate from the observer (i.e., the partial border provided by the brow and nose versus the border provided by the aperture that fully enclosed a region of visual space in all directions).

In conclusion, the results of the present study demonstrate that the type of visual field boundary present can significantly alter the perceived locations of stationary targets in the peripheral visual field. Further exploration of the effects of visual boundaries on spatial localization will help elucidate not only the types of reference frames used in spatial localization but also the spatial metrics within these reference frames.

5. Redefining the Metric of the Retinotopic Coordinate System

The studies described in the previous chapters have focused on measuring changes in the underlying structure of visual space due to manipulations in visual-spatial attention or the type of visual boundaries present. In particular, the results of Chapter 4 demonstrate that visual boundaries play an important role in determining where objects are perceived across the visual field. In the final chapter, we took a different approach. Namely, in this chapter we ask whether the visual field boundaries that define how much of space can be processed within a single glance can influence how incoming visual information is processed at locations far from visual field boundaries. Thus, rather than measuring the perceived metric, or structure of visual space, under a specific experimental condition, we first propose a new way to model the structure of retinotopic visual space and then test whether this model can account for previously reported asymmetries in performance on a crowding task across the upper and lower visual fields.

5.1. Introduction to the Metric of Retinotopic Visual Space

The human visual field is typically mapped in terms of polar coordinates, with the center of gaze (i.e., the fixation point) at the origin (Figure 28, left panel). In this system, two coordinates define locations: polar angle for direction, and radial distance from fixation (i.e., eccentricity), defined in degrees of visual angle. It is well established that the perception of objects is degraded with increasing distance from central fixation (Low, 1951). However, perceptual ability also varies for different visual field locations at equal eccentricities across the horizontal and vertical meridians (Carrasco, Giordano, et al., 2004; Carrasco, et al., 2001; Finger & Spelt, 1947), and between the upper and lower visual fields (Carrasco, Giordano, et al., 2004; Carrasco, et al., 2001; He, et al., 1996; Karim & Kojima, 2010; Previc, 1990; Previc & Intraub, 1997; Skrandies, 1987). Theories proposed to explain these asymmetries have included visual experience/perceptual learning (Karim & Kojima, 2010) and functional specialization within cortical visual maps that reflect both evolutionary and individual histories (Previc, 1990).

Of special interest for the present study is an influential experiment which showed that participants are better able to report the orientation of a grating flanked by similar gratings when the stimuli are presented in the lower visual field than at an equal eccentricity in the upper visual field (He, et al., 1996). Similar results were found using tasks that required differential allocation of attention. He et al. suggested that attentional enhancement of spatial resolution of vision was greater in the lower visual field, where it would benefit object detection in natural scenes. It has therefore been suggested that functional specialization within the visual system underlies this visual field asymmetry (He, et al., 1996; He, Cavanagh, & Intriligator, 1997).

The present study reveals an additional factor that has previously been overlooked: the asymmetrical shape of the human visual field. We show that a new metric of retinotopic visual space can explain the perceptual asymmetry reported by He et al. (1996) and accounts for variance in perceptual capabilities across the visual field in different individuals.

In our model, visual field boundaries define the metric of visual space and the distribution of visual processing capabilities. The binocular visual field is naturally asymmetric, with average borders of 90-100 degrees of visual angle for left and right of fixation, 70° for the

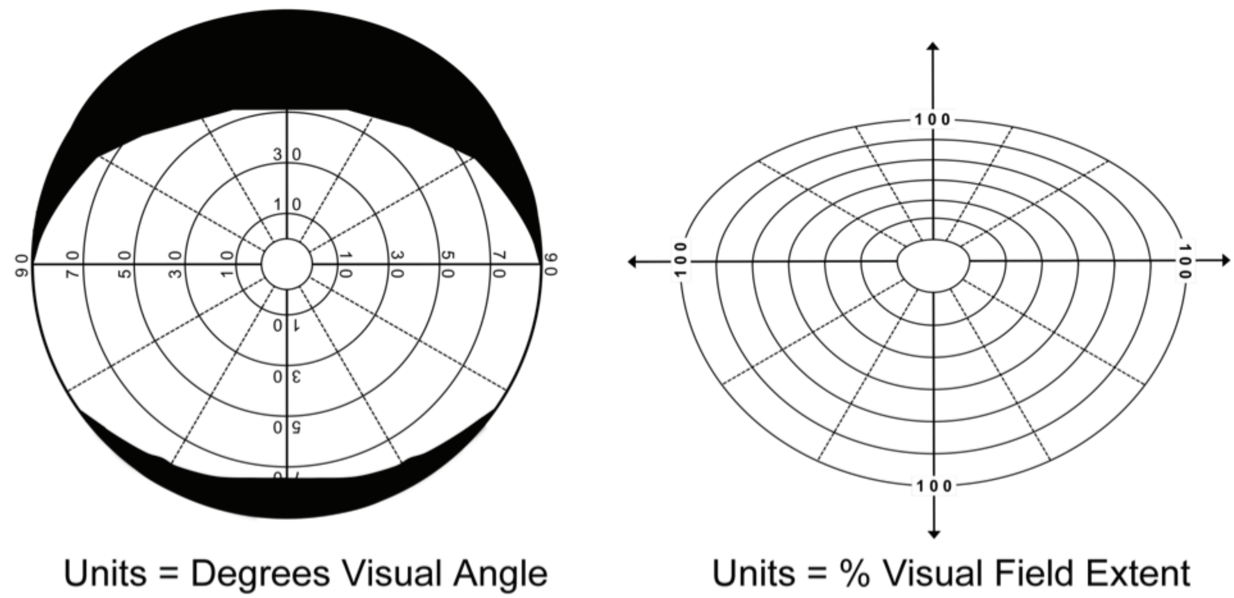

Figure 28. Two Models of Retinotopic Visual Space. The left panel shows a typical binocular visual field, plotted in polar coordinates with distance from fixation in degrees in visual angle. The solid black regions indicate the boundaries of the visual field and the regions outside of the average field of view. The right panel shows the new model of retinotopic visual space, with contours representing equal distances from fixation in % Visual Field Extent (%VFE).

lower visual field, and 50° for the upper visual field (Niederhauser & Mojon, 2002) (Figure 28a, left panel). Thus, the shape of the visual field is better described as a bi-elliptical contour than as a circle. However, upper and lower visual field boundaries also vary across individuals, due to differences in the prominence of the brow and cheeks, relative to the eyes. The metric we propose (Figure 28, right panel) replaces degrees of visual angle with a new unit, percentage of visual field extent (%VFE). We examined whether representing visual field locations as distances from fixation in %VFE can predict perceptual discrimination performance across the visual field. Specifically, we tested two predictions. First, for a given individual, a fixed location in degrees of visual angle will correspond to different values of %VFE, depending on the shape of each individual's visual field, so differences in visual field extent across individuals should predict the magnitude of performance asymmetries. Second, when the locations of stimuli are equated for each participant in terms of %VFE, performance should be equated for axes that have asymmetries when measured in degrees of visual angle.

5.2. Experiment 10: Perceptual Asymmetries and the New Metric of Retinotopic Visual Space

For this task we modified the original paradigm of He et al. (1996). After assessing visual field extents along the vertical meridian, we tested crowding performance in four blocks of trials where the targets gratings were presented at 20º in the upper or lower visual field, or at eccentricities in the upper and lower visual field that matched the locations in the opposite hemifield in terms of % VFE. We tested two hypotheses: 1) the magnitude of the performance asymmetry at the 20º locations across the upper and lower visual fields would correlate with magnitude of visual field asymmetry across individuals and 2) when the locations of the targets in the upper and lower visual field were equated in terms of %VFE, performance would be equated.

5.2.1. Methods

Participants. There were 20 participants (17 females; mean age: 21.3 ± 4.5 years). All but 2 participants were naïve observers who completed the experiment for course credit or were compensated $12 for their time. All participants reported normal or corrected-to-normal vision and did not wear eyeglasses, as eyeglasses have been shown to artificially restrict the visual field (Steel, et al., 1996). Four of the participants were excluded from data analyses after completing the experiment as they performed below chance (50% correct) on multiple conditions. All participants gave informed consent, and the Committee for the Protection of Human Subjects at the University of California, Berkeley, approved the experimental protocol (#2010-04-1159).

Materials and Procedure. Prior to behavioral testing, a Haag-Streit Goldmann kinematic projection perimeter was used to measure the binocular upper and lower visual field extents for each participant. We used the standard III4e test target (0.44° test spot at a viewing distance of 30 cm; 318 cd/m^2 on a background luminance of 10 cd/m^2). While participants maintained fixation at the center of the half dome, the experimenter projected the target light in the far periphery and then slowly moved it toward the fovea along the vertical meridian. The participant pressed a button that elicited a tone as soon as they detected the light in the periphery. Upon hearing the tone, the experimenter recorded the location of the target light. Throughout testing, participants maintained fixation at the center of the perimeter, where a small telescope is located that allows the experimenter, seated on the other side of the dome, to view the participant's right eye and insure that fixation is maintained. If fixation was not maintained, that trial was discarded. At least three repeats were conducted in random order for both the upper and lower vertical meridian. Upper and lower visual field extents were based on data from the final trial for each visual field location.

Stimuli for the behavioral testing were generated and presented on a ViewSonic G225f CRT monitor (refresh rate = 100 Hz) at a viewing distance of 25.4 cm with Presentation software (Neurobehavioral Systems, www.neurobs.com). A chin-and-forehead rest stabilized head position. Participants first completed 10 practice trials with the gratings located 10º above fixation. Throughout testing, eye position was continuously monitored by the experimenter using a commercial infrared camera (LTCMW304C5 from LTS, Houston, TX). If an eye movement was made on any trial, a tone sounded, no response was recorded, and the trial was repeated at a randomly chosen time later in the block. During practice, auditory feedback was given for incorrect responses, and these trials were also repeated. During the experiment, no feedback was provided for incorrect responses.

The task was a modified version of the paradigm of He et al. (1996). Target gratings of varying contrast, oriented 45° or 135°, were presented 20° above or below the fixation cross for 180 ms (Figure 29a). While maintaining fixation on a red cross, participants verbally reported whether the target grating (always centered on the vertical meridian) was tilted to the left or

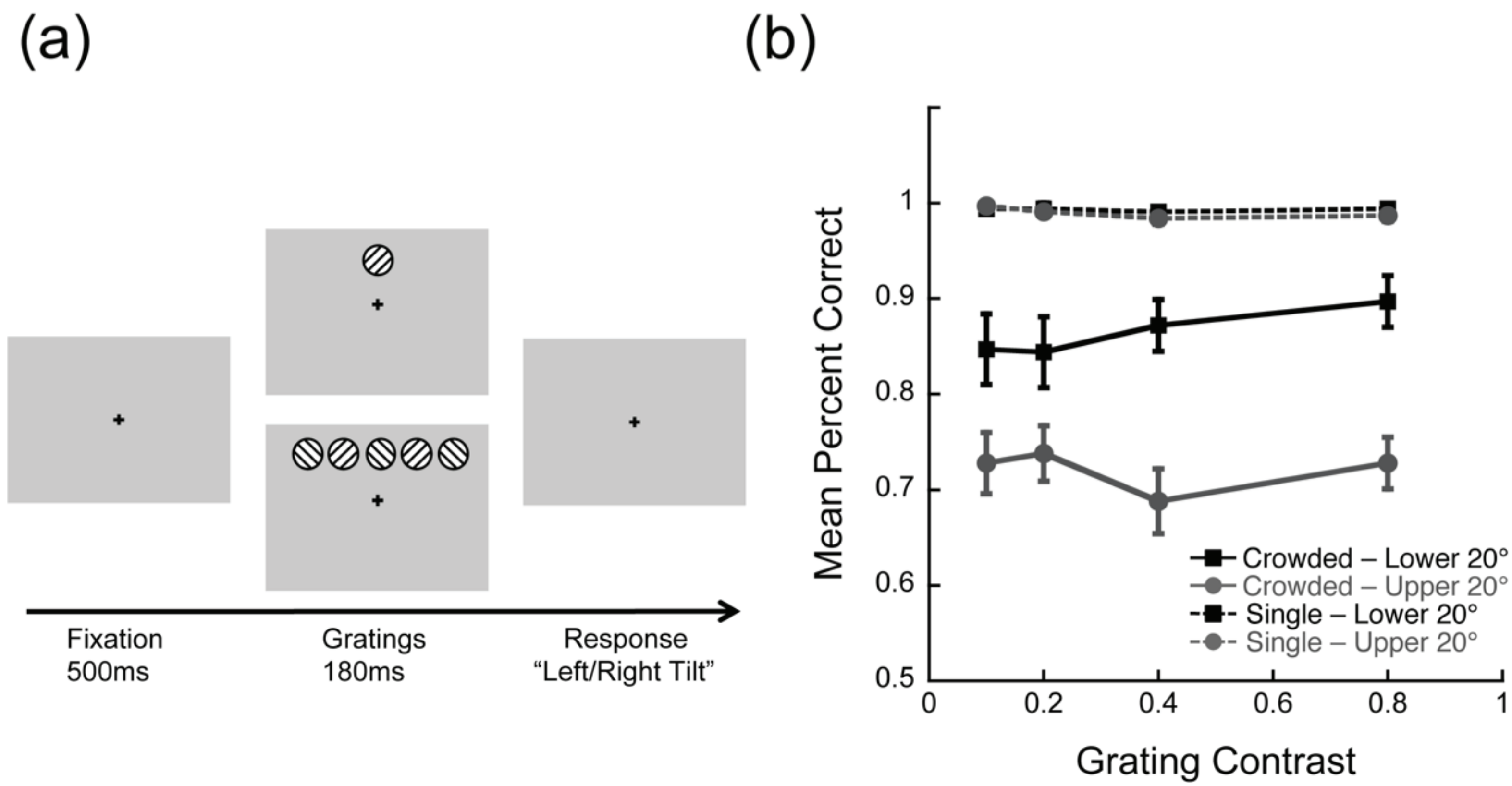

Figure 29. Experiment 10 Behavioral Paradigm. (a) Schematic of trial sequence. After a fixation period, the target grating was presented either alone or with flanker gratings with equal probability on a given trial. Gratings were presented at four vertical meridian locations in separate blocks. (b) Mean accuracy as a function of contrast for targets presented alone or with flankers at 20° above or below fixation. Error bars represent S.E.M. These results replicate the lower visual field advantage in the crowded condition reported by He et al. (1996).

right, and the experimenter recorded responses. Target gratings were either presented alone (single condition) or horizontally flanked by gratings on both the left and right sides (crowded condition). Flanker and target gratings always had the same contrast. Following He et al. (1996), sine-wave gratings were 1 cycle/degree and 2° in radius, with a 5° center-to-center distance between gratings in the crowded condition. Four grating contrast levels were tested: 0.1, 0.2, 0.4, and 0.8. The background of the display was always a neutral gray (27 cd/m^2). A Minolta CS100 Chroma Meter was used prior to testing to measure the luminance of gray values on the monitor used to accurately assess the contrast levels of the gratings and assure that the average luminance of the gratings was also 27 cd/m^2. Target and flanker gratings always had the same contrast level.

Gratings were presented at four target locations (20º upper visual field, 20º lower visual field, Matched upper visual field, and Matched lower visual field), with each location tested in separate blocks. In the Matched lower visual field block, %VFE was computed for the 20° upper visual field stimulus location for each participant, and stimuli were presented at the same %VFE in the lower visual field. In the Matched upper visual field block, the %VFE of the upper visual field location was matched to the %VFE corresponding to the 20° location in the lower visual field for each participant. For example, given a 50° upper VFE and a 75° lower VFE, gratings presented at 20° are at 40% VFE in the upper visual field but only 26.67% VFE in the lower visual field. To match locations in terms of %VFE, targets would be tested at 13.33° (26.67% VFE) in the Matched upper visual field condition and at 30° (40% VFE) in the Matched lower visual field condition.

For gratings at 20° eccentricity, the 1° diameter fixation cross was placed at the center of the screen, and the gratings were placed 20° above or below fixation. For the matched conditions, the fixation cross was either moved closer or farther away from the gratings to decrease or increase grating eccentricity. The monitor was located on a platform with a pulley system that allowed the experimenter to adjust the height of the monitor so that the participant could fixate the cross with his or her head flat against the forehead rest and eyes directed straight ahead, in primary position. Thus, the position of the monitor, not the position of the participants' eyes and head, was modified across blocks.

Block order was counterbalanced across participants with the constraint that each of the four conditions was presented four times with a given temporal order across participants (i.e., 1st block, 2nd block, etc). Within each block, there were 10 repeats of each of the 16 conditions: 2 flanker conditions (single/crowded) x 2 grating orientations (45º/135º) x 4 grating contrast levels (0.1, 0.2, 0.4, and 0.8).

5.2.2. Results and Discussion

A 4(Visual Field Location) x 2(Flanker) x 4(Grating Contrast) x 2(Target Orientation) repeated-measures ANOVA was calculated on the accuracy scores. Results showed no main effect of grating orientation ($p = 0.32$) or interaction of grating orientation with any other factor ($p > 0.1$ for all). Thus, the data were collapsed over this factor in all analyses presented below. The mean percentage correct for gratings presented 20º above or below fixation in the single and crowded conditions as a function of grating contrast are shown in Figure 29b. As seen in Figure 29b, average accuracy was at ceiling when gratings were presented alone in the upper and lower visual fields. To determine whether we were able to replicate the lower visual field advantage in the crowded condition reported by He et al. (1996), a 2(Visual Field Location: 20º upper/lower) x 4(Grating Contrast) repeated-measures ANOVA was calculated on the accuracy scores for the

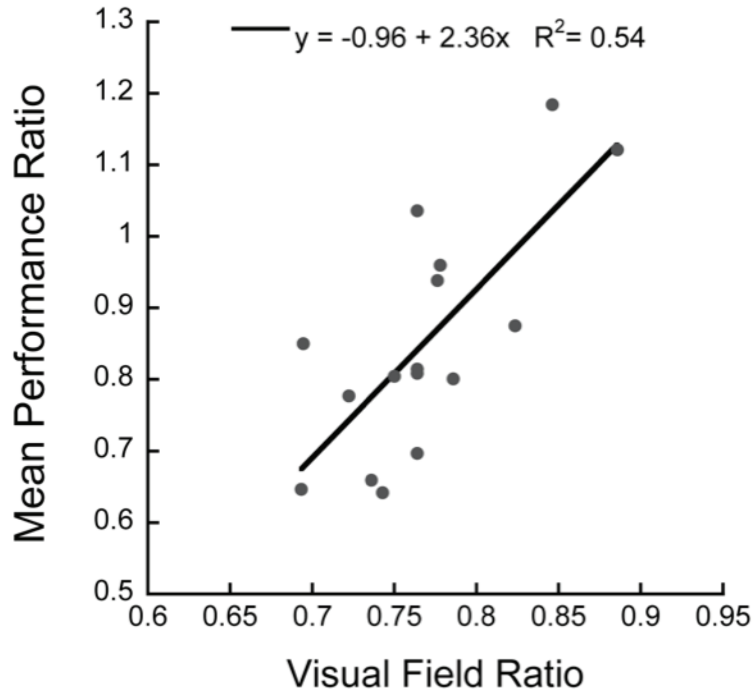

Figure 30. Visual field asymmetries predict magnitude of average perceptual asymmetry across individuals. The magnitude of the performance asymmetry for the crowded conditions at 20° (averaged across contrast levels) is highly correlated with the asymmetry in upper and lower visual field extents. Each data point represents one participant. Solid black line indicates linear regression.

crowded condition only. Results of this analysis showed that, similarly to He et al. (1996), participants were significantly better at discriminating the orientation of the target gratings when they were presented in the lower visual field than the upper visual field, $F(1,15) = 18.15$, $p = 0.001$. Performance did not significantly differ across the four grating contrast tested ($F<1$) and the interaction between visual field location and grating contrast level was not significant, $F(3,45) = 2.45$, $p = 0.08$.

As the previous results showed that we were able to replicate the lower visual field advantage in determining the orientation of gratings in the crowded conditions at 20º eccentricity, we then tested the two predictions put forth if the new metric, based on the borders of each individual's visual field extent, better capture the distribution of processing resources across the visual field. The first prediction was that individual differences in visual field extent should lead to differences in the performance asymmetry across the upper and lower visual field when targets are placed at the same distance from fixation. In order to test this hypothesis, performance ratios were created at each grating contrast level for performance in the crowded

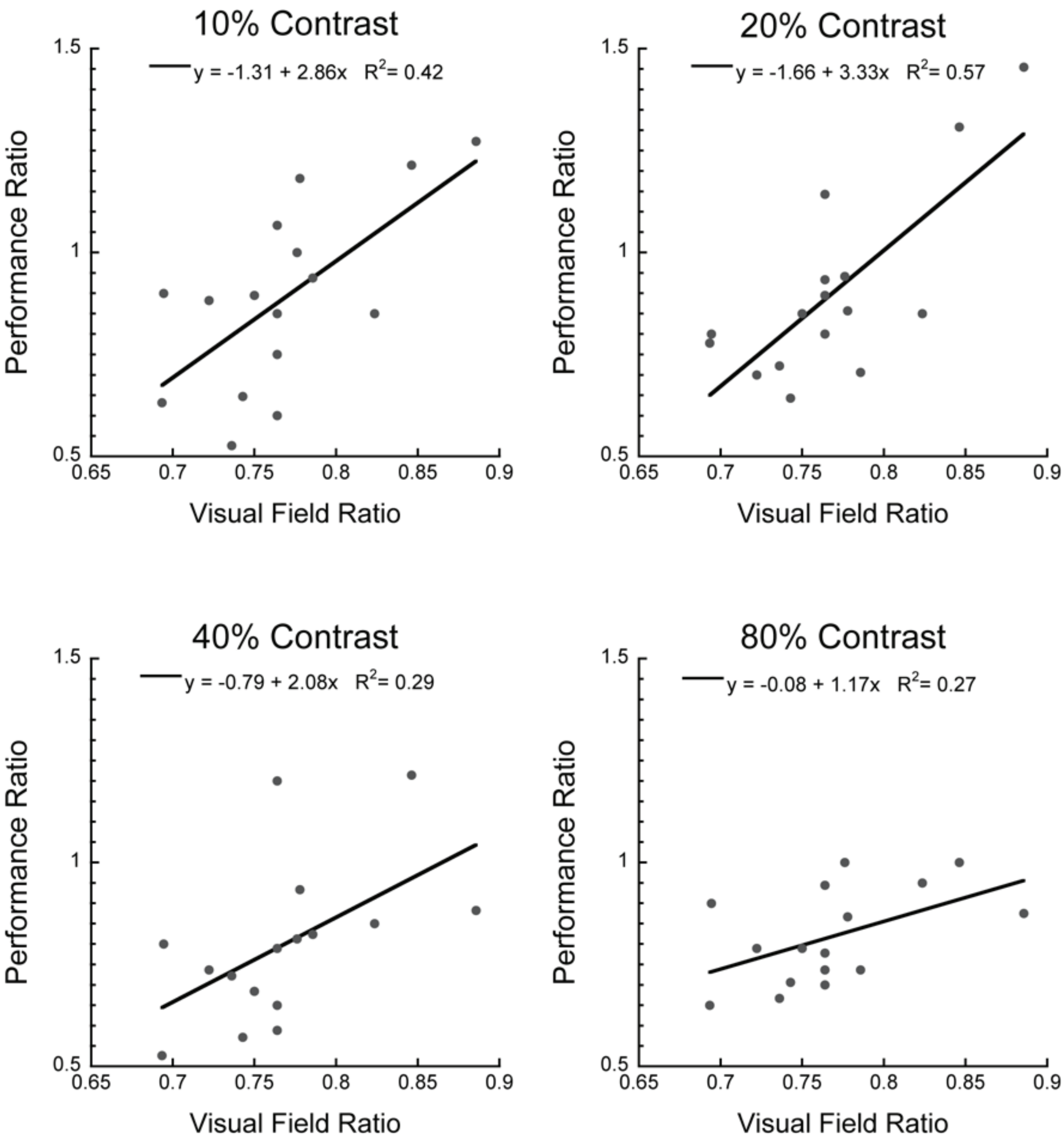

Figure 31. Visual field asymmetries predict magnitude of perceptual asymmetry across contrast levels. Performance asymmetry for the crowded conditions at 20° locations plotted versus visual field ratios for each grating contrast level. Each data point represents one participant. Solid black lines indicate linear regression.

conditions by dividing the percent correct in the upper visual field at 20º eccentricity by the percent correct in the lower visual field at the same eccentricity. Thus, this score reflects how much worse participants performed when target gratings in the crowded condition were presented in the upper visual field than the lower visual field. A mean performance index was calculated by averaging the performance ratios across the four grating contrast levels. We then created a corresponding visual field ratio by dividing each participant's upper visual field extent by their lower visual field extent in degrees of visual angle. Thus, this measure reflects how much smaller each participant's upper visual field extent was relative to their lower visual field extent. Figure 30 shows that the magnitude of the visual field ratio predicts the mean performance ratio. Pearson's R were used to assess the strength of the correlation between these two factors as the results of the Kolmogorov-Smirnov test showed that scores for both factors were normally distributed, $K\text{-}S = 0.18$, $p = 0.20$. Results showed a significant correlation between the visual field ratio and the mean performance ratio, $R = 0.74$, $p = 0.001$.

The relationship between asymmetries in visual field extent and performance in the crowded condition was further tested by examining the correlation at each grating contrast level to ensure that the previous results were not due to averaging across grating contrast. Figure 31 shows the relationship between the visual field ratio and the performance ratios at each grating contrast level separately. As with the mean performance ratio, significant correlations were found between the performance ratios and the visual field ratio at each grating contrast tested (10% Contrast: $R = 0.65$, $p = 0.006$; 20% Contrast: $R = 0.76$, $p = 0.001$; 40% Contrast: $R = 0.54$, $p = 0.032$; 80% Contrast: $R = 0.51$, $p = 0.045$). Kolmogorov-Smirnov tests were calculated on the performance ratio scores at each grating contrast level. All but the scores at the 20% Contrast level were normally distributed (20% Contrast: $K\text{-}S = 0.24$, $p = 0.02$; all other $p \geq 0.20$). We therefore retested the correlations at each grating contrast level using the non-parametric Kendall's tau statistic. Results from this analysis showed that the two factors were still significantly correlated at the 20% contrast level ($\tau = 0.47$, $p = 0.014$), as were the correlations at all other contrast levels ($p < 0.03$ for all).

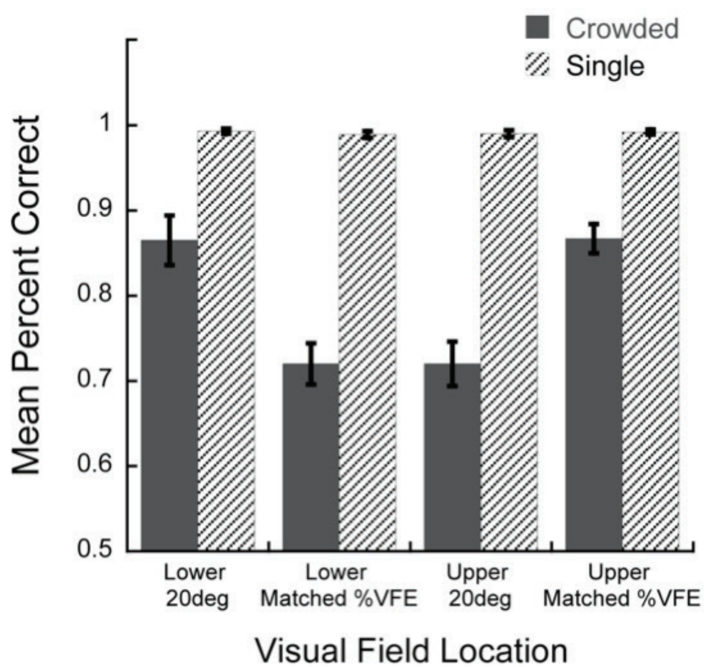

Figure 32. Performance is equated using the %VFE metric. Mean accuracy, averaged over grating contrasts, as a function of tested location. Error bars represent S.E.M.

The second prediction of the new model of visual space was that when the locations of the gratings was moved such that gratings in the upper and lower visual fields were placed at the same distance from fixation in terms of percentage of visual field extent, performance should be equated across the upper and lower visual fields. In other words, performance at the 20º eccentricities should be the same as performance in the matched conditions despite the fact that the locations of the gratings in the matched locations varied in terms of degrees of visual angle across participants with different visual field extents. Figure 32 shows the mean accuracy scores as a function of grating contrast and visual field location for the crowded condition. In order to test this prediction, two separate 2(Visual Field) x 4(Grating Contrast) repeated-measures ANOVAs were calculated on the scores for the crowded conditions only. Considering the 20º lower visual field and upper %VFE-matched locations first, results of the ANOVA showed that there was no difference in performance across the two locations (20º Lower = 86.5% and Upper Matched = 86.7%; $F < 1$, $p = 0.92$). For the 20º upper visual field and lower %VFE-matched locations, performance also did not differ across the two locations (20º Upper = 72.0% and Lower Matched = 72.0%; $F < 1$, $p = 0.98$). For both ANOVAs, no effect of grating contrast or interaction between grating contrast and visual field location was found ($p > 0.05$ for all). However, in order to further compare performance, paired-sample t-tests were calculated comparing performance across the locations at each grating contrast level. For all tests, performance was not found to be significantly different across the paired locations ($p > 0.23$ for all).

5.3. General Discussion of Experiment 10

We have shown that a new metric of retinotopic visual space based on visual field extent can account for both within- and between-participant variability in perceptual asymmetries. In addition, our findings raise the possibility that a metric based on visual field extent may account for known anisotropies in visual field representations in retinotopic cortical areas. Early visual areas contain larger representations of the horizontal than the vertical meridian (Van Essen, Newsome, & Maunsell, 1984) and larger representations of the lower compared to the upper vertical meridian (Liu, Heeger, & Carrasco, 2006; Van Essen, et al., 1984). It is of interest to determine whether re-conceptualizing spatial location based on visual field boundaries can account for these neural asymmetries in visual field representations within and between participants, as it does for perceptual asymmetries.

The model proposed here does not rule out influences of ecological factors or specialization within the visual field on perception. Rather, it suggests a missing factor in previous theories (Karim & Kojima, 2010; Previc, 1990; Skrandies, 1987), namely, that the shape of the binocular visual field is a critical influence on spatial specialization of visual processing. There are also perceptual asymmetries that are not accounted for by the current model, such as upper visual field advantages that have been reported in visual search tasks (Previc & Intraub, 1997). Multiple reference frames are utilized during perception (Robertson, 2004), and different tasks are likely to rely on different reference frames. The current model may not apply to cases involving non-retinotopic reference frames that utilize different metrics, but that is an empirical question for future research. Measuring the visual field extents of participants and matching the locations of stimuli using the %VFE metric may help to illuminate similarities and differences across various perceptual asymmetries, including the types of reference frames underlying these asymmetries. In any case, the current results demonstrate that the shape of our visual fields influences our perception of the world, both within our own visual field and across individuals.

6. General Conclusions

The general aim of the studies described in this dissertation was to explore the role that visual boundaries and visual-spatial attention play in shaping how individuals perceive their environments. As noted in the Introduction, there is not a one-to-one correspondence between visual space and physical space. Overall, the results of the current studies demonstrate that both the shape and size of an individual's visual field as well as their current attentional state significantly alter their perception of objects in an environment.

To briefly summarize the main findings, the results of Chapter 2 showed that changes in the distribution of sustained attention across regions of the visual field alter where objects are perceived. The paradigm used to assess perceived location in these studies found consistent foveal biases, such that targets were perceived to be closer to fixation that they truly were. However, as attention was focused on smaller regions of the visual field, the magnitude of the foveal bias was reduced, consistent with a perceived expansion of space within the attended region. Across eccentricity, regardless of the attention condition, a linear increase in the magnitude of the foveal bias was observed. Overall, results showed a compression of the target eccentricity of approximately 10%. Comparison of the size of the foveal bias in Experiments 1 and 3 suggests that the magnitude of foveal biases is related more to the retinal eccentricity of the targets than the relative position of the target within the aperture, and again the degree of compression was proportional to target eccentricity in all conditions.

In Chapter 3 we showed that rapid shifts in attention lead to transient distortions in the perceived shape of objects. While the experiments in this chapter focused on the perceived shape of an oval frame presented at various times relative to the cues, when coupled with previous research demonstrating similar distortions in the perceived relative locations of two vernier lines (Kosovicheva, et al., 2010; Pratt & Arnott, 2008; Pratt & Turk-Browne, 2003; Suzuki & Cavanagh, 1997), the results are consistent with the assertion that rapid shifts of involuntary attention temporarily distort the underlying structure of visual space. As a result, the perception of a single object or the relative position of multiple objects is subsequently distorted. Collectively, then, the results of Chapters 2 and 3 show that visual attention can significantly alter our spatial perception of the world. Whether this involves extended durations of focused/distributed attention or rapid shifts when involuntary attention is captured by a change in the environment, our attentional state can distort the structure of visual space.

In Chapter 4 the focus of the research shifted to examine the role that visual boundaries play in perceived location. Across three experiments we showed that the type of visual boundaries present alter how participants judge the locations of targets. When judging relative to intrinsic visual field boundaries, peripheral biases and a non-linear scaling of target locations across eccentricity were observed with both motor and verbal response types. When external boundaries are introduced, the scaling of locations changes from non-linear to linear, and in the final case where an enclosed external boundary was provided, errors switched to reveal a foveal bias. Interestingly, the magnitude of the foveal bias observed in Experiment 9 was similar to those observed in Experiment 1. Given that the same task and target locations were used in both experiments, the similarity in the pattern of responses across two different groups of participants (the first of which completed the task using an aperture placed over a computer monitor, while the second completed the task in a Goldmann perimeter) extends the generality of these findings.

Finally, in Chapter 5 we proposed a new model for retinotopic visual space in which the metric, typically based on degrees of visual angle, is replaced with a new metric based on the borders of the visual field with units of distance representing %VFE. Thus, the new metric focuses less on how far away from fixation an object appears and places the emphasis on the relative distance of that object from the edge of the visual field in a specific direction. This new metric takes into account variations in visual field extent within a given visual field as well as variations in visual field extent along a specific direction across individuals. Using a modified paradigm to test performance on a crowding task, we showed that the new metric is able to account for differences in the magnitude of performance asymmetries in the upper and lower vertical meridian across participants and well as within a given visual field. These results suggest that variations in visual field extent can alter visual-processing capabilities across the visual field. However, more research needs to be conducted to determine the extent to which these results generalize to the myriad of perceptual asymmetries reported in the literature. The new metric provides a framework with which to address this question, as well as to begin to investigate how changes in visual field extent that occur due to various visual deficits, such as retinal degeneration, alter perception in remaining parts of the visual field.

While visual-spatial attention and visual boundaries may appear to be arbitrarily identified variables of interest, the common thread between these factors becomes apparent if one considers cases in which normal visual processing is disrupted. Through various retinal diseases, such a retinitis pigmentosa or glaucoma, the visual field can become restricted and visual boundaries can be altered while visual processing in the central visual field remains reasonably intact. Alternatively, lesions resulting from stroke or cortical trauma, such as hemianopsia or quadranopsia, can also lead to visual field loss. Again, in both of these cases, part of the visual field is lost, while vision in other regions is left intact. Research on visual field loss, particularly on peripheral visual field loss from retinitis pigmentosa, has shown that loss of part but not all of the peripheral visual field can lead to a myriad of difficulties completing tasks of daily living, including basic orientation and mobility skills, as well as navigating through novel environments (Fortenbaugh, Hicks, Hao, & Turano, 2006; Fortenbaugh, et al., 2007; Fortenbaugh, Hicks, Hao, & Turano, 2008; Haymes, Guest, Heyes, & Johnston, 1996; Kuyk, Elliott, Biehl, & Fuhr, 1996; Long, Rieser, & Hill, 1990; Marron & Bailey, 1982; Turano, Geruschat, & Stahl, 1998; Turano, Geruschat, Stahl, & Massof, 1999; Turano, Massof, & Quigley, 2002; Turano, Rubin, & Quigley, 1999). Lesions occurring in more parietal and temporal cortical regions can also lead to syndromes such as visual neglect, which is characterized by deficits in attending to regions of space and can be thought of as representing an attentional field loss. While visual neglect is not a primary visual deficit, in that individuals with visual neglect are able under certain conditions to perceive objects presented in the neglected regions of their visual field, under other conditions individuals with visual neglect will perform as if they are functionally blind in the neglected regions, failing to detect objects presented there (List, et al., 2008; Robertson, 2004). Visual neglect can also lead to distortions in the perception of objects that are detected. In particular, line bisection is a task that is often used to assess visual neglect in clinical populations (Marika & Paolo, 2008; Milner, Harvey, Roberts, & Forster, 1993), and patients with visual neglect often demonstrate large biases in their perceived location of the midpoint of lines. Recent research in neurologically intact participants has shown that changes in attention due to involuntary cues can mimic the biases in line bisection tasks observed in patients with visual neglect, although these biases are reduced in magnitude (Toba, et al., 2011).

Given the many difficulties faced by individuals with visual or attentional field losses, there is a need to understand how loss or disruption of vision in part of the visual field alters visual processing in the remaining intact regions. Such information is invaluable for not only understanding how deficits arise in more complex tasks, such as navigation, but also for the development of better rehabilitation protocols to help individuals with these deficits maximize remaining visual processing capabilities. Having a better understanding of the factors that alter space perception and spatial localization is critical to achieving this goal. For example, as found in Chapter 4, the type of boundaries present in a task can lead to changes in the type of biases observed in peripheral localization. Failure to account for differences in experimental set-ups or task conditions can lead to errors in interpreting the results across different studies. An example of this can be found in a recent study by Wittich and colleagues (2011). In this study the authors sought to investigate spatial localization in patients with peripheral field loss from retinitis pigmentosa (RP). In the review of the literature they note two studies in particular. The first, by Turano (1991), was a computer-based bisection judgment task in which patients judged whether a middle bar was located closer to one of two flanker bars presented above or below the middle bar. Results showed either no bias or a foveal bias. That is, the RP patients misjudged the middle of the interval defined by the two flanking bars as being closer to fixation than it really was. The second experiment was the study Temme et al. (1985), the basis for the experiments presented in Chapter 4, which involved presentation of a single dot in a Goldmann perimeter at 10º intervals across the visual field along the cardinal and oblique axes. Participants were required to judge how far out the targets were located, relative to their perceived visual field extent. Here, participants showed a peripheral bias. That is, they overestimated the eccentricity of the targets, and the RP patients showed a larger peripheral bias than the normal-vision controls. While Wittich et al. (2011) based their predictions that their patients would show a peripheral bias on the results of Temme et al. (1985), their task was a bisection task similar to that used by Turano (1991). The results failed to match the predictions (i.e., no peripheral bias was found), and the reasons for this are understandable if one considers differences in the approaches. First, two different frames of reference are used in these tasks. In the study by Temme et al. (1985), participants made judgments within the frame of reference of their visual fields, an egocentric task. In the study by Turano (1991), participants made judgments in an object-centered reference frame where the object was defined by a region bounded by the top and bottom flankers. Given this difference in reference frames, it is likely that there will be differences in the nature of the spaces defined within these reference frames. In the task by Temme et al. (1985), space is bounded by the edges of the visual field in all directions. In contrast, in the study by Turano (1991), space is bounded first by the edges of the computer monitor and then by the edge of the flankers which define the region in which the bisection judgment is made. Based on the findings from Chapter 4, one would expect that even participants with normal vision would show differing biases across these two tasks, because they are employing two different reference frames and metrics. Thus, failure to consider factors such as the visual boundaries present in an experimental set-up or the attentional demand of a task may lead to inconsistent or inconclusive results across studies.

To conclude, the work presented in this dissertation provides evidence for the important roles that both visual boundaries and attentional states play in determining where objects are perceived and how visual processing occurs across the visual field. Though limited to just two of many possible factors, the present work suggests that further empirical studies that attempt to model the underlying structure of visual space will aid our understanding of the many mappings of visual space. The lack of a one-to-one mapping of external space onto visual space should not be seen as an impediment to understanding space perception in the visual domain. Rather, the flexible nature with which we represent space should be seen as a testament to a fundamental way in which the visual system has developed in order to adapt to the complex ways in which we interact with our environments.

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