Perceptual Organization across Retinal Eccentricity

by

Teresa M. Tannazzo

A dissertation submitted to the Graduate Faculty in Psychology in partial
fulfillment of the requirements for the degree of Doctor of Philosophy,
The City University of New York

2008

ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

This manuscript has been read and accepted for the
Graduate Faculty in Psychology in satisfaction of the
dissertation requirement for the degree of Doctor of Philosophy.

Daniel D. Kurylo, Ph.D.

Date Chair of Examining Committee

Joseph Glick, Ph.D.

Date Executive Officer

Frank Grasso, Ph.D.

Aaron Kozbelt, Ph.D.

Karen Ackroff, Ph.D.

Maria Pagano, Ph.D.
Supervisory Committee

THE CITY UNIVERSITY OF NEW YORK

Abstract

PERCEPTUAL ORGANIZATION ACROSS RETINAL ECCENTRICITY

by

Teresa M. Tannazzo

Advisor: Daniel D. Kurylo, Ph.D.

Across all levels of visual processing, from retinal to extra-striate cortex, central visual areas are allocated more cells for processing than peripheral visual areas, producing a reduction in a variety of perceptual capacities for increased eccentricity. This effect has not been explored for perceptual organization. An examination was made here of perceptual organization of stimuli oriented across retinal positions. Four stimulus features were tested across five retinal eccentricities ranging from 0 to 60 degrees. The stimulus features tested were luminance, motion, orientation, and proximity. The size and spacing of stimulus elements were also manipulated. Participants viewed visual patterns that could be perceptually organized into either vertical or horizontal lines. Threshold measurements were obtained through psychophysical techniques while participants fixated different points eccentric to the stimulus. For all stimulus features, no differences existed in thresholds obtained from eccentricities between 0 and 23 degrees. Beyond 23 degrees eccentricity, the features showed different patterns of decline in perceptual capacities. Results do not correspond to cortical magnification factors, found for many other perceptual functions. Results also do not correspond to homogeneous sensitivity, or binocular/monocular distinctions. Instead, perceptual organization follows a unique pattern of functional decline across eccentricity, varying relative to the stimulus feature upon which perceptual organization is based.

Table of Contents

List of Tables

List of Figures

Introduction

Chapter 1. Retinotopic organization and cortical magnification in the visual system

The nervous system's representation of stimuli changes with increasing retinal eccentricity which results in corresponding changes in perceptual abilities. Generally, as one moves away from representations of central vision, fewer neurons are involved in processing. This organization is found at many levels of the visual system, from the earliest retinal areas to higher cortical regions.

Retina

The first representation of the visual world in the nervous system takes place at the photoreceptor layer of the retina. It is here that distortions in the representation of the visual scene are first observed. In the retina, distortions across eccentricity occur in the density of neurons as well as the convergence of one layer of cells onto the next. The distribution of photoreceptors in the retina is not homogeneous. There are more photoreceptors devoted to representing the central vision areas then peripheral areas. The fovea has more than twice as many cones than areas just 3 mm more eccentric (Rodieck, 1998). Conversely, the peripheral areas contain more rods than the central areas, but the overall density of receptors is still less in non-foveal areas.

Photoreceptors synapse with retinal bipolar cells. There is no convergence of photoreceptor signals onto bipolar cells for those serving foveal areas (Rodieck, 1998). Similarly, there is little convergence of bipolar cells signals onto retinal ganglion cells (Rodieck, 1998). But distortions occur in the representation of the visual field at this stage of retinal processing. Many more ganglion cells are devoted to processing foveal stimuli than peripheral stimuli. The density of ganglion cells is greatest between three and six degrees from the fovea (Adams & Horton, 2003). Also, there are more ganglion cells serving the central 3 degrees of the visual field than there are receptors (Sjöstrand, Osson, Popovic, & Conradi, 1999). This suggests the representation associated with the central visual area is being enhanced or magnified by the ganglion cells.

In contrast to the fovea, the signals from the peripheral areas of the retina converge much more as they are processed by the nervous system. For example, in peripheral retina 15 - 50 photoreceptors converge onto a single bipolar cell (Rodieck, 1998). The consequence of this arrangement is that there are many more receptors than bipolar cells serving this area of the visual field. Also, at 19 degrees from the fovea, there is approximately one ganglion cell for every 2 receptors (Sjöstrand et al., 1999). Because receptors are least abundant, there is a loss of spatial information from peripheral areas creating a distortion in the representation at later visual stages of processing.

LGN

The first area of the brain that most ganglion cells (approximately 90%) synapse is in a small area in the thalamus, known as the lateral geniculate nucleus (LGN). Using fMRI scans of human participants, Chen, Zhu, Thulborn, and Ugurbil (1999) have shown the LGN is retinotopically organized. They found a comparable spatial layout in the thalamic representation of visual space as there is in the retina. Specifically, stimulation in the lower visual field activates the superior area of the contralateral LGN. Likewise, visual stimulation in the upper visual field leads to activity in inferior regions of the LGN.

There seems to be very little, if any, distortion of the representation at the LGN. This is based primarily on the fact that the number of cells in the LGN is approximately equal to the known number of ganglion cells projecting into this area (Schein & de Monasterio, 1987).

Area V1

After the LGN, the next step in visual processing is the primary visual cortex, V1. The first map of the brain was made of primary visual cortex by Inouye in 1909 (from Adams & Horton, 2003). Using a participant with cortical damage from a gunshot wound, Inouye mapped the person's visual field deficits. Comparing the cortical lesions with the visual field deficits allowed him to create the first map of area V1. It was established then that the layout of primary visual cortex, like the LGN, is retinotopic.

V1 in humans is an area approximately 4 by 8 cm located at the posterior portion of the occipital lobe. V1 includes and straddles the calcarine fissure. As a stimulus moves in the visual field from the fovea to the peripheral visual field, it activates the posterior most area of V1 and moves to more anterior regions (Wandell, 1999). The horizontal meridian of the visual field is represented at the calcarine fissure. Stimuli in the lower visual field activate cells in the dorsal area of V1, while the ventral side is stimulated by stimuli in the upper visual field (Engel, Glover, & Wandell, 1997; Wandell, 1999). Organization similar to human primary visual cortex has been demonstrated in a variety of animals including the macaque monkey (Azzopardi, Jones, & Cowey, 1999; Tootell, Switkes, Silverman, & Hamilton, 1988), the marmoset monkey (Schielssl & McLoughlin, 2003), the Cebus monkey (Gattass, Sousa, & Rosa, 1987), the hooded rat (Espinoza & Thomas, 1983), and the mouse (Schuett, Bonhoeffer, & Hϋbner, 2002; Wagor, Mangini, & Pearlman, 1980).

Further studies have shown that although the representation in the human cortex is similar to that of the retina, it is not identical. There is a magnification in the representation of the central vision areas in the cortex (Adams & Horton, 2003). Larger areas, and therefore more neurons, are devoted to processing visual information from the central portion of the visual field as compared to the outer visual field. This amplification is known as cortical magnification. Comparing the size of the cortical area to the number of retinal ganglion cells reveals that there is a larger percentage of V1 area than ganglion cells until 20 degrees from the fovea. After 20 degrees eccentric, there is a higher percent of ganglion cells than V1 area.

In general, the cortical magnification of a stimulus decreases as the representation becomes more peripheral (Adams & Horton, 2003; Horton & Hoyt, 1991; Popovic & Sjöstrand, 2001). For example, a stimulus in the center of the visual field is represented in a large percent of V1 and as it becomes more peripheral it is represented on a smaller percent of V1. According to Horton and Hoyt (1991), the central 1 degree of the visual field represents 10% of V1 area, the central 24 degrees of the visual field represents 80% of V1, and the central 30 degrees covers 83% of V1.

However, the cortical representation in V1 not only magnifies the original pattern, but it distorts it as well (Adams & Horton, 2003). The warping of the cortical representation is such that one side of the representation may be magnified more than another. The result is that a perfect square in the visual field may be represented as a rectangle on the surface of V1. The details of the distortion depend upon where in visual field the stimulus originated. Also, regardless of its direction from the fovea, the amount of cortical surface serving 1 deg^2 of visual field is relatively constant at a given eccentricity.

Area V2

Secondary visual cortex (area V2) surrounds V1 and is the next step in the visual pathway. V2 is smaller than V1 (only 1 by 8 cm) and receives most of its input from the ipsilateral V1. V2 is in some ways a mirror image of the representation in V1 and like earlier visual areas, V2 is also retinotopically organized. The dorsal side of V2, like the dorsal side of V1, represents the lower visual field. But, as the stimulus moves to a horizontal position in the visual field the representation becomes more dorsal in dorsal V2, unlike the representation in V1 (Wandell, 1999).

The retinotopic organization in V2 is less precise than V1, possibly due to larger receptive fields found in V2 areas (Gattass, Gross, & Sandell, 1981). However, Gattass et al. (1999) found that the cortical magnification of the visual field in V2 is not significantly different than that of V1. Again, the representation of central visual field is magnified relative to the periphery.

Area V3

V3 borders V2 in the cortex and is similar in size. In some ways V3 appears to be divided into two distinct regions separated by a few millimeters, isolating the area into distinct dorsal and ventral portions (Fize, Vanduffel, Nelissen, Denys, Chef d'Hotel, Faugeras, et al., 2003; Gattass, Sousa & Gross, 1988). In the macaque, ventral V3 represents the central 35 degrees of the upper visual field, while dorsal V3 is dedicated to the central 40 degrees of the lower visual field (Gattass et al., 1988).

The retinotopic organization of V3 is not as obvious as that of earlier visual areas, with the organization in dorsal V3 being more variable and erratic than that of the ventral area. Again, like V2, this loss of precision with the retinotopic organization may be due to the large receptive field sizes with increasing eccentricity in V3. The retinotopic mapping of V3 also shows distortions of the representation similar to earlier cortical vision areas. In general, one degree of central vision is represented in a larger percent of V3 than one degree of peripheral vision (Gattass et al., 1988). Furthermore, Wandell (1999) refers to an additional area, V3A that is adjacent to dorsal V3. Area V3A represents the entire half of the visual field and is retinotopically organized.

Using optical imaging, Lyon, Xu, Casagrande, Stefansic, Shima, and Kaas (2002) found that area V3 is also retinotopically organized in the cortices of owl monkeys. Specifically, the dorsal side of area V3 is a mirror image of dorsal V2, only about half its width. Lyon et al. (2002) verifies that dorsal V3 represents the lower visual field with the horizontal meridian being represented along the V2 and V3 border. Central vision is represented in lateral regions of V3. The V3 representation is a compressed version of that in V2, confirmed by the fact that a stimulus activates a smaller area of V3 than V2 (Lyon et al., 2002).

Area V4

Another cortical area anterior to area V3 is also involved in visual processing and has been labeled V4. V4 extends for 5 - 8 mm in the macaque monkey and represents approximately 35 - 40 degrees of the visual field. Like V3, the upper visual field is represented in the ventral side of V4, while the lower visual field is dorsal for the central 5 degrees of the visual field. The visual field beyond 5 degrees eccentric is represented on the ventral side of V4 near the anterior border (Gattass et al., 1988).

Like V3, the representation of the central visual field in V4 is magnified relative to the periphery. There is a clear distortion in the cortical representation by V4 with central vision represented by an elongated strip of cortex rather than a circular region (Gattass et al., 1988). Furthermore, there is no significant difference between the cortical magnification factors of V3 and V4.

Higher Visual Areas

Using functional magnetic resonance imaging with awake rhesus monkeys, Fize et al. (2003) confirm a similar retinotopic organization in monkey cortex as previous studies with human participants for areas V1, V2, V3, and ventral V4. However, the study does find a difference between monkey and human brains in the organization of dorsal area V4.

In macaque monkeys, the superior temporal sulcus (STS) is involved in motion perception. It includes other motion areas, such as the middle temporal area (MT) and medial superior temporal area (MST). It has been established that both MT and MST are both organized retinotopically although MST has a much more poorly defined retinotopic representation (van Essen, 1987). Another distinction between these sub-regions is that MST has much larger receptive fields, often extending into the ipsilateral visual field which may account for its lack of retinotopic organization.

The equivalent area to monkey STS in human cortex has been called MT+, V5, or ITS (inferior temporal sulcus). The human equivalent to the monkey's MT sub-region has been identified in humans using fMRI experiments. The MT area responds strongly to rotating wedge stimuli indicating small receptive fields and is also shown to be highly orderly in retinotopic organization (Huk, Dougherty, & Heeger, 2002). Another sub-region of MT+ has been identified as corresponding to monkey MST. This area is anterior and dorsal to MT and usually within 5mm of MT (Huk et al., 2002). MST is identified by its strong response to peripheral, ipsilateral stimuli and a lack of coherent responding to retinotopically organized stimuli.

MT and MST are on opposite sides of ITS. MT is approximately 243 mm^2, while MST is estimated to be much smaller (approximately 83 mm^2). The central visual field is largely represented in ventral MT and ventral MST. The peripheral visual field comprises a smaller representation in the dorsal portions, particularly of MT. MST is subject to more noise due to the large size of the receptive fields that often include both central and peripheral visual field areas.

Area V5 is the last cortical area for which there is evidence of retinotopic organization. Studies on areas V6 and V6a have revealed no evidence for retinotopic organization (Dechent & Fram, 2003; Galletti, Fattori, Kutz, & Gamberini, 1999).

In conclusion, it has been established that retinotopic organization is the norm from the retina to area V5 of visual cortex. This organization is evidence that the spatial relationships between visual stimuli are preserved during early processing. However, there is considerable evidence that the representations are not the same as the physical world, but are distorted. The distortions are such that foveal stimuli are allocated considerably more area for processing than peripheral stimuli.

Chapter 2. Perceptual abilities across retinal eccentricity

Differences in retinal anatomy and physiology, as well as differences in cortical magnification, result in differences in perceptual abilities across retinal eccentricity. While viewing images, observers normally position their eyes such that the image falls on the fovea. The fovea is specialized to differentiate fine detail and therefore provides the best acuity of the entire retina. Peripheral retina handles the image quite differently, alerting the viewer of events and objects outside the fovea. Differences in neural representations between central and peripheral viewing result in perceptual differences in both basic and high-order visual functions.

Perceptual abilities are measured in several manners. Commonly, abilities are measured in terms of detection and discrimination. Detection is the ability to observe the presence of an object, and is typically measured as a threshold, or sensitivity. Discrimination is identifying what category the object belongs to. Another common measure of perceptual ability is speed of processing.

For most perceptual measurements, acuity is a factor that must be taken into account. Because acuity may confound performance measures, size-scaling may be used to eliminate this effect. Similarly, luminance and contrast changes across retinal eccentricity may influence other performance measurements, and therefore should also be accounted for with perceptual measurements.

Perceptual functions can be divided into “basic” and “high-order” functions. Basic functions are typically associated with early visual processing whereas high-order functions are associated with later processing. The basic functions are the foundation for later processing.

Basic functions

The low-level, basic functions consist of the first visual processes performed by the nervous system and include such processes as light detection, acuity, depth perception, and letter detection.

Luminance

Light entering the pupil eccentrically appears less bright than light entering from the center of the pupil, known as the Stiles-Crawford effect (Graham, 1965; Levine, 2000). The Stiles-Crawford effect is due to the directional selectivity of the cones. Cones capture more light that enters from the center of the pupil than from outer areas. Foveal cones are 80% less sensitive to light that enters the eye from near the edge of the pupil than from in the center of the pupil (Rodieck, 1998).

Wald (1945, in Graham, 1965) investigated the ability to detect 1 degree circular patches at the fovea and 8 degrees above the fovea. He found that detection thresholds were lower for the fovea than in the periphery, except with very long wavelength stimuli (above 625nm). Wald also found that the periphery area is most sensitive to a different wavelength of light than in the fovea (500nm and 560nm respectively). The stimuli in the fovea appear colored, but not in the periphery.

Lateral Facilitation

Under certain circumstances it is possible to enhance detection by additional, separate stimuli that surround the target to be detected (Stettler, Das, Bennett, & Gilbert 2002). This propensity is known as lateral facilitation by flankers. Giorgi, Soong, Woods, and Peli (2004) studied lateral facilitation across different retinal eccentricities. They found that no lateral facilitation occurs at 12 degrees from the fovea. Also, detection for targets up to 6 degree eccentric is facilitated less by flankers than foveal vision. And, the flankers that best facilitate detection are different for centrally viewed and peripherally viewed stimuli. Central targets are facilitated best by flankers that are closer to the target than in the periphery. The closer flankers do not facilitate targets in the periphery at all. Also, changing the psychophysical procedure from a spatial two alternative forced choice (2AFC) method to a temporal 2AFC procedure eliminated any lateral facilitation in peripheral vision. Clearly lateral facilitation is processed differently in central and peripheral vision.

Acuity

Acuity changes with retinal eccentricity. At only 5 minutes of arc from the fovea, there is a noticeable difference in visual acuity. At 10 minarc there is a 25% loss in visual acuity and a 40% loss by 20 minarc (Riggs, 1965). Virsu, Näsänen, & Osmoviita (1987) provide evidence that for different types of acuity measures, peripheral performance can be equated to foveal performance by magnifying stimuli in the periphery.

Numerosity

Another visual ability affected by retinal eccentricity is numerosity. Numerosity is the ability to identify quantity with briefly presented stimuli. Using high contrast dots of varying spatial frequencies, Parth & Rentschler (1984) found that numerosity performance decreases with increasing eccentricity. But when the size of the stimuli is scaled in accordance with cortical magnification factor, any differences in numerosity between central and eccentric viewing are eliminated. However, even with scaled dots, equating the overall luminance of the stimuli reduces the performance in the periphery but not in the fovea. This suggests performance in the periphery relies on luminance cues but performance in central viewing is dependent upon other cues.

Stereopsis

Stereopsis is another visual ability affected by changes in retinal eccentricity. Stereopsis is the ability to see disparities in the images of the two eyes which give cues to depth perception. Prince and Rogers (1998) looked at stereopsis performance with suprathreshold luminance dots across different retinal eccentricities. The spatial frequency of best sensitivity was found to change with eccentricity. More eccentrically presented stimuli show better performance at lower spatial frequencies. For example, with 21 degree viewing the best stereo sensitivity was with stimuli of 0.06 cy/deg, and for viewing at 3.5 degrees the best sensitivity was with 0.30 cy/deg stimuli. Overall stereopsis ability decreased as eccentricity increased. When data were scaled according to the cortical magnification factor the frequency of best sensitivity became the same for both peripheral and central viewing, but, absolute sensitivity still decreased with increasing eccentricity.

Line detection

Line detection is a basic function also affected by retinal eccentricity. Carrasco, McElree, Denisova, and Giordano (2003) found that discriminating between lines tilted to the left or the right is 87 msec faster when viewed eccentrically at 9 degrees than at 4 degrees. When the stimuli are size magnified according to the cortical magnification factor, the difference in speed between 4 and 9 degrees reduces to 47 msec. One possible explanation for this finding is that the more cortical area involved in the processing requires more time for integrating the information.

It has also been shown that orientation discrimination in the periphery depends on contrast levels (Sally & Gurnsey, 2003, 2004). Performance declines faster with increasing retinal eccentricity when stimuli are well above threshold contrast levels than when contrasts are close to threshold.

Another ability affected by retinal eccentricity is sensitivity to oblique lines. The phenomenon of decreased sensitivity to lines rotated away from the horizontal or vertical meridian (oblique lines) is known as the oblique effect. Westheimer (2003) tested the oblique effect at 20 degrees from the fovea. He found that the oblique effect does exist in the periphery as the best thresholds were observed for vertical and horizontal stimuli. Westheimer (2003) also found slightly better thresholds for stimuli whose orientations were in line with radiating from the fovea (i.e., a 45 degree stimulus in left visual field and 135 degrees in right).

Vernier offset is another visual ability that is changed by peripheral viewing. Vernier offset is tested with two lines aligned with a slight offset. Harris and Fahle (1996) found differences with eccentricity in both the detection of vernier offset and in the discrimination of the direction of the offset. For stimuli aligned in a vertical line, detection and discrimination thresholds increased with increasing eccentricity at the same rate which may be attributable to cortical magnification. But, for stimuli that were oblique, randomly to the left or the right of vertical, as eccentricity increased, detection performance changes more than discrimination. Unlike in the fovea, by 10 degrees eccentric, detection is better than discrimination performance with variable orientated oblique lines.

Letter detection

Letter detection and discrimination is also affected by retinal eccentricity. Higgins, Arditi, and Knoblauch (1996) found that size scaling was enough to normalize peripheral (up to 7.5 degrees) detection and identification of mirror imaged letters to central foveal levels. Melmoth and Rovamo (2003) found that increasing eccentricity to 10 degrees from the fovea reduces sensitivity to letters. Generally, sensitivity increases as a function of letter size for all eccentricities, but then saturates and decreases for the very large sizes. Increasing the number of possible letters to discriminate decreases discrimination but does not affect detection. In addition, contrast scaling is more important than size scaling to equating peripheral vision performance with central vision.

Williams (1984) asked participants to identify letters at eccentricities up to 5 degrees. They used stimuli not scaled for size. When participants were detecting letters from a large set size (24 letters) they were about 10% less accurate and about 200 msec slower than when detection was from a much smaller set size (2 letters). With increasing eccentricity participants were about 40% less accurate and about 200 msec slower than their performance in the fovea. Also, Williams (1984) found that performance was better and faster for stimuli presented either to the left or the right of the fovea than above and below. He also found that there was is slight increase in performance for letters presented in the right visual field than the left, possibly due to the verbal nature of the stimuli. There was no interaction between load and eccentricity.

Anderson and Thibos (2004) found that for stimuli 30 degrees from the fovea, spatial frequencies between 0 and 1.25 cycle/letter are most important for letter discrimination. These low spatial frequencies made the biggest decrement in performance at this eccentricity.

Similarly, Näsänen and O'Leary (1998) measured contrast thresholds and recognition of hand-written digits presented at 0, 5, 10, and 20 degrees eccentric. The stimuli were size-scaled based on cortical magnification and were of different spatial frequencies. At all eccentricities, thresholds were lowest for medium spatial frequency stimuli. For high spatial frequency stimuli, peripheral performance (contrast thresholds and recognition) was nearly equal to foveal performance. With the low spatial frequency stimuli, peripheral performance was significantly below that of foveal performance.

Localization

Visual localization is another ability affected by retinal eccentricity. Bock (1993) found that when peripherally viewing targets, the location of eccentric targets is increasingly overestimated with escalating eccentricity. When an object was presented 2 degrees eccentric, estimates of its location were overestimated by more than 0.5 degree. With an increased eccentricity of the object to 10 degrees from the fovea, localization estimates were overestimated by more than 1.25 degrees.

Motion

Sensitivity to motion is another ability affected by retinal eccentricity. Movement thresholds are higher in the periphery than in the fovea (Graham, 1965). The threshold for foveal viewing is 54 arcsec/sec, whereas at 9 degrees eccentric thresholds rise to 18 minarc/sec. Also, the minimum threshold of displacement perceived as motion increases with increasing retinal eccentricity (Gordon, 1947 in Graham, 1965).

Another visual ability that is affected by peripheral viewing is coherent motion detection. Coherent motion detection is the perception of a group of independent lights flashed sequentially as a single, moving light. A study by van de Grind, van Doorn, and Koenderink (1983) examined coherent movement detection at eccentricities between 0 and 48 degrees in the temporal (outside) visual field. They found that the highest velocity perceived as coherently moving was independent of eccentricity when stimuli were scaled according to cortical magnification factor. However, the velocity of best performance increased linearly, regardless of stimulus size. The velocity of best performance changed from 1deg/sec in the fovea to 8deg/sec at 48 degrees, suggesting the eccentric motion detectors are tuned for different speeds.

The highest frequency at which a light can pulsate and still be perceived as flickering is known as the critical flicker frequency (CFF). At high luminance levels, CFF decreases as viewing goes from the fovea toward the periphery. However, at low luminance levels, CFF increases as viewing goes from the fovea toward the periphery (Brown, 1965).

In sum, for most basic visual functions performance is better in the fovea than in the periphery. Some studies have tried to control for cortical magnification by scaling stimuli. For some functions scaling equates performance between the fovea and the periphery, but for others this is not enough.

High-order functions

The high-order functions consist of the visual processes that occur later in processing, after basic functions have been performed. Some high-order visual functions are word discrimination and face perception.

Word discrimination

Word discrimination is a high-order function in which performance is affected by retinal eccentricity. Lee, Legge, and Ortiz (2003) found that peripherally viewing words 10 degrees in the lower visual field decreases the accuracy of identifying words as compared to foveal viewing. The decrease in performance is shown even when attempting to compensate for cortical magnification by using larger letters in the periphery (3.5 degree stimuli instead of 0.5 degree). Furthermore, this effect can be made more dramatic by identifying longer words. It may be that lexical processing in peripheral areas is similar to that in the central visual field, although processed more slowly.

Face Perception

Another function affected by retinal eccentricity is face perception. Mäkelä, Näsänen, Rovamo, and Melmoth (2001) measured contrast sensitivity to faces at different eccentricities up to 10 degrees from the fovea. They found that sensitivity is about 1.75 times better in the fovea than at all other eccentricities. For equivalent performance in the fovea and peripheral vision both size and contrast needed to increase in the periphery when measuring contrast sensitivities for face perception. At all eccentricities, sensitivity increased with stimuli size but saturated. Peripheral performance with low contrast stimuli (contrasts less than 3%) cannot be equated to foveal performance.

Natural Scenes

Thorpe, Gegenfurtener, Farbe-Thorpe, and Bulthoff (2001), using natural scenes, asked participants to detect if an animal was present in the scene. Without size scaling the stimuli, they found a linear decrease in performance with increasing eccentricity. Accuracy ranged from 93.3% at the fovea to 60.4% accuracy at 70.5degrees eccentric. No difference was found between the left and right visual fields.

Biological Motion

Detection of biological motion is another high-order visual ability that is affected by retinal eccentricity. Biological motion refers to the perceptual phenomenon of perceiving an animate biological individual from just a few, strategically placed, moving points of light. Ikeda, Blake, and Watanabe (2005) studied biological motion perception at 1, 4, and 12 degrees, using 7 stimuli sizes (0.5-16 degrees). In general, they found better performance with larger stimuli. Even magnifying stimuli for eccentric targets could not equate peripheral performance to that of the fovea. This difficult task requires not just seeing the motion but integrating it.

Subjective Contours

There is a decrease in identifying contour paths in the peripheral visual field. Hess and Dakin (1997) found that the fovea has superior performance in this task when compared to performance just 10 degrees eccentric. Furthermore, there is no difference between performance at 10 degrees and 30 degrees eccentric. Scaling the size of the stimuli by factor of 8 also made no difference in performance.

Performance is better in the fovea than in the periphery for all high-order visual functions. Even after controlling for cortical magnification by scaling stimuli, performance between the fovea and the periphery does not equate for these functions.

Conclusion

Research has shown that performance on most basic and high-order tasks declines with increasing eccentricity in the visual field. However, there is evidence that some perceptual abilities, including coherent motion detection, are aided by shifting towards more peripheral vision. Table 1 summarizes the findings of the studies in this review. Although not all studies attempted to control for cortical magnification factors, these studies show that many of the basic visual functions can be improved with scaling, whereas there is no evidence for scaling equating peripheral performance to foveal levels for high-order functions.

What is lacking from this body of research is how performance on intermediate tasks, such as perceptual organization, is affected by retinal eccentricity. It is important to understand the affect of retinal eccentricity on early visual functions because they are a necessary first step in the processing of subsequent functions. In this regard, it is impossible to understand high-order abilities completely without understanding processing at the intermediate and basic levels. Changes in high-order perceptual abilities may simply be influenced by differences at subordinate intermediate- or low- level functions that feed into the higher order processing. Before proposing how this may be explored, a review will be made of literature on the perceptual and physiological basis of perceptual organization.

Table 1: Summary of Perceptual Performance

Visual Function	**Foveal Advantage**	**Equal Performance**	**Peripheral Advantage**	**Reference**
Basic				
Motion	X (high lum.)		X (low lum.)	Brown, 1965
		A		van de Grind et al., 1983
	X			Gordon, 1947
	X			Graham, 1965
Line detection			X (for time)	Carrasco et al., 2003
	X			Harris & Fahle, 1996
	X			Westheimer, 2003
	X			Sally & Gurnsey, 2003, 2004
Letter detection	X	A		Melmoth & Rovamo, 2003
	A (low S.F.)	A (high S.F.)		Näsänen & O'Leary, 1998
		A		Higgins et al., 1996
	X			Williams, 1984
Numerosity	X	A		Parth & Rentschler, 1984
Acuity		A		Virsu et al., 1987
	X			Riggs, 1965
Stereopsis	X and A			Prince & Rogers, 1998
Luminance	X			Graham, 1965
Lateral Facilitation	X			Giorgi et al., 2004
Localization	X			Bock, 1993
Higher-order				
Word Discrimination	X and A			Lee et al., 2003
Face Perception	X and A			Mäkelä et al., 2001
Subjective Contours	X and A			Hess & Dakin, 1997
Biological Motion	A			Ikeda et al., 2005
Natural Scenes	X			Thorpe et al., 2001

A: performance after stimuli were size adjusted for cortical magnification

Chapter 3. Perceptual organization

As soon as the eyes are directed at a scene the visual system begins putting together elements that belong together. The visual system organizes the scene into objects and backgrounds on the basis of simple visual characteristics. This is the process of perceptual organization, which includes all the processes that integrate local features into global shapes.

The input to the visual system is very different than what is ultimately perceived by the observer. An observer perceives separate objects, not patches of color and lines of light. The visual system sorts out which parts of the scene are associated, allowing the observer to perceive coherent objects and surfaces.

Perceptual organization is thought to be an intermediate level process, or processes, accomplished with little effort on the part of the observer. The details of these processes, however, are not fully understood. This chapter will review what is known about the original Gestalt descriptions of perceptual organization, current perceptual theories, and physiological research on where grouping takes place in the brain.

Gestalt Rules

The phenomenon of perceptual organization was studied by the Gestalt psychologists in the 1920s (for a historical account see Westheimer, 1999). They described certain “laws” of grouping, which are rules that describe how stimuli are perceived as an intact set rather than disorganized individual elements. These rules include the following:

Pragnanz – elements that create a good form are grouped as such. Although it has been difficult to precisely define what is meant by this, there is evidence that humans have a preference for shapes that show regularity and symmetry (Feldman, 2000).

Similarity – similar elements are grouped together (e.g., color, luminance, shape, size, and movement)

Good continuation – elements that form smooth extensions are grouped together

Proximity – elements spatially close together will be grouped together

Closure – elements that appeared to be closed figures are grouped together

Common region – elements that are enclosed in an area by lines or color are grouped together (more recently described by Palmer, 1992)

Connectedness – elements connected by a line are grouped together (Palmer & Rock, 1994)

Before the Gestalt movement, psychologists believed perceptions were dictated strictly by sensations. However, their laws have been criticized for only being a description for perception. They did not provide a predictable theory for how stimuli will be perceived that could be investigated experimentally. What remained in question were the mechanisms that govern how elements are grouped together, and how it is decided that forms include some elements and not others. Since the Gestalt movement, psychologists have learned more about perceptual organization and its underlying processes in the nervous system. The laws of grouping have recently inspired experimental research on perceptual organization and how it is accomplished by the nervous system.

Perceptual Theories

It is now accepted that prior knowledge and information about the world plays a role in the interpretation and perception of sensory data (Kimchi & Hadad 2002; Palmer, 1975). Even the presence of other informative stimuli will change percepts (Tadin, Lappin, Blake, & Grossman, 2002). Having organization and a frame of reference leads to the creation of relationships among features and allows the features to be represented more accurately. One question that still remains is exactly when perceptual organization occurs and how much is it influenced by prior experience.

There are many theories designed to encompass what known about perceptual grouping phenomenon. Such theories are similar, varying in their details. Some have been an attempt to quantify the nature of perceptual organization with mathematical models (Ben-Av & Sagi, 1995; Kubovy & Wagemans, 1995; Palmer, 1983). Others are more elaborate and involve bottom-up and top-down visual processes. The bottom-up, or feedforward, approach is generally focused on how the visual system identifies the basic units that will later serve as the input for more elaborate processing (Julesz, 1984; Palmer, 1983). The top-down, or feedback approach, centers on the influence of experience, memory, or other non-stimulus controlled effects (Grossberg & Raizada, 2000; Palmer & Rock, 1994).

Trick and Enns (1997) indicated that grouping is independent of determining shape and, therefore, must be accomplished by different perceptual processes. Their experiments showed that shapes perceived by perceptually grouping small elements together are as easily and accurately counted as shapes created of solid lines. However, when another shape is also are presented in the visual display, only shapes formed by lines are more easily and more quickly enumerated.

Kimchi and Palmer (1985) found that often the global level of the stimulus is totally integrated with the local elements and the observer cannot ignore either. Other times the observer can completely ignore either the global arrangement or the local elements when paying attention to the other. Feldman (1999) has proposed the minimal model theory which states that the minimal interpretation of all possible interpretations is what is perceived. The best explanation of the image will sometimes tend to be compartmentalized into separate, coherent bundles, or objects.

Beck and Palmer (2002) argue that it is faster to discriminate if objects are more similar. For intrinsic grouping factors (similarity of color, proximity) there is little evidence that it is influenced by top-down processes. However, there is more evidence that extrinsic factors (like common region) are affected by knowing the probability of similarity and this makes reaction times quicker. In general, they support a top-down component to grouping as long as enough time is given for feedback to operate, supporting top-down influences.

Lamme and Roelfsema (2000) suggest that there are so many processes occurring in parallel that it becomes extremely difficult to separate the contributions of feedforward and feedback processing. However, they claim that feedforward processes are unconscious and preattentive while feedback processes are conscious and attentive.

An influential theory by Treisman (1986) suggests that only a small number of features are extracted early on in visual processing. Focused attention is important and necessary to group features together and to establish representations of objects and their relations to one another. Also, prior knowledge and expectations help one use attention efficiently in joining features.

Moore and Egeth (1997) argue the grouping is occurring without attention but conflicting results are found because stimuli are not remembered. They presented displays that contained perceptual illusions of line length only if the displays were grouped. Because of short presentation times the participants could not report what stimuli they observed but their responses were consistent with the judgments of line length as if they were affected by the illusions.

Time course

Perceptual organization consists of separate, intermediate-level processes. Because there may be many processes involved in perceptual organization, the time course in which each occurs may be important in understanding how the many processes work together.

Kurylo (1997) found that grouping by proximity occurs before alignment grouping, suggesting that they are different processes. Also, grouping by alignment is a higher level process than proximity grouping and therefore, should be expected to occur within higher levels of brain processing.

Ben-Av and Sagi (1995) found that proximity grouping occurs faster than similarity grouping by shape and by luminance, which further supports separate processes for grouping. Also, proximity grouping is a lower level process than similarity grouping, occurring earlier in the visual system. The researchers also found that as processing time increases, similarity grouping becomes more influential, supporting the idea that it is a later occurring process that needs time to take place. Han, Jiang, Mao, Humphreys, and Qin (2005) also found that participants were faster when responding to grouping by proximity cues then with similarity of shape.

Schulz and Sanocki (2003) found that grouping by similarity of color is initially done early in processing (before color constancy processes) but when participants are given more time, grouping gradually switches to become a later, postconstancy process. Grouping by similarity of color, therefore, can occur both early and later in visual processing. Similarly, when participants are asked to perceptually group using the cues for the later postconstancy process, their reaction times are 175 msec longer than when asked to grouping using cues for earlier processing. Grouping by postconstancy color cues takes longer due to more elaborate processing.

Han, Humphreys, and Chen (1999) found global processing occurs before the processing of local elements if the grouping was accomplished either by similarity of line orientation cues or by closure cues. And, with both types of grouping cues, the local elements did not interfere with the global processing, but the global shape did interfere with the discrimination of the local elements. This finding supports the idea that the processing of the global aspects of the stimulus is occurring before the processing of the local elements. However, decreasing the saliency of the global shape, by embedding the stimuli among similar elements, facilitates processing of local elements and eliminates global advantages in reaction time. Therefore, the sequence of processing global and local elements of stimuli depends upon other factors, such as the background in which the stimuli are contained.

According to Palmer and Rock (1994), uniform connectedness is an early part of the organization of the visual field and classical principles of grouping operate after uniform connectedness. However, others argue that uniform connectedness does not occur before other organizational processes (Kimichi & Hadad, 2002). Using uniform connectedness grouping cues with closed and unclosed figures, Kimchi (2000) found that grouping is significantly stronger for closed figures than unclosed figures. This suggests that uniform connectedness is not necessarily the initial organizational process and its effects are influenced by other processes. For example, closed figures are identified early and are later organized into higher-level units (such as with connectedness) with time.

In summary, although some grouping processes may occur early, the final organized perception is not exclusively controlled by early retinal images. Evidence supports the global aspects of stimuli are processed before local elements. Also, grouping by proximity occurs before grouping by alignment and similarity of shape and luminance. Similarity grouping occurs before color constancy processes but can occur after. Grouping by closure occurs before connectedness. Furthermore, the sequence of processing by different grouping strategies may change as the properties of the stimuli changes. Although there is much evidence that grouping occurs early on, Palmer (2002) reviews research that shows grouping can rely upon binocular depth information, shape completion, and illusory figures processing.

Physiological Mediation of Perceptual Organization

Studies have recently been conducted to explore the neural mechanisms underlying perceptual grouping. One approach is to study disorders of perceptual grouping in brain damaged patients, or with simulated neuropsychological deficits. Other studies use single cell recording, fMRI, PET, or EEG procedures.

Neuropsychological Studies

Apperceptive agnosia is a disorder in which patients cannot recognize objects due to impaired lower-level perceptual processes. Vecera and Behrmann (1997) studied a patient suffering from apperceptive agnosia due brain damage in both occipital lobes and slightly into the right parietal cortex. Using normal participants, Vecera and Gilds (1999) simulated this patient's symptoms of apperceptive agnosia performance by removing the corners of rectangles. With these stimuli, normal participants no longer could group the elements and recognize them as rectangles, performing similarly to the apperceptive agnosia patient. These results suggest that apperceptive agnosia patients have impairments specifically in perceptual grouping and not in other visual processing. Furthermore, if impairment in grouping by closure is related to impairment in occipital lobe, then grouping must involve this area of the brain.

Behrmann and Kimchi (2003) studied two patients suffering from visual object agnosia caused by brain damage. Visual object agnosia is a disorder is in which the patient has an inability to identify familiar objects when they are presented visually. Impairment does not result from deficits with basic visual processing, but specifically deficits in recognizing objects. One patient suffered damage to the right inferior temporal lobe; however, the other patient's damage could not be localized. Both patients performed similar to controls on grouping by proximity and by similarity of luminance tasks. However, one participant could not group small elements into a global configuration. The other patient could only do so with an extended amount of time, suggesting this process is not accomplished as quickly and automatically as it is for controls. Performance on a grouping by closure task was similar to that of global processing. Because the results show that not all perceptual grouping processes are affected the same, they provide support that global processing and grouping by closure are independent of both grouping by proximity and similarity of luminance.

One patient studied by Davidoff and Warrington (1999) suffered from widespread damage to his right tempero-parieto-occipital region with lesser damage to the left frontal pole and the left parieto-occipital boundary. When presented with visual stimuli, the patient could not recognize parts of objects even when he could name the whole object. Furthermore, he could not detect changes in color, shape, or parts of objects. Because this patient suffered impairments only in local processing and not in global processing, it provides evidence that the two processes are independent. Unfortunately, the patient's damage was too widespread to draw specific conclusions as to where these separate processes are occurring in the brain.

Lamb, Robertson, and Knight (1990) compared control participants to participants with lesions on the posterior superior temporal gyrus (STG) while viewing stimuli that contain local and global elements. Unlike controls, the lesion participants showed little interference by global distracters when responding to local targets. This provides further support that global and local processes are independent of one another and that the integration of them involves the STG. Furthermore, the researchers found that the participants with right STG lesions had a large advantage for local targets, whereas the participants with left STG lesions had a global advantage. This is evidence for the dichotomy between local and global processing occurring in different hemispheres in the brain, i.e., local processing occurring in the left hemisphere and global processing occurring in the right hemisphere.

In summary, neuropsychological studies have provided evidence for the existence of separate perceptual organizational processes. Research has shown that the global processing of a stimulus is independent of local processing and that the integration of them involves the STG. Also, the global processing of a stimulus and grouping by closure are independent of both grouping by proximity and similarity of luminance. Evidence also exists for local processing occurring in the left hemisphere and global processing occurring in the right hemisphere. Furthermore, the occipital lobe is necessary for grouping by closure.

Recording Studies

When focusing on objects in the visual field, the eyes align the image on two retinas in corresponding locations. However, objects in the visual field that are at a different distance from the eye than the focused object will create non-corresponding images on the two retinas, this is know as binocular disparity. There are two types of binocular disparities, crossed disparity and uncrossed disparity. Crossed disparity occurs for the images of object that are closer to the eye than the focused object. Uncrossed disparity occurs for the images of objects that are further from the eye than the focused object. Both types of binocular disparity are important cues for depth perception.

Sugita (1999) recorded from V1 neurons of two Japanese monkeys while presenting visual stimuli. He presented a stimulus of two horizontal lines with a gap in the middle and isolated V1 cells that responded. These same cells stopped responding when a darker square was placed between the two lines. However, when the square appeared to be in front of the two lines (presented with crossed disparity) the V1 cells responded, whereas, these same cells stopped responding when the center patch appeared to be further away than the bars (presented with uncrossed disparity). These findings suggest that the V1 cells are using information, possibly through feedback mechanisms, about the depth location of the separate elements of the visual display and respond when the preferred stimulus is also one that is occluded by a closer object. This high-order visual information is influencing the early, basic processing in V1.

Using fMRI, Han, Jiang, Mao, Humphreys, and Gu (2005) found that V1 was involved in proximity grouping but not grouping by similarity of shape. This provides further evidence that these processes are independent and that proximity grouping is occurring earlier than grouping by similar shape. These findings are also consistent with evidence from other psychophysical studies that found proximity grouping to occur faster than grouping by shape (Ben-Av and Sagi, 1995).

Recording ERPs, Han, Jiang, Mao, Humphreys, and Qin (2005) found positive activity increased in medial occipital cortex 100 msec after stimulus onset during proximity grouping tasks. This activity was localized to area V1. When grouping by similarity of shape, negative activity increased over occipito-temporal areas 240 msec after stimulus onset. These two processes are occurring in different areas of the brain and the activity seen for grouping by similarity of shape occurred with a longer latency than grouping by proximity. This study further supports the idea that grouping by similarity occurs independently and later than grouping by proximity.

PET scans of area V2 showed significant increase in blood flow when viewing illusory contour stimuli (ffytche & Zeki, 1996). This area also responded to the real figures represented by the illusory contours. This is further evidence suggesting that early visual areas are involved in perceptual organization of closure.

Using fMRI, Altmann, Bülthoff, and Kourtzi (2003) found an increase in activity in areas V1, V2, VP, V4v, and occipitotemporal cortex (LOC) when participants viewed stimuli with collinear contours, as compared to randomly generated stimuli. They also found similar increases in activity when participants viewed random patterns that had disparity cues for grouping. This suggests that similar neural mechanisms may underlie grouping with these different features. It also suggests that perceptual organization into global shapes involves high-level (LOC) areas as well as early retinotopic regions (V1, V2, VP, and V4v).

Using fragmented pictures of objects to study closure, Doniger, Foxe, Murray, Higgins, Snodgrass, Schroeder, and Javitt (2000) found that ERP activity builds in the occipito-temporal cortex as closure is occurring and the perception is getting closer to object recognition. Specifically, the area within occipito-temporal cortext with increased activity is possibly LO-complex, an area similar to monkey inferotemporal (IT) cortex. The activity shows an onset of 232 msec and peaks at 290 msec. The late onset of the activity may be because closure is served by feedback mechanisms which occur after feedforward mechanisms. Since the occipito-temporal cortex is not a low-level vision area, closure is, at best, an intermediate process that occurs after low level processing has occurred.

Using PET, Fink, Halligan, Marshall, Frith, Frackowiak, and Dolan (1997) found that directing visual attention to global or local stimulus elements affects where brain activity occurs. Paying attention to the global aspect of a stimulus increased activation of the right lingual gyrus, whereas paying attention to local aspects increased activation of the left inferior occipital cortex. This finding is consistent with evidence from neuropsychological studies that found global processing is impaired with damage to the right STG (Lamb et al., 1990).

There is increasing understanding for the physiology underlying perceptual organization. V1 is the site for early processing, including grouping by proximity. V1 also receives feedback from high-order areas, including depth perception areas, to influence perceptual organization. V2 is involved in perception of illusory contours. Evidence also suggests that perceptual organization of collinear contours and grouping by similarity of disparity involves high-level (LOC) as well as early (V1, V2, VP, and V4v) areas. The high-order area, occipito-temporal cortex, shows increased activity as closure is occurring. Also global aspects of stimuli increase activity in the right lingual gyrus, whereas local aspects increased activation of the left inferior occipital cortex.

Conclusion

Since the Gestalt psychologists, perceptual organization has been included in almost every theory of vision. Although current theories on the topic vary in their details, all accept the beginning of perceptual organization starts with bottom-up processes and have top-down influences. There is much evidence from psychophysical, neuropsychological, and recording studies that suggest that perceptual organization is served by many independent processes, each with their own time course and physiological basis.

Much of perceptual organization and how it is accomplished by the nervous system is still unknown. Furthermore, to date the research has focused on central vision and neural areas that serve central vision. Lacking from this research is an exploration of how perceptual organization is affected by changes in visual eccentricity. Given the differences in physiology across the visual fields, and changes in perceptual abilities, differences are likely to occur in perceptual organization at different eccentricities.

Chapter 4. Perceptual organization across retinal eccentricity

Throughout the nervous system, the retinal image is represented very differently for central and peripheral vision. Even at the earliest levels of the visual system, central visual areas are allocated more cells for processing than peripheral visual areas. This trend is found throughout many levels of visual processing. In general, these changes in the neural representations correspond with changes in performance on many perceptual tasks. Specifically, previous research has shown that performance on most tasks declines with increasing eccentricity in the visual field. However, there is evidence that performance on many of these same tasks shows improvement when size compensations are made to peripheral stimuli.

Perceptual organization refers to the processes used by the visual system to sort out which parts of a scene are associated together. There are many different aspects of perceptual organization, each of the different principles of grouping are thought to be separate processes. These organizational processes are thought to take place at intermediate-levels, accomplished with little effort on the part of the observer and after low-level processes have occurred. The phenomenon of perceptual organization is a well described, but under researched topic. Much has been recently learned about the separate processes that influence organization, with evidence from many different types of research including psychophysical and neuropsychological studies.

Although, many perceptual tasks have been studied while investigating the difference between central and peripheral retinal eccentricities, lacking from this research is an exploration of how perceptual organization is affected by changes in visual eccentricity. Knowing how perceptual organization tasks differ based on retinal eccentricity will provide information on neural representations for different retinal regions.

Also, to study perceptual organization across retinal eccentricity it is important to systematically alter the neural representation within a given retinal location by manipulating the size of the stimuli. Using different stimuli to investigate different grouping cues at different retinal eccentricities will provide insight into the operation of the separate processes of perceptual organization.

First, to study perceptual organization from an experimental approach, a quantitative index of perceptual organization ability based upon the metrics of the stimulus is needed. In this way, quantitative comparisons can be made across stimulus conditions and across retinal eccentricities. Second, performance must be based upon the pattern of grouping assigned to ambiguous stimuli. In this regard, when presented with separate elements, there are several possible grouping patterns that compete. The strongest grouping cue is associated with how biased the stimulus is toward that pattern. One method to derive these measurements is to construct stimuli from a pattern of disconnected elements.

Associations among elements can be isolated to a single Gestalt grouping principle, such as proximity or similarity in luminance. The strength of the grouping cue will be associated with the degree of proximity, or the percentage of similarity among elements. As these stimulus features are manipulated, associated changes will occur on the response characteristics of neurons. Each element in a stimulus will activate a localized site on the cortical surface, producing a retinotopic map of the entire stimulus. As the stimulus is presented to greater eccentricities in visual field, the pattern of cortical excitation will shift in accordance with cortical magnification. In this regard, the spacing among activated areas, the degree of neural connectivity among sites, and the density of neurons activated by stimulus elements will shift with eccentricity. These manipulations of cortical activation can then be used to investigate hypothesized neural mechanisms of perceptual organization.

In the following studies, stimulus parameters were manipulated in order to analyze interactions with retinal eccentricity to test hypotheses about perceptual organization. Differences in neural representations across eccentricity were used to test specific hypotheses. The primary hypothesis was that unlike basic visual processing, perceptual organization would be less vulnerable to reduced neural representations with increased eccentricity. The alternative hypothesis associates perceptual organization with object recognition, which is optimal in central vision. In this regard, perceptual organization would decline with increasing eccentricity regardless of compensation for cortical magnification.

General Method

The current studies of perceptual grouping examined the limits to which the intrinsic organization of a stimulus allowed perceptual grouping while systematically altering the neural representation of the stimulus. Participants viewed visual patterns that could be perceptually organized into either vertical or horizontal lines. Threshold measurements were obtained through psychophysical techniques while participants fixated different points eccentric to the stimulus. Four different features cued the grouping of the visual pattern. Each feature was tested at different retinal eccentricities as well as with different sizes and spacing between elements.

Participants

Four trained psychophysical observers participated in the studies (1 female and 3 male). All participants had a best-corrected 14” visual acuity of 20/20 (Snellen).

Apparatus

Stimuli were presented on a standard VGA computer monitor, with a screen resolution of 1024 x 768 pixels. Customized computer software was used to present stimuli and record participant responses.

Experiment 1 - Grouping by Similarity: Foveal

Method

In order to determine if differences exist among different stimulus features in their efficacy to establish grouping, grouping thresholds based upon similarity in luminance, motion, and orientation were compared. Observers viewed stimuli that could be perceptually grouped into specific patterns based upon the similarity among elements in the stimulus array. For each of the grouping features, psychophysical measurements were made of grouping thresholds. To obtain threshold measurements, the level of similarity was progressively reduced until the feature no longer served as a cue for perceptual organization.

Stimuli

Stimuli were presented on a computer monitor for 250 msec. This presentation time was chosen to insure enough viewing time for the observers while also minimizing the possibility of saccadic eye movements during stimulus presentation.

Three different stimulus features were used to elicit perceptual organization: luminance, motion, and orientation. Each stimulus feature was comprised of two different element types. In order to minimize possible sensitivity effects, element types were selected from distinct levels of the stimulus feature domain. Salient differences in these element pairs ensured that perceptual organization measurements were associated with the relationships among elements and not discrimination of the element pairs. The two element types could be sorted along alternate columns or alternate rows. If the two element types were sorted along alternate columns, the stimulus elicited the perception of a series of vertical lines. When the two element types were sorted along alternate rows, the stimulus elicited the perception of a series of horizontal lines.

Luminance. For the similarity of luminance condition, a 20 by 20 array of square elements was presented (Figure 1a). The elements were spaced at regular increments across the array and were aligned along the vertical and horizontal orientations. The luminance of the background display was 16.5 cd/m^2. The luminance for the individual elements of the stimulus array was either higher (49.3 cd/m^2) or lower (0.046 cd/m^2) than the background luminance. These luminance values insured that the contrast between each element type and the background was maximized and therefore they were suprathreshold and salient for all observers.

For each trial, similarity among elements was randomly assigned to either the vertical or the horizontal orientation. For grouping to be biased in the vertical orientation, elements of one luminance type were aligned in columns. Elements of the other luminance type were aligned in alternate columns. The organization of the stimulus was reduced by randomly replacing a percentage of elements with the opposite luminance type. In this regard, the similarity among elements in the organized orientation changed, in increments of 2%, from 100% to 50%.

Motion. For the similarity of motion condition, stimuli consisted of a 20 by 20 array of equiluminant squares that moved along a 45 degree path at a rate of 4 deg/sec (Figure 1b). Motion was produced with five consecutive 50 msec frames, resulting in a total stimulus presentation of 250 msec. The rate of motion was the same as that used in previous research (Kurylo, 2006). The luminance of the background display was 16.5 cd/m^2. Luminance for the individual elements of the stimulus array was 49.3 cd/m^2.

These luminance values assured the stimulus was well above thresholds of contrast sensitivity.

Each stimulus contained two motion directions, selected randomly on each trial from the four possible directions. Elements were initially arranged in an evenly spaced grid. For the vertical condition, each column contained elements that moved in the same direction, alternating between the two directions across columns. This type of stimulus generated a robust perception of a series of moving vertical lines.

The organization of the stimuli was reduced by randomly replacing a percentage of elements with the other motion type. In this regard, the similarity among elements in the organized orientation changed from 100% to 50%, in increments of 2%.

Orientation. For the similarity of orientation condition, stimuli consisted of a 10 by 10 array of rectangular luminance grated elements, orientated either vertically or horizontally (Figure 1c). The luminance of the background display was 16.5 cd/m^2. The individual elements were Gabor patches created by enveloping a sinusoidal grating in a Gaussian distribution. The luminance of the Gabor patches was based on the following equation:

$$\text{Lumin}(x, y) = (\exp(-0.5\, x^2 / SDx))(\exp(-0.5\, y^2 / SDy)(\text{cosine}((2\pi\, x)/\text{cycles})) \qquad (1)$$

For grouping to be biased in the vertical orientation, each column contained elements of the same type, alternating orientation across columns. The organization of the stimuli was reduced by randomly replacing a percentage of elements with the other orientation type. In this regard, the similarity among elements in the organized orientation changed from 100% to 50%, in increments of 2%.

For all stimuli, regardless of the grouping feature, the overall size of each stimulus was 7.8 degrees on each side. The individual elements comprising the stimulus arrays for the features of luminance and motion were 2.0 mm on a side, or 0.20 degrees. Similarly, the spacing between individual elements was the same as the size of one element. The luminance of Gabor patches fades gradually into the background and therefore discrete measurements of size are not available. These stimuli were placed such that their centers were aligned with those of the other stimulus arrays and the overall size of the stimulus array was the same as that of the other grouping features.

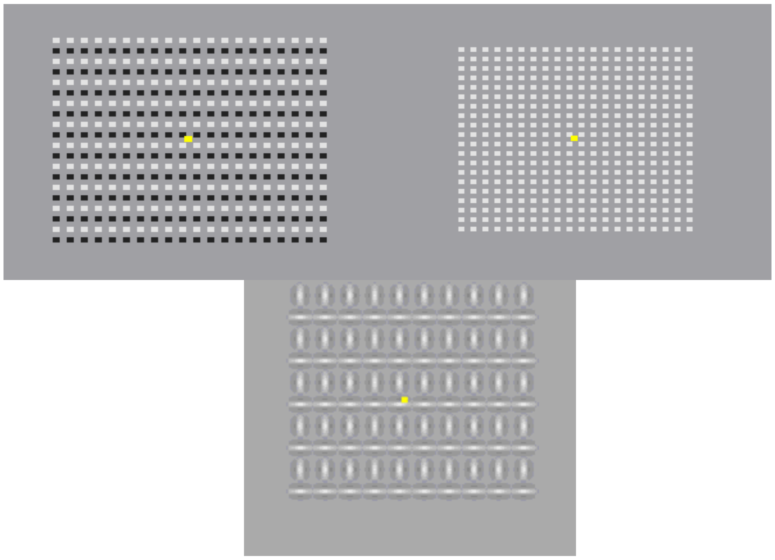

Figure 1 a - c. Examples of stimuli used in the luminance, motion, and orientation conditions. Note: For the motion stimulus, the elements in a single row would move in the same direction and the elements in the adjacent row would move in a different direction.

Procedure

The computer monitor was centered directly in front of the participant in a dimly lit room. Head position was stabilized with a chin rest. All measurements were obtained with monocular viewing using the right eye. The left eye was covered with an opaque eye patch.

Perceptual organization thresholds were obtained in three separate sessions, one for each feature. Each session lasted approximately five minutes and consisted of approximately 60 trials. Participants completed each session in a randomly selected order. Sessions were separated by at least five minutes of rest to reduce monotony and fatigue during experimental sessions.

For each trial, stimulus elements were organized either vertically or horizontally, randomly selected. Participants were presented with the stimulus for 250 msec, fixated on the center of the stimulus, and then indicated at their own pace, via a computer keyboard, whether the stimulus pattern was perceived as a series of vertical or horizontal lines. After the keypress was made, the next trial was presented immediately. After all reversals were completed and a threshold was obtained, the session ended and a new feature would be randomly selected for the next session.

Psychophysical Thresholds. At the beginning of each test, the percent of similarity was 100%, thereby eliciting a strong perceptual grouping to the cued orientation. Across trials, percent similarity was progressively reduced until the stimulus became ambiguous and bi-stable, thereby indicating the limit to which the cue could serve to produce grouping. That is, the percent of similarity was progressively reduced until participants selected the non-cued orientation.

To calculate thresholds, a two-alternative forced choice descending staircase procedure was implemented. The descending staircase algorithm reduced the strength of the grouping cue by 2% after two consecutive correct responses and increased the strength after one error. For every incorrect response preceded by two correct responses, a reversal was recorded. At least five reversals were used to determine the level at which the participant can no longer group the ambiguous stimuli. Grouping thresholds were based upon the mean of the reversals. Any single reversal that was three standard deviations from mean of the remaining reversals was considered an outlier and discarded from the analysis.

Thresholds were defined as the lowest percentage of similarity, or, the highest percent of dissimilarity, among elements necessary to perceptually organize the array. Less similarity among elements at threshold reflects a greater capacity to perceptually organize the stimulus, whereas impairment would necessitate more similarity among elements to perceive grouping.

Results

In order to determine if the different stimulus features differ in their effectiveness to establish grouping, grouping thresholds based upon similarity in luminance, motion, and orientation were compared. Experiment 1 examined grouping thresholds for the three stimulus features, using stimulus arrays with large size and large spaced elements, at foveal viewing. Group means are shown in Figure 2.

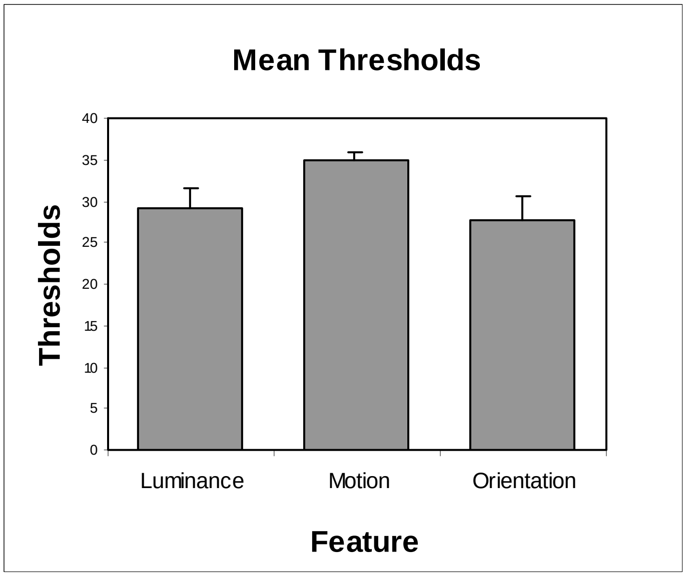

Figure 2. Mean grouping thresholds for three grouping features with foveal viewing. Error bars represent one standard error of the mean (SEM).

A one-way within-subjects analysis of variance (ANOVA) was used to compare thresholds across features. There was a significant difference among the features (F(2, 6) = 56.49, $p < 0.01$, partial $\eta^2 = 0.80$). Post hoc paired t-tests revealed that although thresholds for luminance and orientation did not differ significantly (t(3) = 1.07, $p > 0.05$), motion thresholds differed from both luminance and orientation (t(3) = 3.97 and 3.98, $p < 0.05$, respectively).

The features were fundamentally different, possibly due to scalar differences across stimulus dimensions. Therefore, further analyses were performed separately for each feature.

Experiment 2 - Grouping by Similarity: Retinal Eccentricity

Method

In order to examine the effects of varying stimulus representations on grouping capacities, thresholds were obtained while altering the size, spacing, and retinal eccentricity of the stimuli. The thresholds were compared to see if there was a difference in grouping performance across different grouping features, across different retinal eccentricities, and across different sized and spaced stimuli.

Specifically, this experiment compared grouping capacities for features of luminance, motion, and orientation across five retinal eccentricities. For each feature and at each retinal eccentricity, thresholds were obtained for six different stimulus arrays, in which stimuli varied in element size and spacing. The feature, eccentricity, and stimulus characteristics were randomly selected for each session.

Stimuli

Stimuli were the same as Experiment 1 in regard to grouping features. However, within each feature this experiment used six different stimuli, varying in the size and spacing between individual elements in the array.

For the luminance and motion features, the largest stimulus used element sizes of 2.0 mm on a side, each subtending 0.20 degrees. The spacing between the elements in this stimulus was the same size and visual angle of the individual elements. The overall size of this entire stimulus array was 7.8 degrees on each side. Again, the orientation cue used Gabor patches whose discrete measurements of size are not available but the elements were distributed while maintaining the same overall size.

Two additional stimuli used the same proportion of equal element size and spacing. These stimuli were each reduced in size to produce 5.85 and 3.9 degree stimulus arrays, with 0.15 and 0.10 degree elements and spacing.

The remaining three stimuli increased the spacing between elements resulting in stimuli with different ratios of element size to spacing. These stimuli used medium elements with large spacing, small elements with large spacing, or, small elements with medium spacing.

Specifically, the stimulus using medium elements with large spacing had 0.15 degree elements with 0.25 degree space in between. The overall size of this array was 7.8 degrees. The stimulus using small elements with large spacing had 0.10 degree elements with 0.31 degree space in between. The overall size of this array was 7.8 degrees. And, the stimulus with small elements and medium spacing had 0.10 degree elements with 0.20 degree space in between. The overall size of this array was 5.85 degrees. See table 2 for a complete list of element size, overall size, and spacing.

These arrays were chosen such that the smallest array viewed at the furthest retinal eccentricity was well above acuity limitations based on pilot data. However, another consideration was that to compensate for cortical magnification by doubling the metrics of this array (resulting in the largest array described above) the outcome size was not too large a stimulus such that many retinal eccentricities could not be tested. Furthermore, to more fully describe how the stimulus metrics changes processing, all other possible combinations of size and space were tested.

Table 2. Element size, overall size, and spacing of the stimulus arrays. The size of the individual elements is located in parentheses under element size. The overall stimulus size is in parentheses under element spacing. The space between elements is in the cells.

		Element Spacing (overall stimulus size)		
		Small (3.9 deg)	Medium (5.85 deg)	Large (7.8 deg)
Element Size	Small (0.10 deg)	0.10 deg	0.20 deg	0.31 deg
	Medium (0.15 deg)		0.15 deg	0.25 deg
	Large (0.20 deg)			0.20 deg

Retinal Eccentricity

At the beginning of the session, participants fixated at one of five fixation points which centered the stimuli in the fovea or in the right visual hemi-field at 8, 23, 40, or 60 degrees. The fixation point for the foveal condition was presented on the monitor in the center of the stimulus. All other fixation points were to the left of this center at the appropriate angle.

These eccentricities were chosen to extend as far into the visual field as possible, which was not done in most previous research. Pilot studies showed stimuli viewed at eccentricities beyond 60 degrees could not be perceptually organized above chance levels. Also, no part of a stimulus could fall on the blind spot of the retina (which is located at an eccentricity of approximately 15 degrees). Furthermore, the eccentricities had to be spaced such that there would be reasonable number of areas in the visual field represented but that it would not over-burden the participants by creating too many conditions.

With rotation of the participants' head, the distance from the viewer's eye to the monitor varied between the retinal eccentricity viewing conditions. These changes resulted in up to a 0.20 degree deviation of the overall stimulus size from the foveal measurements described above.

Procedure

Grouping features, procedures, and threshold measurements were the same as Experiment 1 described above, however, in addition to grouping feature, eccentricity and stimulus metric were also randomly selected for each experimental session.

Participants were instructed to fixate at the appropriate fixation point for the duration of the session and then measurements were taken. After all reversals were completed and a threshold was obtained, the session ended and a new feature, eccentricity and metric would be randomly selected for the next session.

Results

In order to examine the effects of varying stimulus representations on grouping capacities, thresholds were compared across retinal eccentricity, the size of elements, and the spacing between elements. Grouping capacities for features of luminance, motion, and orientation were compared across five retinal eccentricities and across six stimulus metrics, in which stimuli varied in element size and spacing.

Luminance. Figure 3 shows mean grouping thresholds for each stimulus metric as a function of eccentricity. Grouping thresholds remained relatively stable for 0, 8, 23, and 40 degree eccentricities, then decline at 60 degrees.

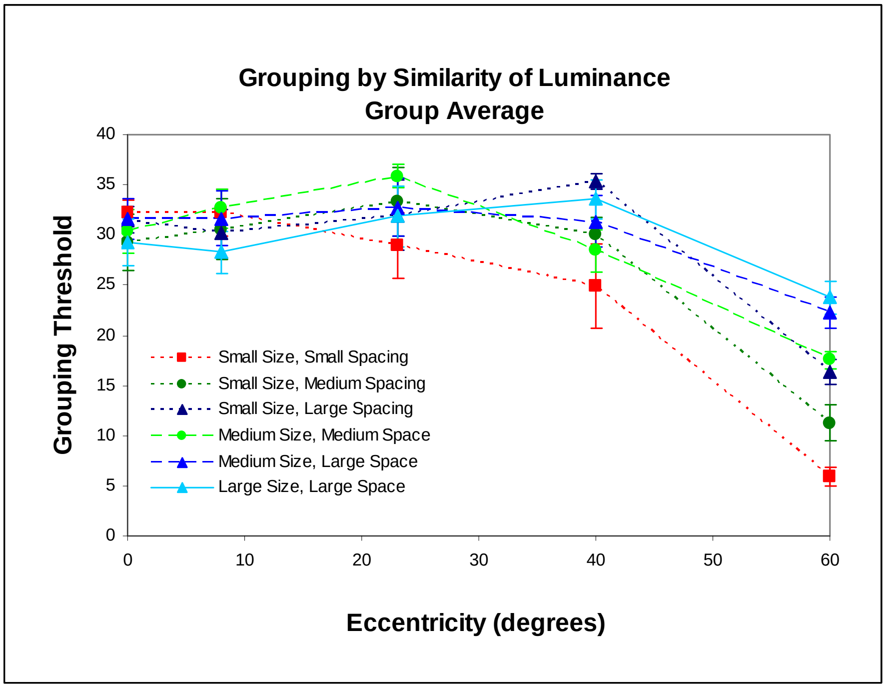

Figure 3. Mean grouping thresholds for the luminance condition for each stimulus metric as a function of eccentricity. Error bars represent one standard error of the mean (SEM).

To assess the effects of eccentricity and stimulus metrics on grouping capacities, a 5 x 6 within-subjects ANOVA was used to compare thresholds across eccentricity and metrics for the luminance condition. There was a significant main effect of eccentricity (F(4, 12) = 25.94, $p < 0.001$, partial $\eta^2 = 0.90$), a significant main effect of metrics (F(5, 15) = 6.27, $p < 0.01$, partial $\eta^2 = 0.68$), and a significant interaction of eccentricity by metrics (F(20, 60) = 4.35, $p < 0.001$, partial $\eta^2 = 0.59$).

To interpret the interaction, the simple effects of metrics at each eccentricity were examined with a one-way ANOVA. At 60 degrees eccentric, there was a significant effect of metrics (F(5, 15) = 26.25, $p < 0.001$). Smaller spaced and smaller sized stimuli were more difficult to group than larger spaced and larger sized stimuli.

All other eccentricities did not show a significant effect of metrics (F(5, 15) = 1.00, 0.91, 2.16, and 2.36, $p > 0.05$ for 0, 8, 23, and 40 degrees respectively). The simple effects of eccentricity for each metric were also examined using one-way ANOVAs. Every level of metric showed a significant difference across eccentricity (Table 3).

Table 3. Results of one-way ANOVA for each stimulus metric across eccentricity for the luminance condition.

		Element Spacing		
		Small	Medium	Large
Element Size	Small	F(4, 12) = 16.80 ***	F(4, 12) = 19.18 ***	F(4, 12) = 17.38 ***
	Medium		F(4, 12) = 19.70 ***	F(4, 12) = 4.50 *
	Large			F(4, 12) = 3.70 *

* $p < 0.05$ ***$p < 0.001$

Visual inspection of the mean thresholds in Figure 4 suggests the effects of eccentricity may be due to performance at 60 degrees. To determine if this was the case, one-way ANOVAs were performed on the data without the 60 degree condition. Without 60 degrees, only one metric (medium size, medium space) showed a significant difference across eccentricity (Table 4).

Table 4. Results of one-way ANOVA for each stimulus metric across eccentricity without the 60 degree condition for the luminance condition.

		Element Spacing		
		Small	Medium	Large
Element Size	Small	F(3, 9) = 1.32	F(3, 9) = 1.77	F(3, 9) = 2.52
	Medium		F(3, 9) = 4.67 *	F(3, 9) = 0.23
	Large			F(3, 9) = 1.85

* $p < 0.05$

Grouping by luminance showed a significant interaction of eccentricity by metrics. Although, all metrics show significant decline with eccentricity, there was only a significant difference between the metrics at an eccentricity of 60 degrees. Furthermore, most significant effects were eliminated by removing thresholds for 60 degrees from the analysis. The results indicate that performance was relatively stable until eccentricity reached 60 degrees, at which point performance declined.

Motion. Figure 4 shows mean grouping thresholds for each stimulus metric as a function of eccentricity. Grouping thresholds progressively declined as eccentricity increased.

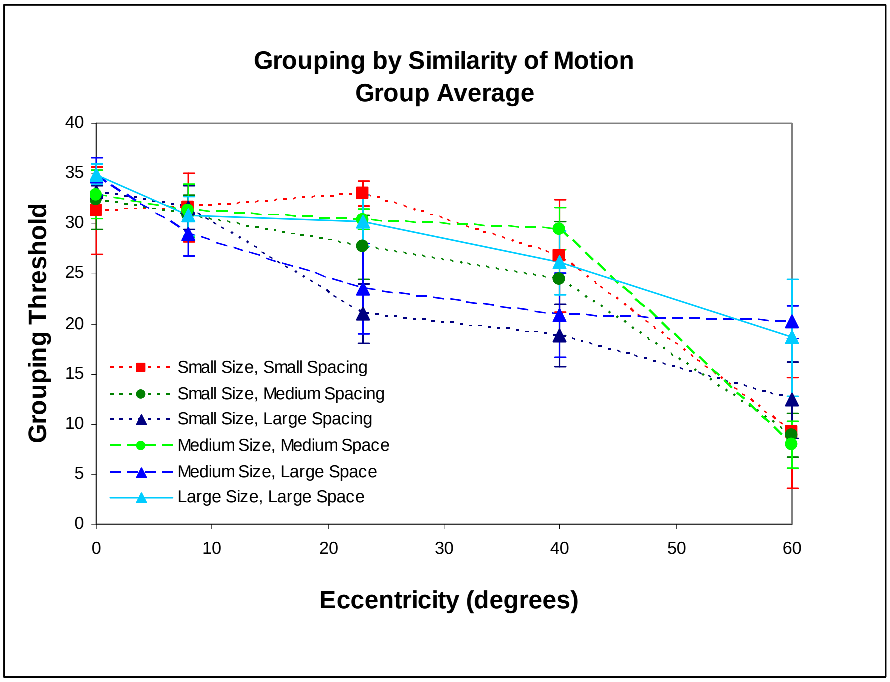

Figure 4. Mean grouping thresholds for the motion condition for each metric as a function of eccentricity. Error bars represent one SEM.

To determine the effects of eccentricity and stimulus metrics on grouping capacities, a 5 x 6 within-subjects ANOVA compared thresholds across eccentricity and metrics for the motion feature. There was a significant main effect of eccentricity (F(4, 12) = 16.44, $p < 0.001$, partial $\eta^2 = 0.85$), a non-significant main effect of metrics (F(5, 15) = 1.26, $p > 0.05$), and a significant interaction of eccentricity by metrics (F(20, 60) = 1.92, $p < 0.05$, partial $\eta^2 = 0.39$).

To further investigate the significant interaction, the simple effects of metrics at each eccentricity were measured using one-way ANOVAs. At an eccentricity of 23 degrees, there was a significant effect of metrics (F(5, 15) = 5.48, $p < 0.01$), in which grouping thresholds for small size stimuli with large spaces were lower than small sized stimuli with smaller spaces. No other eccentricity showed a significant effect of metrics (F(5, 15) = 0.77, 0.89, 0.87, and 2.12, $p > 0.05$, for 0, 8, 40, and 60 degrees respectively).

The simple effects of eccentricity at each metric were also measured using one-way ANOVAs. With one exception (the large size and large spaced metric), all levels of metric showed a significant difference across eccentricity (Table 5).

Table 5. Results of one-way ANOVA for each stimulus metric across eccentricity for the motion condition.

		Element Spacing		
		Small	Medium	Large
Element Size	Small	F(4, 12) = 5.58 **	F(4, 12) = 9.10 **	F(4, 12) = 8.86 **
	Medium		F(4, 12) = 28.17 ***	F(4, 12) = 5.47 **
	Large			F(4, 12) = 3.20

** $p < 0.01$ ***$p < 0.001$

Visual inspection of the mean thresholds in Figure 5 suggests the effects of eccentricity may also be highly influenced by performance at 60 degrees. To examine this possibility, one-way ANOVAs were performed on the data without 60 degrees. Without the 60 degree condition, only metrics with large spacing showed a significant difference across eccentricity (Table 6).

Table 6. Results of one-way ANOVA for each stimulus metric across eccentricity without the 60 degree condition for the motion condition.

		Element Spacing		
		Small	Medium	Large
Element Size	Small	F(3, 9) = 0.44	F(3, 9) = 1.47	F(3, 9) = 17.52 ***
	Medium		F(3, 9) = 0.67	F(3, 9) = 6.31 *
	Large			F(3, 9) = 5.00 *

* $p < 0.05$ ***$p < 0.001$

Grouping by motion showed a significant interaction of eccentricity by metrics. Although most metrics showed a significant decline in function with eccentricity, this effect was due to the 60 degree eccentricity for small and medium spacing.

Orientation. Figure 5 shows mean grouping thresholds for each stimulus metric as a function of eccentricity. Grouping thresholds remained relatively stable for 0, 8, and 23 degrees, but then gradually declined as eccentricity increased to 40 degrees and especially declined at 60 degrees.

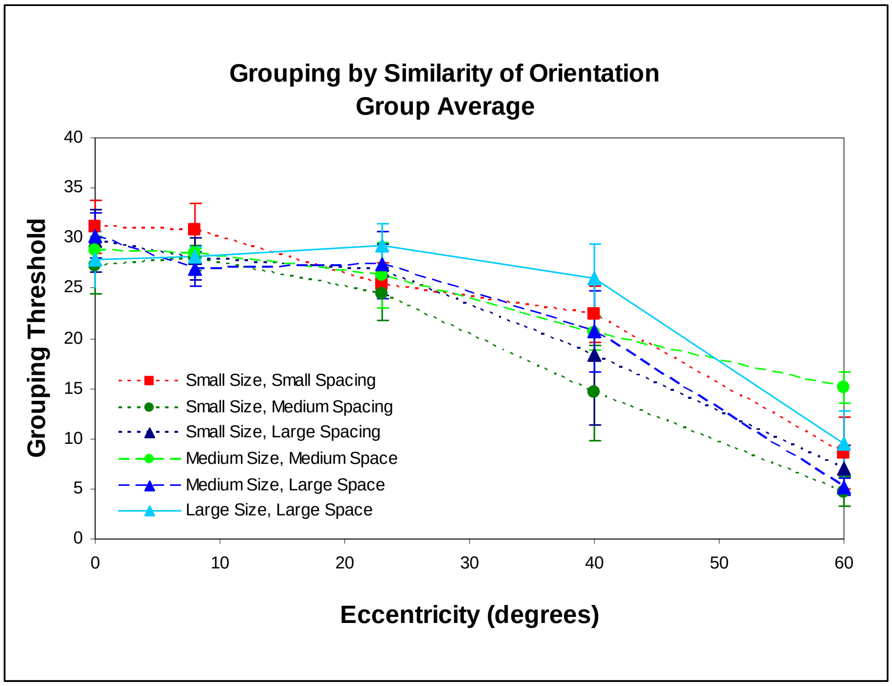

Figure 5. Mean grouping thresholds for the orientation condition for each metric as a function of eccentricity. Error bars represent one SEM.

To determine the effects of eccentricity and stimulus metrics on grouping capacities, a 5 x 6 within-subjects ANOVA compared thresholds across eccentricity and metrics for the orientation condition. There was a significant main effect of eccentricity (F(4, 12) = 21.46, $p < 0.001$, partial $\eta^2 = 0.88$), a non-significant main effect of metrics (F(5,15) = 2.73, $p > 0.05$), and a non-significant interaction (F(20, 60) = 1.55, $p > 0.05$).

To further investigate the eccentricity effect, analyses were also performed on the data without grouping thresholds obtained at 60 degrees eccentricity. A 4 x 6 within-subjects ANOVA was used to compare thresholds across eccentricity and metrics. Without the 60 degree condition, there still was a significant main effect of eccentricity (F(3, 9) = 4.22, $p < 0.05$) and no significant main effect of stimulus metrics (F(5, 15) = 1.55, $p > 0.05$), or eccentricity by metrics interaction (F(15, 45) = 1.08, $p > 0.05$).

Finally, removing the 40 and 60 degree conditions from the analysis and performing a 3 x 6 ANOVA determined that there was no significant difference between 0, 8, or 23 degrees (F(2, 6) = 1.13, $p > 0.05$), indicating that main effects of eccentricity were due to the farthest two eccentricities.

Experiment 3 - Grouping by Proximity: Retinal Eccentricity

Method

Grouping by proximity is based upon the spatial relationships between the elements. Therefore, grouping by similarity and grouping by proximity represent fundamentally different principles of grouping, both perceptually and physiologically. To examine possible differences between these two strategies, Experiment 3 was designed to determine the extent to which spatial relationships could elicit perceptual organization across stimulus size, spacing, and eccentricity. In this regard, participants were asked to view stimuli whose relationship among elements varied in proximity.

For grouping by proximity stimuli contained only one element type that was positioned at differing separation between the vertical and horizontal orientation. Elements closer in the vertical orientation elicit a series of vertical lines. Elements closer in the horizontal orientation elicit the perception of a series of horizontal lines.

This experiment assessed the differences in grouping by proximity across five retinal eccentricities, each using six stimuli of different element size and spacing. As with the similarity conditions, participants fixated one of five points located to the left of the computer monitor. Eccentric fixation points centered the stimuli in the right visual hemi-field at 8, 23, 40, or 60 degrees.

Stimuli

An array of square elements was presented with proximity serving as the grouping cue (Figure 6). The luminance of the background display was 16.5 cd/m^2. Luminance for the individual elements of the stimulus array was 49.3 cd/m^2.

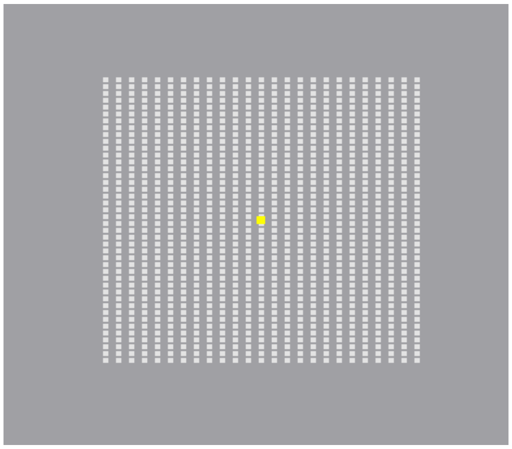

Figure 6. Example of a stimulus used in the proximity condition.

Elements were spaced at regular increments across the array and were perfectly aligned along the horizontal and vertical orientations. The horizontal and vertical orientations differed in the amount of separation between elements. For each trial, the more proximal elements were randomly assigned to either the horizontal or the vertical orientation. For grouping to be biased in the vertical orientation, elements are closer to each other vertically than they are horizontally.

Six combinations of stimulus size and spacing were the same as those used in Experiment 2.

Retinal Eccentricity

Retinal eccentricity conditions are the same as Experiment 2.

Procedure

The computer monitor was centered directly in front of the participant in a dimly lit room. Head position was stabilized with a chin rest. All measurements were obtained with monocular viewing using the right eye. The left eye was covered with an opaque eye patch. Participants were instructed to fixate at the appropriate fixation point for the duration of the session and then measurements were taken.

Thresholds were obtained in separate sessions, one for each eccentricity and metric combination, randomly selected. Each session lasted approximately five minutes and consisted of approximately 60 trials. Participants completed each session in a randomly selected order, separated by at least five minutes of rest to reduce the monotony and fatigue during experimental sessions.

For each trial, stimulus elements were closer to each other either vertically or horizontally, selected randomly on each trial. Participants were presented with the stimulus for 250 msec and then indicated at their own pace, via a computer keyboard, whether the stimulus pattern was perceived as a series of vertical or horizontal lines. After the keypress was made, the next trial was presented immediately. After all reversals were completed and a threshold was obtained, the session ended and a new eccentricity and metric would be randomly selected for the next session.

Psychophysical Thresholds. At the beginning of each test, the separation of elements along the more distant separation (S_dist) was fixed at 0.38 degrees and the separation of elements along the more proximal separation (S_prox) was set at 0.20 degrees. This elicited a strong perceptual grouping to the cued orientation. Across trials, S_prox was progressively increased until the stimulus became ambiguous and bi-stable, thereby indicating the limit to which the cue could serve to produce grouping. That is, S_prox became closer to S_dist until participants selected the non-cued orientation.

To calculate thresholds, a two-alternative forced choice staircase procedure was implemented. The staircase algorithm increased S_prox after two consecutive correct responses, in increments of approximately 10%. S_prox was decreased after one error. For every incorrect response preceded by two correct responses, a reversal was recorded. At least five reversals were used to determine the level at which the participant can no longer group the ambiguous stimuli. Grouping thresholds were based upon the mean of the reversals.

Thresholds were defined as the percentage of S_prox to S_dist among elements necessary to perceptually organize the array. The higher S_prox is, and therefore the percentage of S_prox to S_dist, at threshold reflects a greater capacity to perceptually organize the stimulus, whereas impairment would necessitate a greater difference between elements to perceive grouping.

Results

Grouping by similarity and grouping by spatial relationships represent fundamentally different principles of grouping, both perceptually and physiologically. To examine possible differences between these two strategies, Experiment 3 was designed to determine the extent to which spatial relationships could elicit perceptual organization across stimulus size, spacing, and eccentricity.

The mean grouping thresholds for each stimulus metrics as a function of eccentricity are shown in Figure 7. Grouping thresholds remained relatively stable for 0, 8, and 23 degrees but then gradually declined as eccentricity increases to 40 degrees, and then more dramatically declined at 60 degrees.

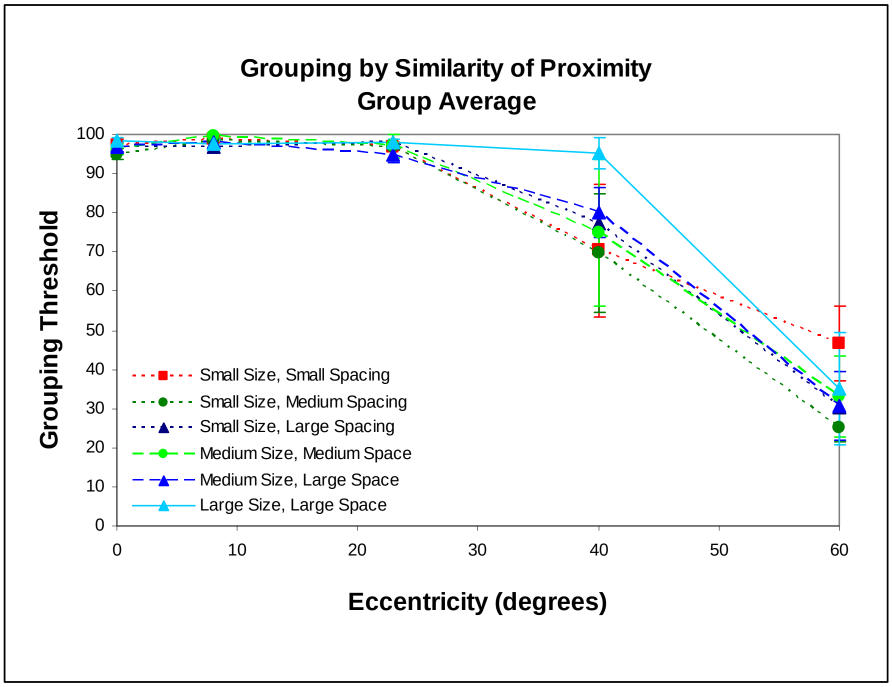

Figure 7. Mean grouping thresholds for the proximity condition for each metric as a function of eccentricity. Error bars represent one SEM. Grouping thresholds reflect the proportion of distances between the closer and the further orientations.

To determine the effects of eccentricity and stimulus metrics on grouping capacities, a 5 x 6 within-subjects ANOVA compared thresholds for the proximity condition across eccentricity and metrics. There was a significant main effect of eccentricity (F(4, 12) = 22.16, $p < 0.001$, partial $\eta^2 = 0.88$). The main effect of metrics and the interaction of eccentricity by metric were not significant (F(5, 15) = 2.24 and F(20, 60) = 1.14, $p > 0.05$).

Analyses were also performed on the data without grouping thresholds obtained at the 60 degrees eccentricity. To compare thresholds for the proximity condition across eccentricity and metrics a 4 x 6 within-subjects ANOVA was used. There still was a significant main effect for eccentricity (F(3, 9) = 3.92, $p < 0.05$). The main effect of metrics and the interaction of eccentricity and metric were not significant (F(5, 15) = 1.12 and F(15, 45) = 0.97, $p > 0.05$).

Finally, removing the 40 and 60 degree conditions from the analysis and performing a 3 x 6 ANOVA determined that there were no significant differences between 0, 8, or 23 degrees (F(2, 6) = 1.27, $p > 0.05$).

Grouping by proximity thresholds were significantly different across eccentricity. Specifically, there were no differences between 0, 8, and 23 degrees, but these were different than 40 and 60 degrees.

Experiment 4 - Laterality Effects of Perceptual Grouping

Method

This experiment assessed the difference in the four grouping features between the right and left visual hemi-fields. This was done to determine whether the features used in the previous experiments, which used nasal visual fields, would show different performance when observed with the opposite side of the retina as well. Thresholds may differ based on the role the process serves in object recognition. Thresholds for features of luminance, motion, orientation, and proximity were measured for stimuli centered 23 degrees eccentric both to the right and left sides of the computer monitor.

Stimuli

Grouping features were the same as those described above for grouping by similarity of luminance, motion, orientation (Experiment 1) and grouping by proximity (Experiment 3). Thresholds were obtained for stimuli with equal element size and spacing in between elements. Specifically these were the small size and small spacing, medium size and medium spacing, and the large size and large spacing arrays.

Procedure

Procedure and threshold measurements were the same as those used in Experiments 1, 2, and 3.

Results

This experiment assessed the difference in the four grouping features between the right and left visual hemi-fields to determine whether results acquired from the previous experiments, which used the right visual hemi-field (left cerebral hemisphere), could be generalized to the left visual hemi-field (right hemisphere).

The mean grouping thresholds for each feature are shown in Figure 8. In nearly all cases, a trend existed for a left hemi-field advantage. For each of the four stimulus features measured, a 2 x 3 ANOVA compared hemi-field and metrics. The luminance feature showed a significant main effect of metrics (F(2, 6) = 7.06, $p < 0.05$, partial $\eta^2 = 0.70$). The medium sized and spaced stimuli have better thresholds than the large stimuli, which in turn have better thresholds than the small stimuli.

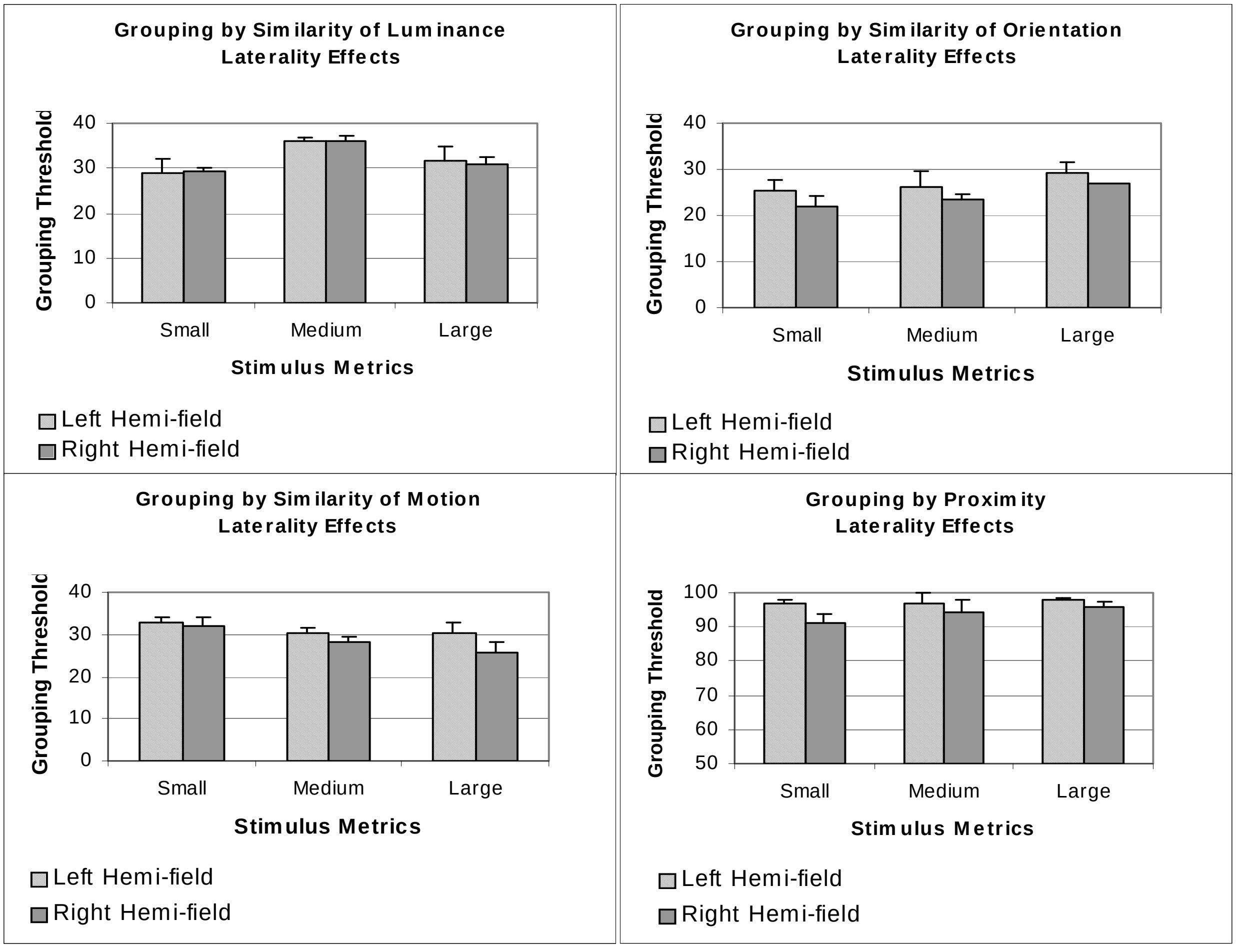

Figure 8. Mean thresholds for each feature and each hemi-field as a function of stimulus metrics. Error bars represent one SEM.

Motion was the only feature to show a significant main effect of hemi-field (F(1, 3) = 45.21, $p < 0.01$, partial $\eta^2 = 0.94$). For all features, the left hemi-field had higher grouping thresholds than the thresholds for the same metrics from the right hemi-field. All other tests were not significant ($p > 0.05$).

Experiment 5 - Acuity

Method

Potential decline in grouping ability with small elements size, close element spacing, or farther retinal eccentricities may result from limitations in visual acuity and not because of factors specific to perceptual grouping. In order to assess the effects of acuity on perceptual organization thresholds, acuity measures, based upon discriminating solid lines, were obtained at five retinal eccentricities. Observers viewed stimuli that consisted of a series of solid lines oriented either horizontally or vertically. To obtain threshold measurements, the size and space between the lines was progressively reduced until the observer could no longer discriminate the orientation of the lines.

Stimuli

Stimuli consisted of solid lines, oriented either vertically or horizontally, selected randomly on each trial (Figure 9). Stimuli were presented for 250 msec. Each stimulus contained 20 lines, alternating between dark and light lines. The luminance of the background display was 16.5 cd/m^2. The luminance for the lines in the stimulus array was either higher (49.3 cd/m^2) or lower (0.046 cd/m^2) than the background luminance.

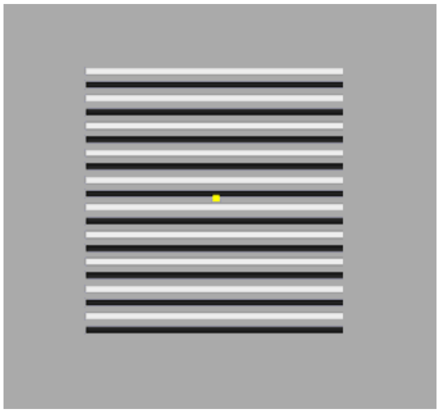

Figure 9. Example of a stimulus used in the acuity condition.

For acuity, 20 parallel lines were presented. The luminance of the background display was 16.53 cd/m^2. The luminance of the lines was either higher (49.3 cd/m^2) or lower (0.046 cd/m^2) than the background luminance, alternating across lines.

The lines were spaced at regular increments across the array and were aligned along the horizontal or vertical orientations. For each trial, the lines were presented either horizontally or vertically. The orientation was randomly selected on a trial by trial basis.

At the beginning of each test, the overall size of each stimulus was 6.24 degrees on each side. The individual lines comprising the stimulus array, and the spacing between the lines, were 0.16 degrees wide. Across trials, the size and spacing of the lines were reduced until the observer could no longer discriminate the orientation of the lines. The width of the lines and the spacing between the lines decreased in the following sizes: 0.16, 0.135, 0.11, 0.09, 0.07, 0.045, and 0.024 degrees. As the spacing decreased, the overall size of the stimulus also decreased. These sizes, corresponding to the spacing list above were: 6.24, 5.27, 4.29, 3.51, 2.70, and 1.76 degrees.

Procedure

The Procedure was the same as used in Experiments 1, 2, and 3.

<u>Psychophysical Thresholds.</u> To calculate acuity thresholds, a two-alternative forced choice descending staircase procedure was implemented. The descending staircase algorithm reduced the visual angle between the lines after two consecutive correct responses and increased this space after one error. For every incorrect response preceded by two correct responses, a reversal was recorded. Acuity thresholds were based upon the mean of the reversals.

Results

Decline in grouping ability at the farther retinal eccentricities may have resulted from limitations in visual acuity and not due to factors specific to perceptual grouping. In order to assess the effects of acuity on perceptual organization thresholds, measures of discriminating solid lines were obtained at each of the five retinal eccentricities.

Visual inspection of the data shows that acuity was best at 0 and 8 degrees and worsens as retinal eccentricity increases (Figure 10). At all eccentricities, acuity thresholds were below the acuity limit used in the grouping conditions (0.10 degrees). A one-sample t-test revealed that the acuity limits for the previous grouping experiments are significantly different than the mean acuity at 60 degrees ($t(3) = -3.516$, $p < 0.05$). Therefore, differences in perceptual grouping across retinal eccentricity were not due to acuity factors.

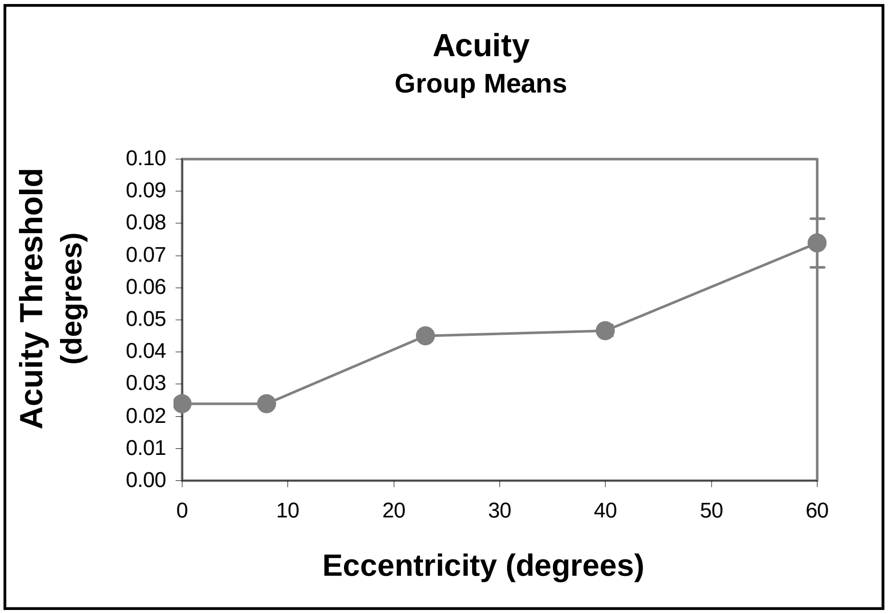

Figure 10. Mean thresholds for acuity as a function of eccentricity.

Error bars represent one SEM.

Discussion

Psychophysical, neuropsychological, and electrophysiological studies have shown that perceptual organization is mediated by many interacting processes, each with their own time course and physiological basis. This is consistent with the results of this study. Although all of the grouping features show a decline with retinal eccentricity, Experiment 1 shows that the features used for grouping by similarity are fundamentally different from each other. This was further supported in Experiment 2, as each feature showed different performance patterns when retinal eccentricity and stimulus metrics were changed.

Luminance. Similarity of luminance grouping thresholds remained stable until a sharp drop-off at 60 degrees eccentric. Statistically, there was a significant decline in thresholds with eccentricity for all stimulus metrics but almost all of these differences were eliminated without the eccentricity of 60 degrees. In addition, there was a significant interaction of eccentricity by metrics, in which at 60 degrees eccentric, there was a significant difference between the metrics such that the large spaced and larger sized stimuli were easiest to group.

Motion. Similarity of motion grouping thresholds gradually declined as retinal eccentricity increased. There was a significant interaction of eccentricity by metrics, in which at 23 degrees eccentric, there was a significant difference between the metrics such that the stimuli with small size elements with large spacing are harder to group than the small elements with small spacing. Furthermore, half of the significant differences across eccentricity for each metric were eliminated when thresholds for 60 degrees are removed from the analysis.

Orientation. Similarity of orientation grouping thresholds remained stable until a decline at an eccentricity of 40 degrees. At 60 degrees, thresholds declined more considerably. Grouping thresholds did not show a significant interaction of eccentricity by metrics. However, there were significant differences in thresholds across eccentricity. Specifically, thresholds at 0, 8, and 23 degrees were not different from each other, but were different than thresholds at 40 and 60 degrees.

Proximity. Proximity grouping thresholds did not change for eccentricities up to 23 degrees. There was a decline in thresholds at 40 degrees and a drastic decline at 60 degrees. Grouping thresholds did not show a significant interaction of eccentricity by metrics. However, there were significant differences in thresholds across eccentricity. Specifically, thresholds at 0, 8, and 23 degrees were not different from each other, but were different than thresholds at 40 and 60 degrees.

Although all features showed different patterns across retinal eccentricity, what was common of all features was that they were all stable, for all metrics, from 0 to 23 degrees. Luminance and motion showed an interaction between eccentricity and metrics, however, orientation and proximity did not. What is common amongst all features is the sharp decline in thresholds at 60 degrees. Furthermore, for all features tested at foveal viewing, there was no difference in performance for any of the six different stimulus metrics.

It is unlikely the decline in performance at 40 or 60 degrees is due to acuity differences. Firstly, acuity levels sharply drop at eccentricities of 3 degrees, whereas performance on perceptual organization tasks measured here did not decline until around 40 degrees. Secondly, Experiment 5 verifies that acuity limits were well below the limits used in the perceptual organization tasks.

The primary hypothesis of these studies was that unlike basic visual processing, perceptual grouping would be less vulnerable to changes in neural representations, indicating that neural processing of grouping is not related to the amount of cortex involved in the processing. In this regard, perceptual grouping capacities would not change with increased eccentricity, or with alterations in the size or spacing of elements. The hypothesis was partially supported in that performance on perceptual organization tasks generally did not decline until 40 or 60 degrees. Therefore, eccentricities up to 23 degrees support the predictions of the primary hypothesis.

An alternative hypothesis was that perceptual organization operates similarly to object recognition, which is optimal in central vision, but declines sharply with eccentricity. This hypothesis is based on the model that the amount of processing by the nervous system is proportionate to the amount of cortical area served by the process. Because less cortical area is devoted to peripheral processing, performance declines. In addition, with this pattern of performance across eccentricity, increasing the scale of the stimulus with greater eccentricity should compensate for cortical magnification and thereby equate performance to foveal levels. However, the pattern of results found here for perceptual grouping did not correspond to the pattern found with object recognition.

In the current studies, even with compensation for cortical magnification, performance in far peripheral vision did not improve by increasing the stimulus scale. This is in contrast to the many studies that have found improvement when size compensations are made to peripheral stimuli. Specifically, peripheral performance can be equated to foveal levels when size-scaling is used in motion detection (van de Grind et al.,1983), letter detection (Melmoth & Rovamo, 2003, Näsänen & O'Leary, 1998, &

Higgins et al., 1996), numerosity (Parth & Rentschler, 1984), and acuity (Virsu et al., 1987).

Although not all past studies attempt to control for cortical magnification factors, performance at eccentric viewing of many basic visual functions can be improved with scaling, whereas this enhancement does not occur for high-order functions. In the current experiments, even after compensation for cortical magnification, the declining perceptual organization performance in far peripheral vision did not improve by increasing the stimulus size, which makes perceptual grouping similar to high-order tasks. Grouping is known to occur at an intermediate level of processing but at far eccentricities, grouping abilities resemble high-order vision. Therefore, these results are consistent with the model that perceptual organization processes takes place after many basic visual functions have completed. This is especially surprising for grouping by proximity, which is considered to be a very low-level process, occurring very early in the stages of the visual system.

One major difference between the current studies and other studies of more basic visual processes are the size of the stimuli. To study perceptual organization, the stimuli must be relatively large, whereas, with more basic visual processes, a small light will generally serve as the stimulus of interest. With perceptual organization tests, the goal is to measure the amount of integration among smaller elements, and therefore must be very much larger than the smaller elemental units. In the studies presented here, the smallest stimulus arrays were 3.9 degrees, so such a stimulus centered at 23 degrees is actually subtending the area 21 to 25 degrees eccentric of the fovea, not just a point at 23 degrees.

Neural Substrate

The neural mechanisms underlying these results are unknown. Perceptual grouping capacities across eccentricity found here do not follow changes predicted by known physiology at the level of the retina or primary visual cortex. The spacing among cortical sites activated by stimulus elements, the degree of neural connectivity among these cortical sites, and the density of neurons activated are all altered with even a slight change in retinal eccentricity, particularly near foveal and para-foveal areas. However, grouping thresholds did not change across eccentricity up to 23 degrees, indicating independence of perceptual grouping from these physiological factors.

Similarly, manipulating the metrics (element spacing and element size) is also associated with changes in the neural representations. Nevertheless, the current studies did not find the changes predicted by what is known of this retinotopic representation.

Furthermore, the decline in performance found at 40 degrees does not correspond to known differences in retinal or cortical features. For example, binocular to monocular borders occurs at 80 degrees. In addition, if these changes in perceptual organization were due to an acuity limit, we would expect the decline in performance to occur in at eccentricities immediately outside the fovea, which was not the case with the current measurements.

In the current studies, Experiment 5 only found differences in laterality for the motion feature. Specifically, performance for left hemi-field viewing was better than performance for right hemi-field viewing. This is consistent with previous studies of motion (Casco & Spinelli, 1988). However, some of the other features were expected to have laterality effects. For example, luminance, with its role in object recognition, would be expected to produce better performance in the left hemi-field. However, psychophysical procedures used here might not have been sensitive enough to detect differences in laterality.

Perceptual Strategies

An important factor with perceptual studies of retinal eccentricity is the ability of participants to fixate in the correct location for the duration of experimental sessions. Participants participating in these experiments were highly trained, motivated observers, and therefore fixation variance was unlikely a factor.

One possible confound of this research, as is common of many psychophysical studies, is that participants may have adopted different perceptual strategies for solving the discrimination task. For example, an observer did not necessarily have to pay attention to all elements in a stimulus array. Observers may have solved the discrimination task by attending to strings of elements that form contours along one orientation. For example, with the proximity grouping cue, observers may have found strings by the density of elements. A strategy for the luminance condition may have been to look at contrast borders of the two element types. Similarly, participants may have attended to only strings of high luminance while ignoring low luminance elements. For motion stimuli, observers may have localized strings of coherent moving dots. Finally, for the orientation condition, participants may have attended to strings of co-linear or co-axial elements. Using local strings to solve the grouping task, instead of globally processing the entire stimulus array, would be more difficult for the 60 degree eccentricity condition because smaller strings at this eccentricity would likely approach the limits of acuity or contrast sensitivity.

Role in Locomotion

A possible explanation for the pattern of results found here is that retinal eccentricities up to 40 degrees have different ecological significance for animals. When looking and moving forward, objects included in the visual field 40 degrees on each side are the objects in one's path. Grouping is therefore important for locomotion in order to analyze objects in or near the path of movement. For these conditions, object recognition is the goal.

In contrast, in the far periphery (past 40 degrees), object recognition, and therefore perceptual organization, is less important. Instead, the role of the far periphery is to alert the visual system to the presence of an object so that eye movements can be made to foveate these objects.

Future Research

Based upon the current research, perceptual grouping declines somewhere between an eccentricity of 23 and 40 degrees. However, the stimuli used in the current studies are too large to precisely describe the nature of the decline. Future research should use smaller stimuli at more levels of eccentricity to better specify the precise retinal location and the pattern at which perceptual organization declines. It will be important to more fully understand perceptual organization and the neural mechanisms that serve such processes if the pattern of grouping performance across retinal eccentricity can be more fully explained.

Also, it is important to investigate performance across retinal eccentricities of other perceptual organization tasks, such as similarity of color and flicker, or other spatial relationships, such as good continuation. Color analysis includes higher levels of processing than any of the tasks investigated in these studies and it is therefore important to compare performance to the tasks explored here. Flicker detection and motion detection are processed similarly in the visual system and, therefore, perceptual grouping by similarity of flicker should be similar to that of motion.

Another possible line of research would be to investigate if reducing luminance levels of the stimulus elements effects perceptual grouping performance across retinal eccentricity. The studies of perceptual grouping presented here were done with luminance levels well above threshold and therefore the results cannot be generalized to perceptual grouping with luminance at or near threshold level.

Finally, it will be important to further study the laterality effects. One obvious study will be to test thresholds at eccentricities above and below the fovea. These areas also correspond to known differences in physiology and therefore, thresholds obtained at these eccentricities will provide crucial information about the underlying neural substrate that serves perceptual organization.

In the studies of perceptual organization presented here, thresholds from all four grouping features declined with retinal eccentricity, although not in the pattern predicted by the primary hypothesis. Each feature showed a unique pattern as a function of retinal eccentricity and, for all features, there was no difference between performance at 0, 8, or 23 degrees. Furthermore, the expected differences between the stimuli with different metrics were not found. The results are inconsistent with what is known about the retinotopic organization and cortical magnification of the early stages of visual processing.

References

Adams, D. L., & Horton, J. C. (2003). A precise retinotopic map of primate striate cortex generated from the representation of angioscotomas. The Journal of Neuroscience, 23 (9), 3771-3789.

Altmann, C. F., Bülthoff, H. H., & Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in human visual cortex. Current Biology, 13, 342-349.

Anderson, R. S., & Thibos, L. N. (2004). The filtered Fourier difference spectrum predicts psychophysical letter discrimination in the peripheral retina. Spatial Vision, 17, 5-15.

Azzopardi, P., Jones, K. E., & Cowey, A. (1999). Uneven mapping of magnocellular and parvocellular projections from the lateral geniculate nucleus to the striate cortex in the macaque monkey. Vision Research, 39, 2179-2189.

Beck, D. M., & Palmer, S. E. (2002). Top-down influences on perceptual grouping. Journal of Experimental Psychology: Human Perception and Performance, 28, 1071-1084.

Behrmann, M., & Kimchi, R. (2003). What does visual agnosia tell us about perceptual organization and its relationship to object perception? Journal of Experimental Psychology: Human Perception and Performance, 29, 19-42.

Ben-Av, M. B., & Sagi, D. (1995). Perceptual grouping by similarity and proximity: Experimental results can be predicted by intensity autocorrelation. Vision Research, 35, 853-866.

Bock, O. (1993). Localization of objects in the peripheral visual field. Behavioural Brain Research, 56, 77-84.

Brown, J. L. (1965). Flicker and intermittent stimulation. In C. H. Graham (Ed.), Vision and Visual Perception (pp. 251-320). New York: Wiley.

Carrasco, M., McElree, B., Denisova, K., & Giordano, A. M. (2003). Speed of visual processing increases with eccentricity. Nature Neuroscience, 6, 699-700.

Casco, C. & Spinelli, D. (1988). Left-right visual field asymmetry in bistable motion perception. Perception, 17(6), 721-727.

Chen, W., Zhu, X.-H., Thulborn, K. R., & Ugurbil, K. (1999). Retinotopic mapping of lateral geniculate nucleus in humans using functional magnetic resonance imaging. Proc Natl Acad Sci USA, 96, 2430-2434.

Davidoff, J., & Warrington, E. K. (1999). The bare bones of object recognition: implications from a case of object recognition impairment. Neuropsychologia, 37, 279-292.

Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., Schroeder, C. E., & Javitt, D.C. (2000). Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. Journal of Cognitive Neuroscience, 12, 615-621.

Dechent, P., & Frahm, J. (2003). Characterization of the human visual V6 complex by functional magnetic resonance imaging. European Journal of Neuroscience, 17, 2201-2211.

Engel, S. A., Glover, G. H., & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. Cerebral Cortex, 7, 181-192.

Espinoza, S. G., & Thomas, H. C. (1983). Retinotopic organization of striate and extrastriate visual cortex in the hooded rat. Brain Research, 272, 137-144.

Feldman, J. (2000). Bias toward regular form in mental shape spaces. Journal of Experimental Psychology: Human Perception and Performance, 26, 152-165.

Feldman, J. (1999). The role of objects in perceptual grouping. Acta Psychologica, 102, 137-163.

ffytche, D. H., & Zeki, S. (1996). Brain activity related to the perception of illusory contours. Neuroimage, 3, 104-108.

Fink, G. R., Halligan P. W., Marshall, J. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1997). Neural mechanisms involved in the processing of global and local aspects of hierarchically organized visual stimuli. Brain, 120, 1779-1791.

Fize, D., Vanduffel, W., Nelissen, K., Denys, K., Chef d'Hotel, C., Faugeras, O., et al. (2003). The retinotopic organization of primate dorsal V4 and surrounding areas: a functional magnetic resonance imaging study in awake monkeys. The Journal of Neuroscience, 23, 7395-7406.

Galletti, C., Fattori, P., Kutz, D., F., & Gamberini, M. (1999). Brain location and visual topography of cortical area V6A in the macaque monkey. European Journal of Neuroscience, 11, 575-582.

Gattass, R., Gross, C. G., & Sandell, J. H.(1981). Visual topography of V2 in the macaque. The Journal of Comparative Neurology, 201, 519-539.

Gattass, R., Sousa, A. P. B., & Gross, C. G. (1988). Visuotopic organization and extent of V3 and V4 of the macaque. Journal of Neuroscience, 8, 1831-1845.

Gattass, R., Sousa, A. P. B., & Rosa, M. G. P. (1987). Visual topography of V1 in the Cebus monkey. The Journal of Comparative neurology, 259, 529-548.

Giorgi, R. G., Soong, G. P., Woods, R. L., & Peli, E. (2004). Facilitation of contrast detection in near-peripheral vision. Vision Research, 44, 3193-3202.

Graham, C. H. (1965). Perception of movement. In C. H. Graham (Ed.), Vision and Visual Perception (pp. 575-588). New York: Wiley.

Grossberg, S., & Raizada, R. D. S. (2000). Contrast-sensitive perceptual grouping and object-based attention in the laminar circuits of primary visual cortex. Vision Research, 40, 1413-1432.

Han, S. E., Humphreys, G. W., & Chen, L. (1999). Parallel and competitive processes in hierarchical analysis: perceptual grouping and encoding of closure. Journal of Experimental Psychology: Human Perception and Performance, 25, 1411-1432.

Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Gu, H. (2005). Attentional modulation of perceptual grouping in human visual cortex: functional MRI studies. Human Brain Mapping, 25, 424-432.

Han, S., Jiang, Y., Mao, L., Humphreys, G. W., & Qin, J. (2005). Attentional modulation of perceptual grouping in human visual cortex: ERP studies. Human Brain Mapping, 26, 199-209.

Harris, J. P., & Fahle, M. (1996). Differences between fovea and periphery in the detection and discrimination of spatial offsets. Vision Research, 36, 3469-3477.

Hess, R. F., & Dakin, S. C. (1997). Absence of contour linking in peripheral vision. Nature, 390, 602-604.

Higgins, K. E., Arditi, A., & Knoblauch, K. (1996). Detection and identification of mirror-image letter pairs in central and peripheral vision. Vision Research, 36, 331-337.

Horton, J. C., & Hoyt, W. F. (1991). The representation of the visual field in human striate cortex. A revision of the classic Homes map. Archives of Ophthalmology, 109, 816-825.

Huk, A. C., Dougherty, R. F., & Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. Journal of Neuroscience, 22, 7195-7205.

Ikeda, H., Blake, R., & Watanabe, K. (2005). Eccentric perception of biological motion is unscalably poor. Vision Research, 45, 1935-1943.

Julesz, B. (1984). A brief outline of the texton theory of human vision. Trends in Neuroscience, 6, 41-45.

Kimchi, R. (2000). The perceptual organization of visual objects: a microgenetic analysis. Vision Research, 40, 1333-1347.

Kimchi, R., & Hadad, B.-S. (2002). Influence of past experience on perceptual grouping. Psychological Science, 13, 41-47.

Kimchi, R., & Palmer, S. E. (1985). Separability and integrality of global and local levels of hierarchical patterns. Journal of Experimental Psychology: Learning, Memory, and Cognition, 11, 673-688.

Kubovy, M., & Wagemans, J. (1995). Grouping by proximity and multistability in dot lattices: A quantitative gestalt theory. Psychological Science, 6, 225-234.

Kurylo, D. D. (2006). Effects of Aging on Perceptual Organization: Efficacy of Stimulus Features. Experimental Aging Research, 32, 137-152.

Kurylo, D. D. (1997). Time course of perceptual grouping. Perception and Psychophysics, 59, 142-147.

Lamb, M. R., Robertson, L. C., & Knight, R. T. (1990). Component mechanisms underlying the processing of hierarchically organized patterns: inferences from patients with unilateral cortical lesions. Journal of Experimental Psychology: Learning, Memory, and Cognition, 16, 471-483.

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. Trends in Neuroscience, 23, 571-579.

Lee, H.-W., Legge, G. E., & Ortiz, A. (2003). Is word recognition different in central and peripheral vision? Vision Research, 43, 2837-2846.

Levine, M. (2000). Levine and Shefner's Fundamentals of Sensation and Perception, 3rd ed. New York: Oxford University Press Inc.

Lyon, D. C., Xu, X., Casagrande, V. A., Stefansic, J. D., Shima, D., & Kaas, J. H. (2002). Optical imaging reveals retinotopic organization of dorsal V3 in New World owl monkeys. Neuroscience, 99, 15735-15742.

Mäkelä, P., Näsänen, R., Rovamo, J., & Melmoth, D. (2001). Identification of facial images in peripheral vision. Vision Research, 41, 599-610.

Melmoth, D. R., & Rovamo, J. M. (2003). Scaling of letter size and contrast equalizes perception across eccentricities and set sizes. Vision Research, 43, 769-777.

Moore, C. M., & Egeth, H. (1997). Perception without attention: evidence of grouping under conditions of inattention. Journal of Experimental Psychology: Learning, Memory, and Cognition, 23, 339-352.

Näsänen, R., & O'Leary, C. (1998). Recognition of band-pass filtered hand-written numerals in foveal and peripheral vision. Vision Research, 38, 3691-3701.

Palmer, S. E. (1975). Visual perception and world knowledge: Notes on a model of sensory-cognitive interaction. In D. A. Norman & D. E. Rumelhart (Eds.), Exploration in Cognition (pp. 279-307). San Francisco: Freeman.

Palmer, S. E. (1983). The psychology of perceptual organization: a transformational approach. In J. Beck, B. Hope, & A. Rosenfeld (Eds.), Human Machine Vision (pp. 269-339). New York: Academic Press.

Palmer, S. E. (1992). Common region: a new principle of perceptual grouping. Cognitive Psychology, 24, 436-447.

Palmer, S. E. (2002). Perceptual grouping: It's later than you think. Current Directions in Psychological Science, 11, 101-106.

Palmer, S. E., & Rock, I. (1994). Rethinking perceptual organization: The role of uniform connectedness. Psychonomic Bulletin & Review, 1, 29-55.

Parth, P., & Rentschler, I. (1984). Numerosity judgments in peripheral vision: Limitations of the cortical magnification hypothesis. Behavioural Brain Research, 11, 241-248.

Popovic, Z., & Sjöstrand, J. (2001). Resolution, separation of retinal ganglion cells, and cortical magnification in humans. Vision Research, 41, 1313-1319.

Prince, S. J. D., & Rogers, B. J. (1998). Sensitivity to disparity corrugations in peripheral vision. Vision Research, 38, 2533-2537.

Riggs, L. (1965). Visual acuity. In C. H. Graham (Ed.), Vision and Visual Perception (pp. 321-349). New York: Wiley.

Rodieck, R. W. (1998). The First Steps in Seeing. Sunderland, MA: Sinauer Associates, Inc.

Sally, S. L., & Gurnsey, R. (2003). Orientation discrimination in foveal and extra-foveal vision: effects of stimulus bandwidth and contrast. Vision Research, 43, 1375-1385.

Sally, S. L., & Gurnsey, R. (2004). Orientation discrimination across the visual field: matching perceived contrast near threshold. Vision Research, 44, 2719-2727.

Schein, S. J., & de Monasterio, F. M. (1987). Mapping of retinal and geniculate neurons onto striate cortex of macaque. Journal of Neuroscience, 7, 996-1009.

Schiessl, I., & McLoughlin, N. (2003). Optical imaging of the retinotopic organization of V1 in the common marmoset. NeuroImage, 20, 1857-1864.

Schuett, S., Bonhoeffer, T., & Hübener, M. (2002). Mapping retinotopic structure in mouse visual cortex with optical imaging. The Journal of Neuroscience, 22, 6549-6559.

Schulz, M. F., & Sanocki, T. (2003). Time course of perceptual grouping by color. Psychological Science, 14, 26-30.

Sjöstrand, J., Osson, V., Popovic, Z., & Conradi, N. (1999). Quantitative estimations of foveal and extra-foveal retinal circuitry in humans. Vision Research, 39, 2987-2998.

Stettler, D. D., Das, A., Bennett, J., & Gilbert, C. D. (2002). Lateral connectivity and contextual interactions in macaque primary visual cortex. Neuron, 36, 739-750.

Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. Nature, 401, 269-272.

Tadin, D., Lappin, J. S., Blake, R., & Grossman, E. D. (2002). What constitutes an efficient reference frame for vision? Nature Neuroscience, 5, 1010-1015.

Thorpe, S. J., Gegenfurtener, K. R., Farbe-Thorpe, M., & Bulthoff, H. H., (2001). Detection of animals in natural images using far peripheral vision. European Journal of Neuroscience, 14, 869-876.

Tootell, R. B. H., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988). Functional anatomy of macaque striate cortex. II. Retinotopic organization. Journal of Neuroscience, 8, 1531-1568.

Treisman, A. (1986). Features and objects in visual processing. Scientific American, 254, 114-125.

Trick, L. M., & Enns, J. T. (1997). Clusters precede shapes in perceptual organization. Psychological Science, 8, 124-129.

van de Grind, W. A., van Doorn, A. J., & Koenderink, J. J., (1983). Detection of coherent movement in peripherally viewed random-dot patterns. Journal of the Optical Society of America, 76, 1674-1683.

Vecera, S. P., & Behrmann, M. (1997). Spatial attention does not require preattentive grouping. Neuropsychology, 11, 30-43.

Vecera, S. P., & Gilds, K. S. (1999). What processing is impaired in apperceptive agnosia? Evidence from normal subjects. Journal of Cognitive Neuroscience, 10, 568-580.

Virsu, V., Näsänen, R., & Osmoviita, K. (1987). Cortical magnification and peripheral vision. Journal of the Optical Society of America A, 4, 1568-1578.

Wagor, E., Mangini, N. J., & Pearlman, A. L. (1980). Retinotopic organization of striate and extrastriate visual cortex in the mouse. The Journal of Comparative Neurology, 193, 187-202.

Wandell, B. A. (1999). Computational neuroimaging of human visual cortex. Annual Review of Neuroscience, 22, 145-173.

Westheimer, G. (2003). The distribution of preferred orientations in the peripheral visual field. Vision Research, 43, 53-57.

Westheimer, G. (1999). Gestalt theory reconfigured: Max Wertheimer's anticipation of recent developments in visual neuroscience. Perception, 28, 5-15.

Williams, L. J. (1984). Information processing in near peripheral vision. The Journal of General Psychology, 111, 201-207.