Understanding the mechanisms of flicker defined form processing

by

Deborah Goren

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Abstract

Flicker defined form (FDF) is a temporally-dependent illusion created by the counterphase flicker of randomly positioned element dots, that preferentially stimulates the magnocellular system. Previous studies have found improvement with peripheral presentation, a resistance to blur and a dependence on high temporal frequencies (Quaid & Flanagan, 2005a; Quaid & Flanagan, 2005b). Although it is seemingly very different from most luminance defined, static stimuli, it is still unknown in what ways it differs. The current study aimed to determine how FDF varies or is similar to static, luminance defined stimuli. Current results showed that FDF could be matched to particular spatial frequencies, and improved with increasing background structure and area. Shapes could be discriminated from each other and recognized. These results suggest that although FDF is dependent on motion pathways for temporal dynamic perception, it could also benefit from the input of form perception pathways, depending on the cues present in the stimulus (*e.g.* background structure, area). Results also showed that FDF does not benefit from Gestalt rules of contour closure, unlike some static stimuli, although related studies have shown that FDF could still be detected in spite of blur. These studies suggest that FDF appears to rely on motion perception pathways, areas such as MT, but is easier to perceive at times due to overlap in function with shape perception pathways, areas such as IT. As such FDF shares many characteristics with other motion-defined-form stimuli, but uniquely shares aspects of form vision.

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Dedication

I dedicate this thesis to my aunt who would have been the first one to throw my celebratory party.

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Chapter 1

Introduction: What is FDF and why is it special?

1.1 FDF: What is it and why is it special?

Many visual stimuli are defined by differences in luminance that create edges between background and the stimulus, or within an image. Flicker defined form (FDF) is an illusory contour stimulus that cannot be perceived using purely luminance differences. The luminance differences between the background and stimulus elements are being constantly flickered in counterphase. Randomly placed dot elements within the stimulus are always the ‘opposite’ luminance to background dots. Whenever the background dots are a particular magnitude above the average luminance, the stimulus dots are that same magnitude below the average. The background and stimulus alternate between these two luminance levels which represent different phases in the square wave modulation, creating counterphase flickering regions of dots (stimulus and background) at a high temporal frequency. The visual system’s temporal limitations are such that very high temporal frequencies prevent the ability to see the two alternations that make up the flickering. It is this limitation that ensures that above 15Hz FDF’s two phases (above and below the average luminance) cannot be distinguished. This means that luminance cues cannot be used as a primary cue to distinguish background from the stimulus. If the luminance differences between background and stimulus were entirely ‘invisible’ then there would be no cues at all to distinguish background from stimulus. Flickering inside and outside of the stimulus are occurring at the same times, so that the temporal phases are the same. Only the luminance phases are misaligned temporally. Although the luminance phases cannot be distinguished, they likely contribute to FDF perception.

Originally referred to as the phantom contour illusion by Rogers-Ramachandran and Ramachandran (1998), this illusion has a number of distinctive properties which distinguish it from other, static illusory contour stimuli. Among these is the importance of luminance to define the two regions. As mentioned above, luminance is often used as a cue to distinguish a stimulus from a background. This original study found that the same high temporal frequency alternation with patches that varied according to hue, instead of luminance were incapable of creating the percept. Although contrast is important, this study also found that even at low contrasts such as 10%, the percept can be seen. Another study has shown that not only simple shapes, but also letters can be detected (Flanagan et al., 1995).

Temporal modulation is also necessary for perception of FDF (Rogers-Ramachandran & Ramachandran., 1998). Temporal frequencies above 15Hz produce the percept, whereas for frequencies between 7 and 15Hz the phases (luminance phases above and below average luminance) can be discriminated. The visual system is capable of discriminating light from dark in the FDF stimulus, between 7Hz and 15Hz (phase durations: 143ms and 67ms) because the duration of each phase is long enough to be perceived individually. Fifteen Hz results in a duration that is not long enough to be perceived, possibly due to the constant masking effects of one phase following another. If the phases can be discriminated, the temporal modulation is the major cue to the contour and is no longer illusory. Thus, the temporal frequency must be above 15Hz.

Both the original study and many studies following have shown that FDF is easier to perceive farther into the periphery (Quaid & Flanagan., 2005; Rogers-Ramachandran & Ramachandran, 1998). Quaid and Flanagan (2005) showed a complicated relationship between stimulus size, dot density and eccentricity. The variability in contrast thresholds (measured in log Michelson contrast units) increases with increasing task difficulty. Smaller dot densities and target sizes increased both thresholds and variability of these thresholds. In more limiting cases, such as low dot densities (less than 2 dots per degree) the improvement with increasing peripheral presentation (>3˚) is apparent. More favourable conditions, such as higher dot densities (~3 dots/degree), show much less effect of eccentricity.

Depth can also be perceived when flicker frequencies are between 5 and 31.3Hz (Iwabuchi & Shimizu, 1997). Smaller areas are perceived in front, which means that the FDF target will most likely be perceived in front. Increasing density of dots which is known to improve detection (Quaid & Flanagan, 2005), also improves depth perception of the illusion (Iwabuchi & Shimizu., 1997).

1.1.1 Magnocellular dominance

Many of the characteristics of FDF point to a dominance of the magnocellular system. Although magnocellular and parvocellular cells respond to similar frequencies, magnocellular cells are more sensitive to high temporal frequencies and low spatial frequencies (Derrington & Lennie, 1984). These properties reflect retinal anatomy and physiology such as a greater proportion of magnocellular ganglion cells as compared to parvocellular cells in the peripheral retina that may contribute to a strong role in peripheral perception (Azzopardi et al., 1999), transient responses (shorter latency to respond, but faster to stop responding), and larger receptive fields (Derrington & Lennie, 1984). Physiological evidence points to the importance of the role of magnocellular input into the medial temporal area (MT), responsible for recognizing the motion of objects. A study which inactivated the magnocellular layers of the lateral geniculate nucleus (LGN- responsible for connecting retinal structures to cortical structures) showed that neurons in MT showed large decreases in activation, whereas most neurons showed a much smaller effect for parvocellular inactivation (Maunsell et al., 1990). Some neurons were sensitive to parvocellular activity, but the decreases in activation were still significantly smaller than those seen in magnocellular cells.

Lesioning of the M layers of the LGN showed a greater detriment for flicker perception, as compared to drift perception (Merigan et al., 1991). Effects of magnocellular deactivation can be seen as an increase in motion thresholds, but not a complete loss of motion perception. The finding that motion perception was not entirely extinguished means that the magnocellular pathway is not the only pathway contributing to motion perception. This is not surprising given that the two major pathways (dorsal and ventral) receive information from both magnocellular and parvocellular input (Ferrera et al., 1994; Nealey & Maunsell, 1994; Maunsell et al.; 1990; Merigan et al., 1991). The study by Merigan et al. (1991) showed that when contrast of the stimulus was increased, motion perception improved, in spite of a lack of magnocellular input. This study suggests, contentiously so, that if an increase in stimulus contrast can compensate for the lack of magnocellular input, the role of the M pathway is to increase contrast for motion perception. Leonards and Singer (1997) suggest that the magnocellular system is sensitive to contrast, but its most important role is in the perception of precise temporal structure.

1.2 Mechanisms for FDF processing

It is still unclear what mechanisms are responsible for FDF perception. Luminance information cannot be used explicitly because the differences between the phases can not be distinguished. Still, when the stimuli are made isoluminant (equal luminance for stimulus and background) with colour differences between the regions, the illusion can no longer be perceived, suggesting a reliance on luminance information. This seeming paradox means that it is difficult to determine the cortical pathways involved. Based on the importance of temporal and spatial information, it seems likely that both the ventral and dorsal streams are involved.

Primary visual cortex is a relay centre for information which comes from the LGN and is passed onto other cortical structures. It makes sense that an area such as V1 which does some primitive processing and passes on signals to other visual areas, both dorsal and ventral, receive input from magnocellular and parvocellular pathways. Livingstone & Hubel (1984) attempted to show segregation between parvocellular and magnocellular pathways by demonstrating that these pathways send their information to different regions of the visual cortex. Blobs, which contain cytochrome oxidase (a mitochondrial enzyme), are most prominent in layers 2 and 3, of area 17 in primates (a physiological correlate of human V1). These blobs project to the thin stripes of area 18 (a physiological correlate of human V2, Livingstone & Hubel, 1984). Livingstone & Hubel (1984) could not determine the origin of information for blobs. Interblobs (the regions between blobs) project to the interstripe areas of area 18 and receive information from parvocellular cells. Livingstone & Hubel proposed that the segregation of information suggested a separation between magnocellular and parvocellular pathways.

More recent evidence suggests that magnocellular and parvocellular information is used by many cortical regions both early and late in processing. In primate V1 the signals from magnocellular cells are sent to many different areas within the superficial layers, including both blob and interblobs, allowing information to 'mix' within these areas. Also, many neurons in V1 receive information from both parvocellular and magnocellular pathways (Nealey & Maunsell, 1994).

The dorsal stream, previously believed to receive all information from magnocellualr projections (Livingstone & Hubel, 1984), receives input from both magnocellular and parvocellular pathways. By inactivating layers of the LGN receiving magnocellular input, Maunsell et al. (1990) showed that the responses of neurons within MT decrease and perception of motion is compromised. Inactivating parvocellular input to MT had minimal impact. Although these results lend strength to the segregation of the two pathways, some neurons in MT received parvocellular input (Maunsell at al., 1990). Behaviourally, motion perception, compromised when magnocellular input is removed, is still possible with compensatory contrast (Merigan et al., 1991), suggesting a role for the parvocellular pathway in motion perception.

The ventral stream regions also receive input from both pathways. V4, a region in the ventral stream which is believed to be responsible for colour and basic shape perception, receives input from magnocellular and parvocellular pathways. When either of the two pathways is blocked a large reduction in response is found for neurons in V4 (Ferrera et al., 1994). In fact, the amount of reduction is similar for both pathways, suggesting a similar role for the two pathways. These results, in combination with above results, suggest that even highly specialized cortical regions, which might appear to benefit from signals from only one pathway, receive input from both, and rely on both pathways for a complete response.

A number of pieces of evidence point to the dominance of the magnocellular pathway in FDF perception. As mentioned earlier, the improvement in performance with increasing eccentricity, resistance to blur and reliance on high temporal frequencies point to the role of the magnocellular system (Livingstone & Hubel, 1987).

1.3 Figure ground segregation

At first glance, FDF seems to be very similar to figure ground segregation. Perceptual binding of elements which are spatially separated is improved by a number of different characteristics. Other forms of figure ground segregation include stimuli in which figure and background are defined in different ways (*e.g.* different orientations, motion directions). In all of these tasks the background serves to distract from the form elements because of similarity between figure and background elements.

1.3.1 What is it?

Figure ground segregation benefits from a number of spatial characteristics. Among them is the spacing of elements (Bex et al., 2003b), phases of the individual elements and curvature of the contour. Hess et al (2001) showed that greater curvature slows the contour extraction system and makes it more difficult to perceptually bind elements when they are being temporally modulated at higher temporal frequencies (*e.g.* orientation modulations). This study also found that contour extraction is more duration-dependent for curved than straight contours (Hess et al., 2001). Perception of curvature is also less tolerant of variation in spatial frequency between contour elements. Octaves, a measure of the amount of bandwidth (variation between frequencies), represent a factor of two in variation (*i.e.* Bandwidth = 2^{octaves}). A straight contour can tolerate 1.3 octaves of variation (a factor of 2.5 times), whereas a curve with 30° of curvature can only tolerate 0.7 octaves (a factor of 1.6 times, Dakin & Hess, 1998). This difference in tolerance for spatial frequency bandwidth is important because it suggests differences in how straight and closed contours are processed. Larger bandwidths indicate that a larger range of spatial frequency variation can be tolerated within the contour. Straighter contours, which are still perceivable with larger spatial frequency bandwidths than curved contours, most likely represent more convergence of spatial frequency channels. Conversely, curved contours, which tolerate a smaller bandwidth, represent less convergence between spatial frequency selective V1 cells.

One of the important structural characteristics which improves perception of figure ground is closure (Kovacs & Julesz, 1993). Kovacs & Julesz (1993) found that contours which create enclosed shapes are easier to detect. This study also found that objects which appear inside of a closed contour are easier to detect.

1.3.2 Mechanisms

One of the mechanisms for figure-ground perception is the association field. Lying outside the boundaries of the classic receptive field, are regions that respond to the connection between separated elements. The spatial extent of these effects is still debated. A range of 3 to 10° has been found, although some of the discrepancies may be due to methodological differences (Marcus & Van Essen, 2002; Rossi et al., 2001; Zipser et al., 1996).

Typically, contextual modulation works to increase the salience of an element that is more difficult to see. One of the mechanisms that help to promote the increased salience of elements which are spatially separated is filling-in. Filling-in is a process which ‘connects’ spatially separated elements , to create a more continuous contour. Filling-in is more likely in cases where elements are located close to each other, particularly when orientations are the same (Polat & Sagi, 2007). Facilitation between elements which are probably part of a common path (*e.g.* share similar orientations, are located within limits listed above) is created between the neurons that are activated by the individual elements. The connection between these two neurons creates the percept of a more connected contour. Lateral interactions are believed to be antagonistic within close proximities (double the spatial extent of the target), and facilitative within farther distances (10 times the spatial extent of the target, Polat & Sagi, 1993). The strength of the lateral interactions is also dependent on spatial frequency and orientation of the elements. Filling-in has been proposed as the mechanism for illusory contour perception. In the case of FDF, filling-in could be creating perceptual ‘bridges’ between the spatially separated elements, creating a more connected percept.

1.3.3 Where and when

In order to determine the common processing element for all figure ground tasks, which can rely on different ‘grouping’ mechanisms, one common element that has been proposed is an enhancement of activity in V1 neurons (Lamme, 1995). Using figure ground tasks which rely on orientation and motion-based variation, individual cell responses in V1 of monkeys was enhanced when the figure was present in a cell’s receptive field, as compared to the background (Lamme, 1995). The fact that enhancement is found for one area of the image, even though both contain images with similar elements, suggests that the figure is treated in a special way. This enhancement is seen at a latency of 30-40ms after the first response. Given that this is a second response, following the initial response, coupled with the short latency hints at feedback from V2. Figure ground percepts have been attributed to horizontal connections between cells in V1. Longer range connections, such as those that span more than a few millimeters, link cells with similar orientations, particularly those that are collinear (Lamme, 2003). These connections explain the majority of the effects of association fields, such as the facilitation that is seen for elements which are spaced up to 10 times the length of each element (Polat & Sagi, 1993).

Most figure ground separation research shows a strong role of V1 and V2 (discussed above) which are involved with basic contour perception. Some research shows the involvement of higher order cortical areas. Once the extrastriate areas were removed, figure ground perception was impaired. In contrast, detection of luminance defined contours were unaffected. These findings suggest two things. First, figure ground stimuli are processed differently than non-figure ground stimuli (*e.g.* contours that are not composed of separated elements). Second, V1 and V2 are not the only regions necessary for figure ground perception (Super & Lamme, 2007). In this same study, cueing the target location improved performance markedly, suggesting that higher cortical areas contribute to cuing in figure ground tasks, but this same cueing is not as important for non-figure ground tasks.

The term figure ground segregation encompasses a number of different types of stimuli that may rely on different mechanisms. Thus, one particular pathway may not account for all of the different stimuli that are considered figure ground. It may be that simple figure ground tasks, such as pop-out tasks (recognizing an aberrant element) do not require feedback from higher cortical areas, but that more complex figure ground tasks such as contour binding require some feedback (Lamme, 2003).

1.3.4 Implications for FDF

FDF is a good example of why figure ground tasks can vary so significantly. FDF varies from many of the typical figure ground segregation tasks in two important ways which makes it potentially mechanistically different. Although FDF is similar to some figure ground tasks which constitute an entire patch that is different from the background, but varies from those tasks which require contour completion. Second, the addition of a shared temporal component to elements which define the contour improves binding and contour perception. Although some figure ground tasks use motion as a cue to segregation, this motion is distinguishable, FDF has a luminance cue to segregation which, although not perceptually distinguishable, may be contributing to the segregation process.

1.4 Illusory contours

1.4.1 Mechanisms

Mechanistically, static illusory contour perception is poorly understood. A number of different theories have been proposed. Among them are models based on: different perceived depths of the fore and background (cues-to-depth); the position of an object in relation to the world (object-cue); completion of surfaces (gestalt completion); differences in brightness between figure and background (brightness-contrast); and edge detector processing of both real and illusory contours (feature-edge detection, Seghier & Vuilleumier, 2006).

One of the mechanisms responsible for a particular category of illusory contours is end stopping (Peterhans & von der Heydt, 1989). End stopping can be used to explain abutting line gratings (von der Heydt & Peterhans, 1989). These gratings are defined by luminance in one orientation, but the illusory contour is created orthogonally to the lines that create it. End stopping is a phenomenon which suppresses cortical signals which extend beyond the classical receptive field. A line which is ‘too’ long will actually produce a smaller signal than a smaller line of the same width, orientation, and spatial frequency. These types of effects are commonly found in V1, particularly in layers 2&3, and 4. The mechanisms that control the ability of these layers to perform end stopping seem to reside in layers 6 of V1 and the dorsocaudal claustrum, which projects primarily to layer 4 of V1 (Bolz & Gilbert, 1986; Sherk & LeVay, 1983). End stopping is a function that can be attributed to the extra-classical receptive field. The extra-classical receptive field which can extend up to 13° is believed to be dependent on horizontal connections within V1 and feedback from V2, V3 and MT (Angelucci & Bullier, 2003).

Filling-in, as mentioned earlier, has also been proposed as a mechanism for illusory contour perception (Polat & Sagi, 2007). The perceptual bridging of gaps may help to complete incomplete figures.

1.4.2 Static Illusory contours: Time course

Illusory contour stimuli are processed later than non-illusory stimuli, probably due to more feedback. Ringach and Shapley (1996) showed the time course of processing of Kanisza illusory figures through the use of psychophysical backward masking. Kanisza figures were stimuli that created the percept of a figure due to the placement of inducers. These inducers were typically placed at corners, or in other salient regions of the figure. Ringach and Shapley's backward masking paradigm involved presenting the Kanisza figure, followed by a luminance defined shape, or a series of inducers that do not create a Kanisza figure, or another illusory contour. Each mask type affected the processing of the original illusory contour at a different time. Masking effects due to the masking of inducers was found at 117ms (Ringach et al., 1996). Masking found at 140-200ms was most effective for illusory figure masks, suggesting that this period was when the illusory component of the stimulus, not the inducers, was being processed.

Using backward masking techniques, Imber and Shapley (2005) showed that illusory contours are indeed processed differently than non-illusory contours. This study used illusory contours reliant on inducers, similar to Kanisza squares. Masking studies rely on the principle that in order for one image to mask another, the two images must be processed in the same region at the same time in order for perception of the target image to be affected (Anbar & Anbar, 1982). In the case of illusory contours, Imber et al. (2005) found that the masking effects of illusory contours occur more than 117ms after stimulus onset (Imber et al., 2005), similar to the previous study (Ringach et al., 1996). The masking of inducers, without a corresponding illusory contour, did not have the same effect. Ringach et al. suggest that processing of illusory contours takes at least 117ms, and that the region responsible for processing these illusory contours at 117ms is separate from the region which processes non-illusory contours. This effect is only seen until approximately 400ms, when illusory and non-illusory contour masks have equal effect on illusory contour perception. This 400ms limit may reflect the amount of time that the illusory contour is still being processed.

1.4.3 When and where: The role of V1 and V2

The roles of V1 and V2 for static illusory contour perception are widely debated. Some of these discrepancies may be due to methodological differences between the studies.

Static illusory contours are believed to be processed primarily in V2, which then feeds back to V1. This is different from non-illusory contours which are processed in V1, which then sends its information to V2. Thus, the sequence of visual areas involved is seemingly backwards for illusory contours. A study of abutting line gratings in monkeys showed that V2 is more active than V1 for processing this illusory contour. Abutting line gratings are those created by two groups of parallel lines that are offset from each other, creating the percept of a line. For this particular type of illusory contour, more salient abutting line gratings created greater activation in V2 than in V1 (von der Heydt et al., 1984). According to a single cell recording study in monkeys, both V1 and V2 are involved in illusory contour perception, although the time course and importance of each region is different (Lee & Nguyen, 2001). When viewing Kanisza figures, cells in V2 were activated at 70ms. Cells in V1 were activated at 100ms. Activation in V1, which occurs after V2, was also much smaller than in V2. Similar to Von der Heydt's findings, these results suggest a stronger role for V2 in illusory contour perception. Also of note is that these two studies used different static illusory contour stimuli, which were processed using similar mechanisms. One of the possible explanations for this finding is that V2 is activated before V1, and sends its information to V1 in a feedback pattern.

End stopping-dependent contours such as abutting line gratings show activation by almost all V1 cells by inducing lines, whereas the illusory contour created by the inducing lines activated approximately half of V2 cells. Some V2 cells respond to the orientation of the inducing lines, whereas some don't (von der Heydt et al., 1989). Using an illusory moving bar, created by inducers, showed that neurons in V2 responded to the moving 'bar' when it was present in the receptive field of a neuron. When lines were present within the area of the illusory bar, or one of the necessary inducers was missing, perception of the illusion was disrupted. This perceptual disruption was reflected in decreased activation. A limit of 1 to 3.5 degree separation between the inducers was found for centrally positioned targets. Linear summation and summation to threshold models were unable to explain effects of additional lines and length summation curves. Again, these effects were attributed to end stopping (Peterhans & von der Heydt, 1989). V1 responses were very different than V2 responses, such as no responses when the bar appeared in the receptive field and no effect of additional lines. The differences between V1 responses and the resulting perceptions, suggest that V2 is most likely the more important region for illusory contour perception.

1.4.4 When and where: V3, V4 and LOC

In contrast to many of the above findings, an fMRI study found two pieces of evidence that point to higher level involvement during illusory contour processing: no preference in V1 or V2 for illusory as compared to luminance defined contours and no preference for stimulus size (size invariance, Mendola et al., 1999). This study found a strong preference for illusory contours in V3A and V7. This suggests that although lower level cortical areas such as V1 and V2 may be involved with illusory contour processing, more specialized regions may be responsible for a large part of its processing.

In support of the importance of higher cortical areas, Kanisza figures can be masked by other Kanisza figures of different sizes (Imber et al., 2005). The presence of masking effects when target and mask are not spatially overlapped, suggests that processing the target occurring in an area which is size invariant, such as more complex shape processing areas. In these cortical areas the basic shape processing has occurred and minor variations of particular shapes (*e.g.* size) are processed in the same areas. Among these areas is the Lateral occipital complex (LOC), an object processing region in the ventral pathway.

The role of LOC in static contour perception is unclear. Using fMRI one study compared LOC activation for illusory figures and other less-salient-illusory contours. The less salient illusory contours were similar to the illusory figures in that both were Kanisza-type figures involving inducers. The inducers in the less salient figures were rounder, which prevented a robust perception of the illusory figure. The Kanisza figures were perceptually more salient than the modified less salient versions of these figures, LOC was activated similarly by illusory contours and these other stimuli, (Stanley & Rubin., 2003). The lack of preference in LOC activation for illusory contours, suggests that LOC is not the most important region for the perception of these illusory contours.

1.4.5 Differentiating FDF from static illusory contours

One current theory is that depth order and contrast polarity allow illusory contour perception. Depth order reflects the presence of cues to depth within the stimulus. According to one study, counterphase flicker of elements, similar to FDF, can lead to depth perception (Iwabuchi et al., 1997). It is possible that depth cues may help FDF perception. Contrast polarity reflects the presence of differences in luminance within the stimulus. The inability of humans to discriminate the phases of the dots within the FDF stimulus means that contrast cannot be differentiated between figure and background dots (Rogers-Ramachandran & Ramachandran, 1998). If perceived contrast variation is needed to detect illusory contours, then FDF may lack this information. Another consideration is that although the observer cannot differentiate between the phases (represented by dots inside versus outside of the figure), the neurons can still respond differently to the phases, allowing this cue to be used.

1.5 Temporally defined stimuli

Temporal structure and synchrony seem to be important from an evolutionary perspective. In order to survive, humans had to identify food and danger. The recognition of both predator and prey would benefit from a system which can bind individual points with temporal structure. Most moving objects, such as animals have elements which either move in synchrony (such as points within a face), or in relation to each other according to a predictable pattern (such as the movement of limbs). Thus, in order to survive, the human visual system had to evolve a mechanism to identify moving objects.

1.5.1 Form from motion

1.5.1.1 What is it?

Form-from-motion stimuli are stimuli in which the form is defined by a dynamic characteristic. Stimuli can be composed of individual elements that move with similar temporal (*e.g.* timing) or spatial (*e.g.* direction) dynamics. A number of different form-from-motion stimuli exist, which are most likely processed in different ways, depending on what defines the form.

1.5.2 Coherent motion

Coherent motion is motion in which the individual elements of a dot pattern are moving together. Using full field dot arrays and displacing elements, Lappin and Bell (1976) showed that with decreasing spatial and temporal separation the arrays could be seen as moving coherently. Typically coherent motion stimuli are composed of elements which do not provide spatial cues to figure versus background. For example, unlike figure ground stimuli composed of Gabor elements, there is no orientation information. Even within this category of form-from-motion, there are a number of different types of coherent motion, with different saliencies.

Motion coherence is manipulated by altering the proportion of elements within the array which move according to a common element (*e.g.* speed, direction). The addition of motion coherence to randomly positioned elements groups them and creates the percept of a shape. This has been shown in many different forms. According to one study, the motion of elements is most salient when the shared characteristic is direction (versus speed, Ledgeway & Hess, 2006).

When grouping of common elements is based on the elements moving in a shared direction the type of motion affected stability of the illusion. Two different types of motion were studied in this experiment. The first was when elements moved along a contour, versus in the same direction. The second was when all of the elements of a contour moved in the same direction (making the contour move). Motion along the contour is more effective as a cue to form-from-motion than motion in a common direction. The study also found that the first type of motion was much more sensitive to changes in curvature within the contour (shown in earlier studies to make contour detection more difficult). The second type of motion was much less sensitive to changes in curvature (Ledgeway & Hess, 2002). Although motion along the contour is more detectable, its ability to be degraded by curvature suggests that it is not very robust. This sensitivity suggests that local variations in direction of motion are important in order to create temporal dynamics (*e.g.* elements moving in the same direction) that allow form from motion to be perceived.

Some studies in dot movement have shown that moving contours are not subject to all of the same rules as static contours (Bex et al., 2003b). The ability to identify coherently moving contours is aided by increasing contour length, increasing density of dots, and decreasing curvature. These are all characteristics that also benefit static contour perception. In contrast to static stimuli, this study found that contours defined by motion do not show a contour-angle-dependent bandwidth. This means that the range of tolerable angles is equal for both smaller (0˚) and larger (40˚) contour angles. This finding suggests, similar to the findings of Lee & Blake (1999b), that the motion binding process makes perception of dynamic stimuli less dependent on spatial cues than similar static stimuli. This study suggests that in order to see the contour, a narrow band process must be used. A local motion averaging system is incapable of extracting the contour.

1.5.2.1 When and where

Form-from-motion's cortical processing mechanisms have been studied using a number of different techniques. Cowey and Vaina (2000) studied an individual with damage to ventral extra striate cortex (responsible for object recognition). They showed a disconnect between motion perception and form-from-motion perception. This patient was unable to name shapes, but able to match them. This inability suggests a deficit in object recognition (agnosia). Motion perception was unaffected, including perception of speed and direction. In contrast, form-from-motion and biological motion perception were impaired. Both form-from-motion and biological motion perception rely on the temporal dynamics of individual elements in order to extract salient shapes. Because motion perception is intact, object perception is impaired and form-from-motion perception is impaired, it implies that form-from-motion shares some common pathways with object perception that are impaired when ventral extra striate cortex is damaged. These results suggest that the ventral stream is necessary for extraction of form-from-motion (Cowey & Vaina, 2000).

The importance of both form and motion cues to the perception of form-from-motion makes it different than static contours which seem to rely heavily on V2. Cells that respond to motion-defined-contours are found more often as one moves from V1, to V2 and then V3/V3a (Peterhans et al., 2005). Cells sensitive to motion-defined-contour seem to be responsive to a lot of the properties that first order cells are responsive to (*e.g.* orientation, density of elements, element spacing), and unresponsive to motion properties such as speed and direction of motion, suggesting a strong role in object perception.

V4 of monkeys contains a significant portion of cells (10-20%) within the central 10˚ of the visual field, which are responsive to contours defined by motion. V4 cells were responsive to the orientation of the lines created by the motion. In contrast, V2 cells were most responsive to the orientation of the motion itself (Mysore et al., 2006). These V4 neurons were activated by specific orientations, independent of how that orientation was defined. Cue invariance is the ability of a neuron to encode a property (*e.g.* orientation, shape) independent of the cues which define (*e.g.* motion, luminance). Another cue invariant region is the LOC.

Shape perception occurs primarily in LOC, which is one of the final areas in the ventral stream. Using fMRI, one study found that shapes defined by colour and motion are similarly activated in LOC, demonstrating cue invariance (Self & Zeki, 2005). Although V4 and LOC are cue invariant, and probably have little to do with the processing of the motion in form-from-motion stimuli, they are still required in order for shapes to be perceived. The role of the dorsal stream in form-from-motion can be inferred from its importance in motion integration. According to one study, different motion-related-tasks are probably processed in specialized regions of extrastriate cortex (Vaina et al., 2005). Dissociation between form and motion recognition tasks implies that one function can be impaired while the other is still functional. Form from motion is among the special class of tasks which can be impaired when simple motion tasks are unimpaired. Williams syndrome is a condition known to affect visuospatial perception. A study of patients with this condition showed that basic motion perception remained intact *(e.g.* direction, coherence and speed discrimination, Mendes et al., 2005). More complicated motion-related tasks, such as frequency doubling (low spatial frequencies flickered at high temporal frequencies creating the illusion of higher spatial frequencies) and 3D form from motion perception, which rely on the extraction of structure using motion cues, are significantly impaired (Mendes et al., 2005). Another study showed that individuals with parietal cortex damage who were impaired at a form-from-motion task (biological motion), were able to perceive form (a ventral stream task), coherent motion (a dorsal stream task) and even background-noise-free-biological motion (ventral & dorsal stream task). These authors suggest a role for parietal cortex in form-from-motion perception, since these patients showed function which suggests a spared MT (dorsal stream tasks) and impaired form-from-motion perception (Schenk & Zihl., 1997).

1.5.2.2 Stimulus and Neural Synchrony

Recent psychophysical evidence in humans contradicts early evidence which suggests that temporal synchrony, without spatial information, is sufficient for separating figure from ground (Lee & Blake, 1999b). Evidence suggests that more cues than just temporal synchrony are being used in order to make the separation (Morgan & Castet, 2002). This second study showed that when elements within the target area equal spatial similarities as those in the background (*i.e.* all Gabor elements' phases are randomly generated), and only the presence of lack or synchrony is defining figure versus ground, the task is only possible under certain conditions. Specifically, only certain temporal frequencies can be used. This study, based on limited data, shows an ability to perceive figure versus ground, based solely on synchrony above 60Hz and below 20Hz. Interestingly, the FDF stimulus permutations used in the studies reported below rely on temporal frequencies below 20Hz, suggesting that synchrony may be able to act independently of other cues under this condition.

1.5.3 Temporal Structure

The presence of motion coherence is so strong that it can overcome the lack of spatial structure, even when the sole cue is temporal synchrony (versus motion direction, Lee & Blake, 1999b). Temporal structure, when combined with good continuation, improves perception greater than spatial summation would predict (Lee & Blake, 2001). Random events that share a common timing can be bound to create a percept, especially when the elements that are being modified are aligned to create a contour. These results have been extended to include temporal dynamics which are not synchronous, but share common temporal structure (Guttman et al., 2007). The additional benefit of temporal–structure-binding as compared to temporal-synchrony-binding is the robustness to variation in latency between the patterns. This means that one pattern can be offset in time much more when the cue to binding is temporal structure, than for synchrony. Although FDF does not rely on temporal structure, but rather synchrony, temporally-structured stimuli may help us to understand the neural mechanisms underlying FDF perception.

Motion as a mechanism for segregation of elements by temporal cues seems to operate faster than some other characteristics (*e.g.* colour). In one study, segregation of stimulus from background based on motion was faster than segregation based on colour (Bartels & Zeki., 2006). Another study found that detection of contours that rely on temporal information to segregate stimulus from background occurs within 200-400ms. (Poom & Borjesson, 2004). FDF elements, which have equal luminance to other elements within their patch, seem to be most dependent on the temporal information as the phase cannot be discriminated when the area between the two patches is covered (Rogers-Ramachandran & Ramachandran, 1998).

Temporal asynchrony, as a specific form of temporal structure, has been proposed as one of the cues to contour extraction. Although asynchrony is capable of contour extraction and structure perception, it is not a robust system. Asynchronous temporal structure is detected best at lower durations. In some cases detection is more difficult at longer durations. This is surprising because the perception of most stimuli improves with increasing duration. Masking can disrupt processing of this stimulus if presented at the onset or offset (Dakin & Bex, 2002). Ramping the contrast of the stimulus on and off also minimizes the improvement seen for asynchronous as compared to synchronous structure. The lack of robustness to both onset/offset and duration manipulations suggests that the most important component of asynchronous temporal structure is the onset and offset. According to other studies, this onset asynchrony creates a priming effect that improves when the stimulus is presented before the background (Beaudot, 2002)

1.5.4 Motion and spatial cues

Although it may be possible for temporal synchrony to segregate stimulus from background without spatial cues, the presence of spatial information has been shown to impact perception. Both spatial and temporal phase can act together to improve perception. The alignment of phase information improved perception when ‘snake’ and ‘ladder’ structures were tested using various modes of temporal information. Snakes, representing contours with parallel elements were found to be more detectable than ladders, representing contours with perpendicular elements. The addition of in-phase flicker as compared to random flicker or static elements improves detectability. Drifting of elements also improves perception. Individual elements can be moving at different speeds. Up to three octaves of speed were tolerated within the same contour, allowing an almost 8-fold range of speeds (Bex et al., 2001). The authors suggest that contour integration can use both sustained (spatial structure) and transient (temporal structure) information, even when the two types of input are segregated. For random dot patterns, motion can be perceived in spite of varying the spatial frequency peaks of individual elements (up to 4 octaves! Bex & Dakin., 2003a). This result suggests integration across spatial frequencies in order to identify motion within contours.

Contour detection was unaffected by the spatial frequency of the elements, but affected by the spatial frequency variation between elements. Contour detection was also affected by spacing and speed of the elements and overall patterns of motion (Bex et al., 2003b). This finding suggests that discrete and independent motion detectors allow perception of contours defined by motion.

According to one study, peak subtract phase, which has the least contrast between stimulus and background, can be the most visible. Temporal correlation of this contrast modulation strengthens the salience of the percept (Lee & Blake, 1999a). Temporal and spatial information can interact, to improve salience.

1.5.5 Neural synchrony as a mechanism

The importance of neural synchrony to figure ground perception is unclear. Some studies show that during a period of perceptual texture segregation (*i.e.* when background and stimulus are perceptually segregated), pairs of neurons which are responsible for the processing of background/stimulus do not show more synchronous activity than pairs of neurons which correspond to stimulus/stimulus (Lamme & Spekreijse, 1998). If texture segregation is not coupled with neural synchrony, and cannot be used to reliably predict figure vs. ground, then coordinated neural activity is probably not the mechanism responsible for differentiating stimulus from background.

According to more recent research, the role of synchrony is probably more complicated than simply figure vs. ground creating synchronous neural activity. Studying the correlation between neural synchrony and performance during the pre-stimulus and during-stimulus phases showed that during stimulus presentation a shift occurs in synchrony to narrower (more tuned) and lower magnitude correlation peaks (van der Togt et al., 2006). When the stimulus is perceived, this shift is even larger, meaning more desynchronization. The authors believe that this shift represents a honing of neuronal activity from global to local mechanisms (less to more specialized). The authors suggest that that synchrony is involved with perception of figure ground and texture segregation.

1.5.6 Differentiating form from motion from FDF:

Although FDF is seemingly very similar to form-from-motion tasks, it differs in some important ways. First, the phases of the flicker (*i.e.* black versus white) that define FDF is imperceptible to viewers when the frequency is above 15Hz (Rogers-Ramachandran & Ramachandran, 1998). Specifically, if asked which dots are dark or light at any given time, the motion that defines form-from-motion tasks can be identified (*e.g.* direction, speed). This means that the underlying cue for form perception is not perceived in one case (*i.e.* FDF). Nevertheless, the visual cortex must be able to take the phase information that cannot be perceived and use it to create the FDF percept.

1.6 A special region for kinetic contour processing?

Still under debate is the possibility that contours defined by motion are processed in a specialized cortical region. It is possible that this region, named the kinetic occipital region (KO), may be part of the family of V3 regions, which are responsible for boundary perception, or a part of lateral occipital complex (LOC), which is responsible for object processing. An fMRI study by Van Oostende *et. al* (1997) showed that gratings defined by motion activated KO more than luminance defined gratings, or other types of motion (uniform, transparent). This study found that KO was separate from MT and V3 both in structure and in function. In contrast, some functional overlap was found between KO and LO. Similar to LO, KO's responses were found to be size and spatial frequency invariant, and responsive to different kinds of kinetic boundaries.

In an fMRI study by Zeki *et al.* (2003) of human KO area, a small number of individual cells were found that were selective for kinetic contours versus luminance defined (static) contours. This study found that averaging across the entire region, cells were not selective for kinetic contours as compared to luminance defined contours. Most cells showed similar activation and tuning functions for kinetic and luminance defined contours. This lack of preference was found in spite of preferences for motion as compared to colour stimuli. The authors concluded that this region was, most likely, not responsible for the selective processing of kinetic contours.

1.7 Versatility of the visual system

Although physiologically different from humans, lizards' behaviour may prove to be a useful model for how the visual system can adjust its behaviour depending on the conditions it is presented with (Peters et al., 2007). According to this study, during noisier conditions (*i.e.* more windy conditions) tail flicking increases in duration, not speed. This increases the likelihood the signal will be noticed, without distortion (*e.g.* speed). Also, during noisier conditions, the signals are intermittent. Peters et al. (2007) propose that the intermittence is implemented in order to ensure sustained salience and prevent adaptation.

This finding is particularly important because, as reported above, a number of different types of cues can be used to identify contours. A number of different mechanisms, that are processed by different cortical pathways, using different timelines, are used by each of these stimuli. FDF represents a distinct class of stimulus that shares properties with each of these stimuli. It is likely that FDF has its own pathway, different than all of those reported above, but that use similar areas. Perhaps future research will help us to understand the connections between cortical regions that allow FDF to be perceived.

1.8 Implications for glaucoma detection

Although FDF's role in glaucoma detection is not the intention of the current thesis, FDF is a stimulus designed with the intention of being used to detect glaucoma in the early stages, when current tests fail to detect it. Structural loss has been shown to occur before function loss can be seen using current tests. If FDF truly targets magnocellular processing, then a loss of magnocellular cells may lead to detectable functional losses.

1.9 Study Rationale

FDF is special because of the proposed magnocellular dominated perception. Many motion-defined-form stimuli are either composed of Gabor patches, which contain phase information, or rely on motion information, in contrast to the flicker information in the current stimulus. This thesis intends to determine whether FDF is subject to similar rules as first order static stimuli, giving us a better idea of how FDF behaves and the mechanisms behind its perception.

A number of the studies employed in this thesis have implications for magnocellular/parvocellular processing. The first, a subjective experiment of the perceived spatial frequency of the illusion, has implications for both the pathway employed and differences from other static stimuli. The second experiment aimed to determine whether spatial structure of the elements can influence perception of FDF, which has implications for feedback and attentional mechanisms. The third experiment addresses the importance of contour versus area, which is important because the salient component of the illusion has previously been considered to be the region between the two out-of-phase dot regions (Rogers-Ramachandran & Ramachandran, 1998). An importance of surface places emphasis on the non-illusory surface component of the stimulus. The fourth experiment attempted to determine whether the Gestalt rule of closure applied to this temporally driven illusion. The fifth experiment intended to determine whether FDF targets can be discriminated and resolved. This experiment revealed a number of mechanisms that are present in the processing of this stimulus, such as filling-in over small distances.

1.10 Considerations

1.10.1 Sample size

A major consideration for this thesis was the use of a small sample size. All of the subjects tested were young, trained observers who produced consistent data. Each of these subjects was tested numerous times, over a number of sessions, and was maintained for most of the experiments. By maintaining a small, but consistent subject pool, comparisons can be made within and across experiments.

Had a larger sample size been used, a smaller number of trials would have been conducted. In order to gauge trends, the data would be averaged, which can eliminate subtle and individual effects. According to Movshon and Kiorpes (1988), tasks with greater variability between subjects produce pooled data that is significantly different from individual data. The current studies contain at times, high levels of variability, inherent in the design of some of the difficult, visual tasks. Thus, for this study a greater number of trials per subject, with subjects being consistent through the majority of the studies, allowed greater comparison within and across studies.

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Chapter 2

The perceived spatial frequency of flicker defined form (FDF); A temporally defined illusion

2.1 Abstract

Purpose: Flicker defined form (FDF) is an illusory percept created by the counterphase flicker of neighbouring random dot fields. Perception of this illusion is believed to be dominated by the magnocellular pathway. Methods: Using a grating patch positioned next to a line form of the FDF stimulus, subjects were asked to match FDF to a sine wave grating of a particular spatial frequency. The effects of random dot density, contrast and eccentricity were tested. Results: Results show that baseline conditions are matched to between 1.5 and 2 cpd. Effects of eccentricity, dot density and contrast are minimal, and suggest that the same spatial frequency channels are most likely processing the stimulus, across the different viewing conditions.

Keywords: Spatial frequency; Eccentricity; Illusory contour; Temporal frequency

2.2 Introduction

Flicker defined form (FDF) is an illusory contour created by the flickering of randomly positioned dots. Flickering two adjacent regions of dots in counterphase at a high flicker frequency creates the perception of an illusory boundary, originally termed the “phantom contour” illusion (Flanagan et al., 1995; Rogers-Ramachandran & Ramachandran, 1998). Studies have found that this illusion is particularly robust in the periphery as compared to central viewing, is insensitive to blur, and occurs only when the flicker frequency is greater than approximately 15Hz (Quaid & Flanagan., 2005a; Rogers-Ramachandran & Ramachandran, 1998). At lower temporal frequencies (lower than 7Hz), the individual temporal phase characteristics of the dots are discernable. When the temporal frequency is above 15Hz the flickering dots look perceptually identical, yet an illusory border is perceived. The FDF percept has thus been classified as an illusory border as it is generated from elements which are perceptually identical. The shift from perception of surface phase characteristics (*e.g.* seeing individual dark and light phases) to the percept of the illusory contour has been suggested to represent a shift from parvocellular to magnocellular dominated processing (Quaid & Flanagan., 2005a; Rogers-Ramachandran & Ramachandran, 1998). Robustness in the periphery (Quaid & Flanagan, 2005a), insensitivity to blur (Quaid & Flanagan, 2005b) and the absence of the illusory contour at chromatic isoluminance (Quaid & Flanagan, 2005a) also suggest that this illusion is strongly dominated by the magnocellular pathway, which is more sensitive to lower spatial frequencies and higher temporal frequencies (Merigan et al., 1991).

Most of what is known about the mechanisms of FDF is based on processing that occurs before the lateral geniculate nucleus (LGN). However, the notion that this illusory contour is magnocellular dependent, tells us very little about the post-LGN processing mechanisms involved. As no studies have been conducted to date to determine the higher cortical areas involved in FDF perception, we must make predictions based on other illusory stimuli. Static illusory contours, such as Kanizsa squares, create stronger cell responses in area 18 (monkey homologue of V2) compared to area 17 (monkey homologue of area V1, von der Heydt et al., 1984). This finding suggests that illusory contours are treated differently than luminance-defined contours, the latter of which depend on area V1 more than area V2. Another mechanistic difference between illusory contours as compared to luminance-defined contours is the lag in processing time. In a masking study (Imber et al., 2005) the effect of illusory contour masking was seen at long stimulus onset asynchronies (~300ms), which suggests that processing is dependent on involvement of higher cortical regions. When considering the processing of such static illusory contours, it is possible that the mechanisms are quite different from those of FDF. Flicker defined form is a stimulus which depends on temporal dynamics in order to be perceived (Quaid & Flanagan, 2005a; Rogers-Ramachandran & Ramachandran, 1998). This suggests a greater involvement of the dorsal stream. Thus, it is currently unknown how these mechanisms differ, if at all, from FDF mechanisms.

No studies to date have examined the importance of spatial frequency components of the FDF illusion. Although, the illusory edge, which is a product of the limitations of the visual system, is most likely a narrow band stimulus, the perceived spatial frequency of this illusory contour has never been reported. Given that this illusory edge is the most important component of the FDF stimulus as it is believed to create the illusory image, it is of value to determine the perceived spatial frequency. If FDF is dominated by the magnocellular pathway, then the perceived spatial frequency is likely to be ‘low’. Although there is much overlap between the functions of magnocellular and parvocellular cells, the upper spatial frequency limit of the magnocellular system is approximately 10 cpd (Derrington & Lennie, 1984; Merigan et al., 1993). A spatial frequency higher than 10 cpd would indicate a role for the parvocellular system. Although magnocellular cells are more sensitive to low spatial frequencies than parvocellular cells, the current task cannot distinguish whether a spatial frequency below 10 cpd is due to primarily magnocellular function. Many properties of FDF point to magnocellular processing (Quaid & Flanagan, 2005a; Quaid & Flanagan, 2005b), suggesting that FDF should be matched to a spatial frequency compatible with this pathway.

Flicker defined form is a contour binding task which relies on temporal dynamics. Contour binding, and particularly figure-ground segregation, is a task that occurs when disconnected elements must be perceptually connected in order to complete a whole line segment. These tasks can be aided by spatial elements such as collinear orientations, or temporal dynamics, *i.e.* asynchrony, of the individual elements within the array (Beaudot, 2002; Bex et al., 2001). FDF shares similar properties because the individual elements of the display must be perceptually bound to create the difference between stimulus and non-stimulus elements. Both figure ground segregation and FDF perception processes rely on the connection between disconnected elements and are aided by temporal dynamics. According to Dakin and Hess (Dakin & Hess, 1998), detection of static curved contours was only possible if the spatial frequency of the elements composing that contour were within 0.7 octaves of each other. For static straight contours the range was slightly larger (~1.5 octaves). Thus, only small ranges of spatial frequencies were tolerable. Detection of moving contours relies on elements within the pattern to be similar in spatial frequency (Bex et al., 2003). If a similar mechanism is being used to process both figure ground segregation and FDF contour binding (i.e. connecting spatially disconnected elements), then the dependence of figure-ground segregation connections on small ranges of spatial frequencies (Dakin & Hess, 1998) may be reflected in the perceived spatial frequencies of FDF. Namely, if figure-ground segregation tasks are processed similarly to FDF contour binding, then similar cortical channels may be involved. If similar channels are involved, then the dependence on particular bands of spatial frequency seen in figure-ground segregation tasks may also be present in FDF stimuli. If FDF stimuli can only be composed of a narrow band of spatial frequencies in order to perceive the illusory contour, this would suggest that the perceived spatial frequencies should also fall into a narrow band. If the perceived spatial frequency differs by more than 1.3 octaves (Dakin & Hess, 1998), when the density of dots within the display is manipulated, it may suggest that more than one mechanism is involved in processing the illusion. Thus, the primary intention of this paper is to investigate the relationship between perceived spatial frequency, random dot density, eccentricity and contrast.

The second intention of this experiment is to determine if shifts in spatial frequency act predictably according to salience. Namely, do spatial frequency ranges correlate with robustness of the illusion? If the illusion is highly dependent on the magnocellular system, the greater salience of the illusion would be dependent on lower spatial frequencies. Thus, the aspects of the illusion that improve contrast thresholds (*e.g.* higher dot density, further eccentricity, increasing contrast) should be shifted to lower spatial frequencies (Quaid & Flanagan., 2005a). We expect that increasing dot density, eccentricity and contrast will shift the perceived spatial frequency of the illusion to a lower spatial frequency than when the illusion was created by lower dot densities, more central eccentricities and decreasing contrast.

2.3 Methods

2.3.1 Subjects

Three subjects, two female and one male, ages 27, 23 and 25 respectively, from the University of Waterloo served as participants for the experiments. All subjects were trained visual observers. Each subject had corrected visual acuity of 6/6 or better and there were no known ocular abnormalities.

2.3.2 Experimental setup

To view the FDF stimulus, subjects were seated 32cm from a Sony Trinitron Multiscan CPD-G500 monitor with a resolution of 768 x 1024 pixels and pixel pitch of 0.37mm. The screen subtended 48 x 62º of visual angle. Refresh rate was 100Hz. Luminance values varied between 0cdm^{-2} and 100cdm^{-2} which were used to create 23 log Michelson percent contrast levels that fluctuated symmetrically around 50 cdm^{-2}, most of which were not used in this particular study.

2.3.3 Stimulus

The FDF target was composed of 0.34˚ diameter randomly positioned circular dots. All dots were luminance modulated at 16.67Hz (square wave). An illusory line was created by counterphase flickering dots. The illusory contour was positioned horizontally across the display extending from the right edge of the screen to 2.5cm (2.24˚) from the fixation point (Fig 2-1) within the inferior nasal quadrant.

A white fixation point was positioned on a uniform, matte black background. Black cardboard was used to cover the FDF screen and allow a neutral surface for the comparison grating (Fig 2-1).

A second computer system displayed the gratings which were used to match the spatial frequencies. The Cambridge research system running PSYCHO v.4.11 (1992) was used to display a suprathreshold (50% contrast) square grating of 8˚ diameter. The monitor was positioned 37cm from the eye (sum of distance from the screen to the beam splitter and from the beam splitter to the eye). Using a 50:50 beam splitter, the grating was superimposed onto the screen displaying the FDF stimulus (Fig 2-1) within the inferior temporal quadrant. In order to prevent the subject performing a direct matching task between the two stimuli, the grating was always drifting at 0.5Hz. This slow speed prevented direct matching, but was also slow enough to allow subjects to perceive the grating. Drifting also prevented the grating pattern from fading.

In order to test multiple eccentricities, the targets were kept at the same locations. Only the fixation point was moved. The fixation point was moved directly vertical from the fixation location and this distance was calculated based on the distance from the fixation point at 0˚. Four different eccentricities were used, which correspond to the same eccentricities tested in other FDF studies (4.2˚, 12.7˚, 21.2˚). For the fixation target subjects were able to look back and forth at FDF target and grating.

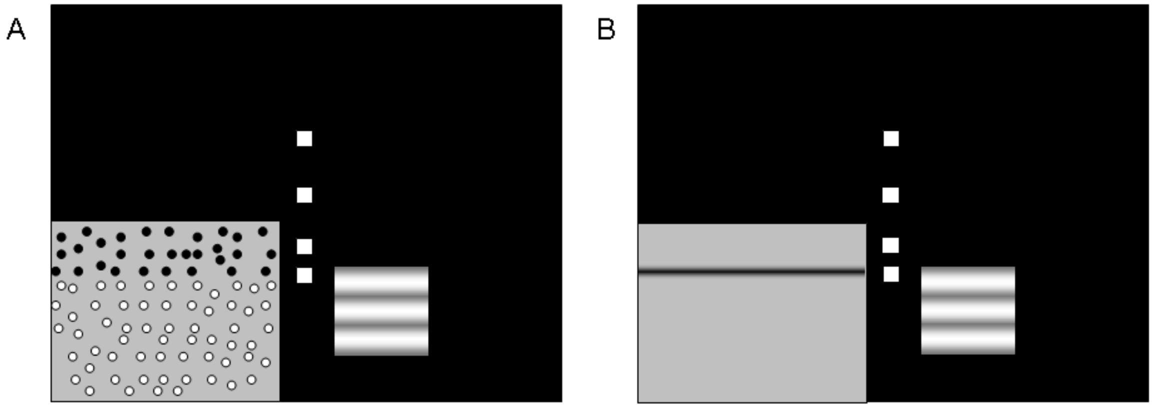

Figure 2-1. Schematic of experimental setup.

Panel A shows the physical appearance of the stimulus. Panel B shows the perceived appearance of the stimulus (*i.e.* an illusory periodic line and dots with perceptually indistinguishable phases). The white boxes represent the fixation point where the subject is instructed to look (Fixation, 4.2˚, 12.7˚, and 21.2˚). The two other boxes show how the two stimuli were positioned with respect to one another (the distance between the two targets was 5cm, 4.5˚). The box on the left is the FDF stimulus, which appeared as a ‘fuzzy’ straight line, between the sets of counterphase flickering dots. Note that distances and sizes are only roughly to scale.

2.3.3.1 Effects of contrast

When effects of contrast were manipulated the density of dots was kept constant. For baseline conditions the target was composed of a ‘standard’ dot density (2.1 dots/degree^2) with a suprathreshold contrast level (1.3 log Michelson percent). Contrast manipulations were performed at fixation for two additional contrast levels (0.9 and 1.7 log Michelson percent) which varied from near threshold (0.9), above threshold (baseline: 1.3) and suprathreshold (significantly above threshold: 1.7). Baseline contrast of 1.3 log Michelson percent units is suprathreshold for most of the manipulations performed in this study (*e.g.* dot density and eccentricity) and typically used as the initial testing value for staircases (Quaid & Flanagan, 2005a). Two additional values were added which represent a larger and a smaller contrast value (0.9 and 1.7).

2.3.3.2 Effect of dot density

Four manipulations for the density of dots were performed including 1.6 dots/degree^2, 2.1 dots/degree^2, 2.6 dots/degree^2 and 3.2 dots/degree^2. For all of these dot densities, the same contrast level was used (1.3 log Michelson percent).

The choice to keep contrast the same was made in spite of some difficulties experienced by the subjects in perceiving the illusion. First, although perception is more difficult with the lower dot densities used in the current study, all should be perceived at the contrast level used (Quaid & Flanagan., 2005a). Changing the density of dots within a stimulus may alter the mechanisms responsible for its processing. By keeping the contrast constant, the only changes in mechanisms will be due to the density of the dots.

2.3.3.3 Effect of Randomness

A control experiment which determined the effects of the type of background was performed. Two types of 'randomness' were employed. The first involved randomly seeding the locations of individual points (random). The second involved moving points from a grid-like structure according to randomly seeded directions, for a randomly defined but upper limit constricted distance (organized). Note that both are random, but the second maintains a more consistent density of dots and a more organized appearance.

2.3.4 Procedure

Subjects viewed the stimulus monocularly, using the right eye. They were given a keyboard which allowed them to scroll through the different spatial frequencies at their own rate and as many times as they chose. Subjects were instructed to choose the wavelength which most closely matched the illusory line using a method of adjustment. An initial range of spatial frequencies (0.25, 0.5, 1, 2, 4 and 8 cpd) was tested. These initial values were chosen to mirror the octave steps used in the assessment of spatial frequency perception. After this initial choice the range was narrowed by using adjacent values as the new lower limit and halving the difference. This halved difference value was used as the step size for the second iteration. This process was repeated, making the step sizes continually smaller, until the step size was 0.125cpd. For higher spatial frequencies the initial step sizes were larger, so more iterations were required to achieve the 0.125 step size.

All conditions were tested three times, the second two times in random order. Aberrant trials were repeated.

2.3.5 Analysis

Means and standard errors were calculated for within and across subject comparisons. Data were analyzed using repeated measures ANOVA (Huynh Feldt corrections to epsilon degrees of freedom were used when sphericity was violated). Significant effects were followed by Tukey's HSD post hoc analysis.

2.4 Results

2.4.1 Perceived spatial frequency, baseline

The first intention of this experiment was to determine if the FDF illusory contour could be matched to a particular spatial frequency. The baseline condition used a medium dot density (~2.1 dots/degree^2). At 4.2° the perceived spatial frequency of the illusory contour under baseline conditions was found to be 1.65±0.13 cpd. Greater variation was present between than within subjects, even when the characteristics of the FDF stimulus were varied.

There was a concern that the perceived spatial frequency would be simply dependent on the distance between the dots. If this were true the perceived spatial frequency should be predictable from the distance between dots. In addition, the difference in perceived spatial frequency between the lowest and highest dot densities tested should be double! Only minimal changes were seen in the perceived spatial frequency even with the largest variations in dot density. These findings suggest that subjects were not responding to the distance between dots.

2.4.2 Contrast

The second intention of this experiment was to determine whether the factors which affect detection, affect the perceived spatial frequency. Would contrast, which is the metric used to determine visibility of the stimulus, have an equally strong effect on the perceived spatial frequency? At low contrast levels the FDF stimulus was difficult to detect (Quaid & Flanagan, 2005a). The characteristics that define the stimulus (*e.g.* dot density, eccentricity) affect the amount of contrast required to detect the stimulus.

No effect of contrast was found ($F_{(2,4)}$=0.57, p=0.61, observed power=0.1, Fig. 2-2). No interaction between contrast and eccentricity was found ($F_{(6,12)}$=1.27, p=0.34, observed power=0.32). The greatest difference between high and low contrast was found at 21.2º (low contrast: 1.40±0.11; high contrast: 1.57±0.16). The smallest difference due to contrast was found at 12.7 º (low contrast: 1.69±0.12; high contrast: 1.68±0.15). Subjects noticed that the FDF target was harder to see at low contrast, and easier to see at higher spatial frequencies, but subjects matched to very similar spatial frequencies.

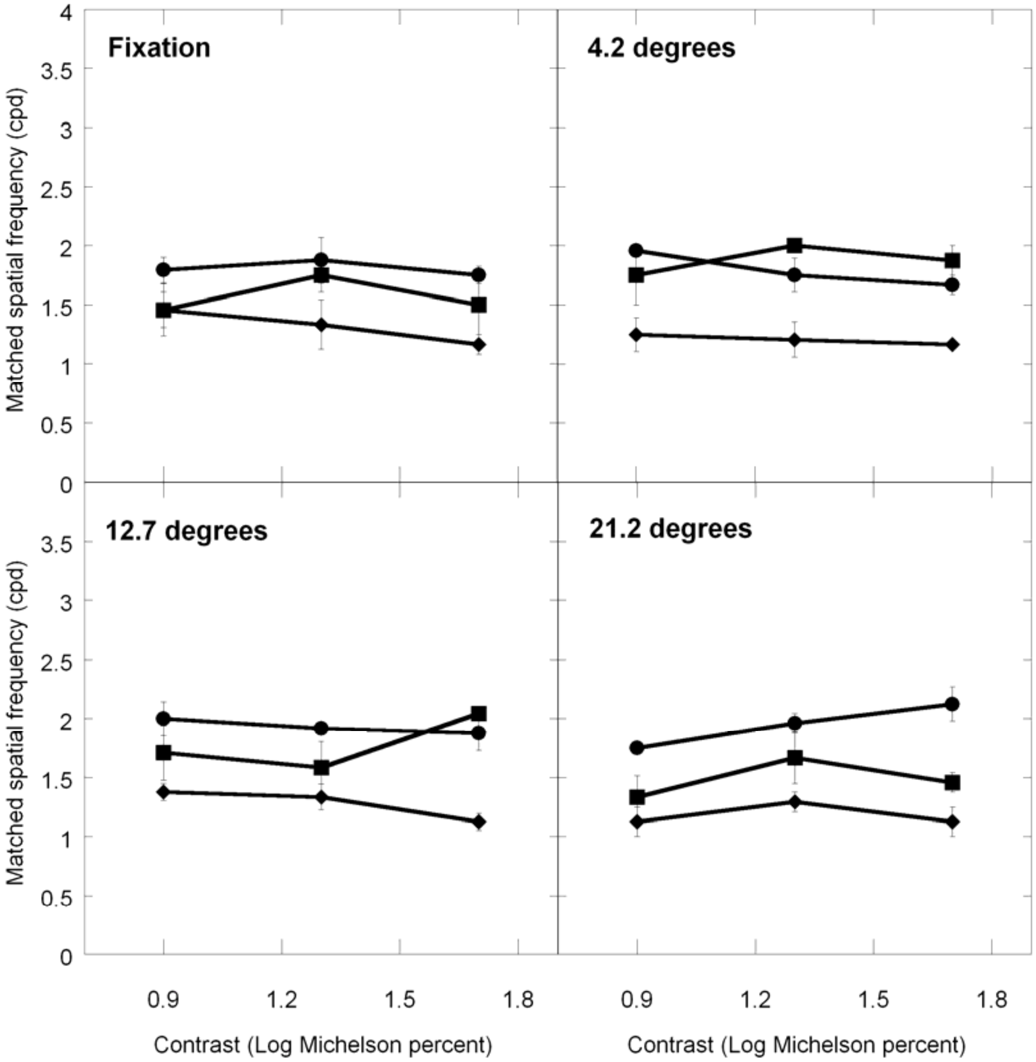

Figure 2-2. The effect of contrast on perceived spatial frequency of FDF.

Mean for three subjects and standard errors are shown.

2.4.3 Density of random dots

The density of random dots (dots/degree^2) has previously been shown to be one of the most important factors in determining detectability of the illusion (Quaid & Flanagan, 2005a). A larger density of dots makes the illusion more visible at lower contrasts.

An effect of dot density was found ($F_{(3,6)}$=7.40, p=0.02, Fig. 2-3). Two important comments can be made about this finding. First, although sphericity is not violated for this condition (p=1.0), when a Huynh Feldt correction is applied, no significant effect is found ($F_{(1,2)}$=7.40, p=0.06). Huynh Feldt, being a less conservative test, suggests that this effect is minimal. Tukey's HSD supports this observation. A difference of approximately 0.22cpd is found between 2.1 and 2.6 dots per degree, when collapsing across eccentricity.

No effect of interaction between dot density and eccentricity was found ($F_{(9,18)}$=0.78, p=0.64, observed power=0.26).

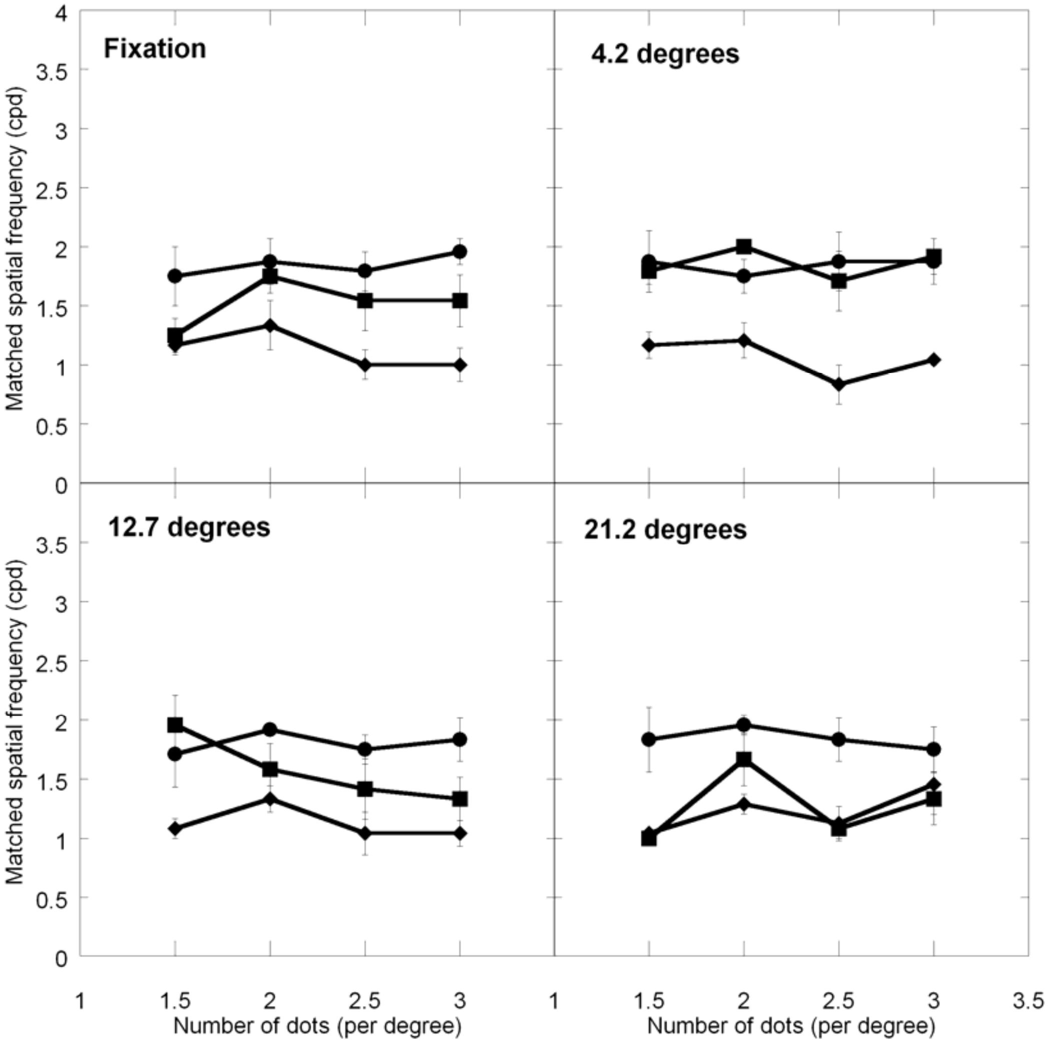

Figure 2-3. The effect of density of dots per degree on perceived spatial frequency at 4 different eccentricities.

Eccentricities are listed in the upper left corner of each box. Each symbol represents the mean and standard error for each individual subject.

Examining results averaged across subjects (Fig. 2-4), similar effects can be found. Some slight differences can be seen for the lowest dot density between fixation (mean: 1.39±0.13) and 21.2º (mean:1.29±0.16) and between 4.2º (mean: 1.61±0.14) and 12.7º (mean: 1.58±0.17). These differences were less than half of a cycle and standard errors showed overlap between these points. Across dot density small variations could be seen, although within the boundaries of standard errors.

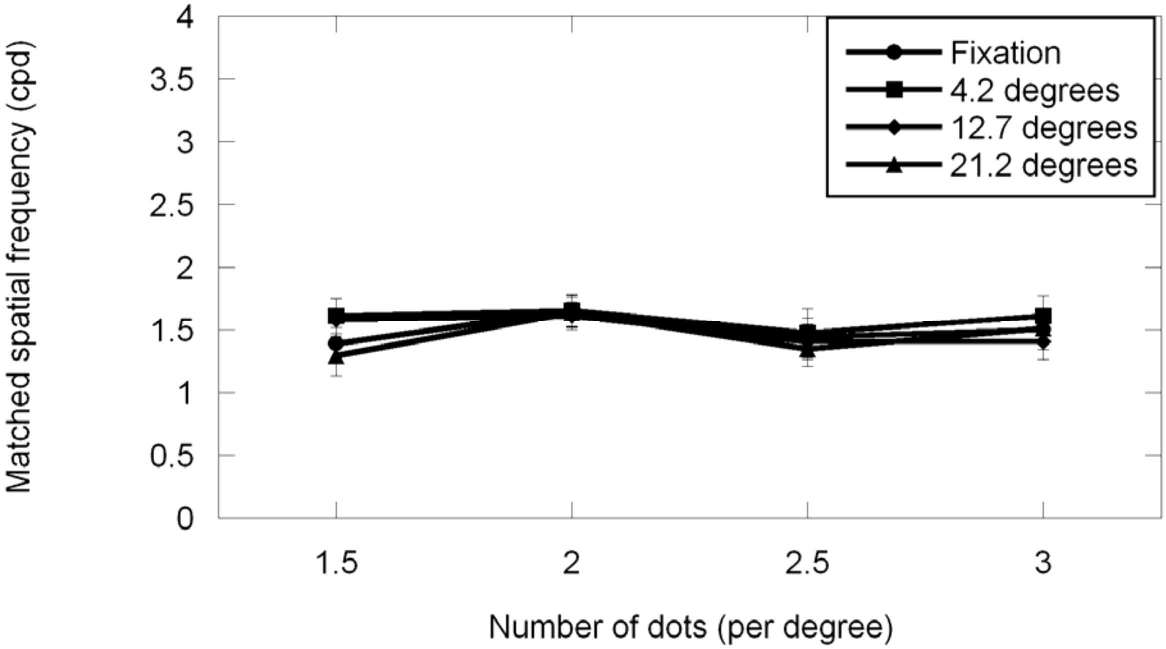

Figure 2-4. The average effect of density of dots per degree on perceived spatial frequency at 4 different eccentricities.

Each symbol represents the mean and standard error collapsed across 3 subjects.

2.4.4 Effect of randomness

No effect of randomness was seen ($F_{(1,2)}$=1.08, p=0.41, observed power=0.1, Fig. 2-5). No interaction between randomness type and eccentricity was found ($F(_{3,6)}$=2.28,p=0.18, observed power=0.33). Collapsing across eccentricities, organized backgrounds were matched to 1.79±0.09cpd whereas random patterns were matched to 1.64±0.06cpd. One subject showed a difference between the two types of randomness, but only at fixation. This is probably due to the difficulty of seeing the illusion near fixation, and the variability of perception near fixation.

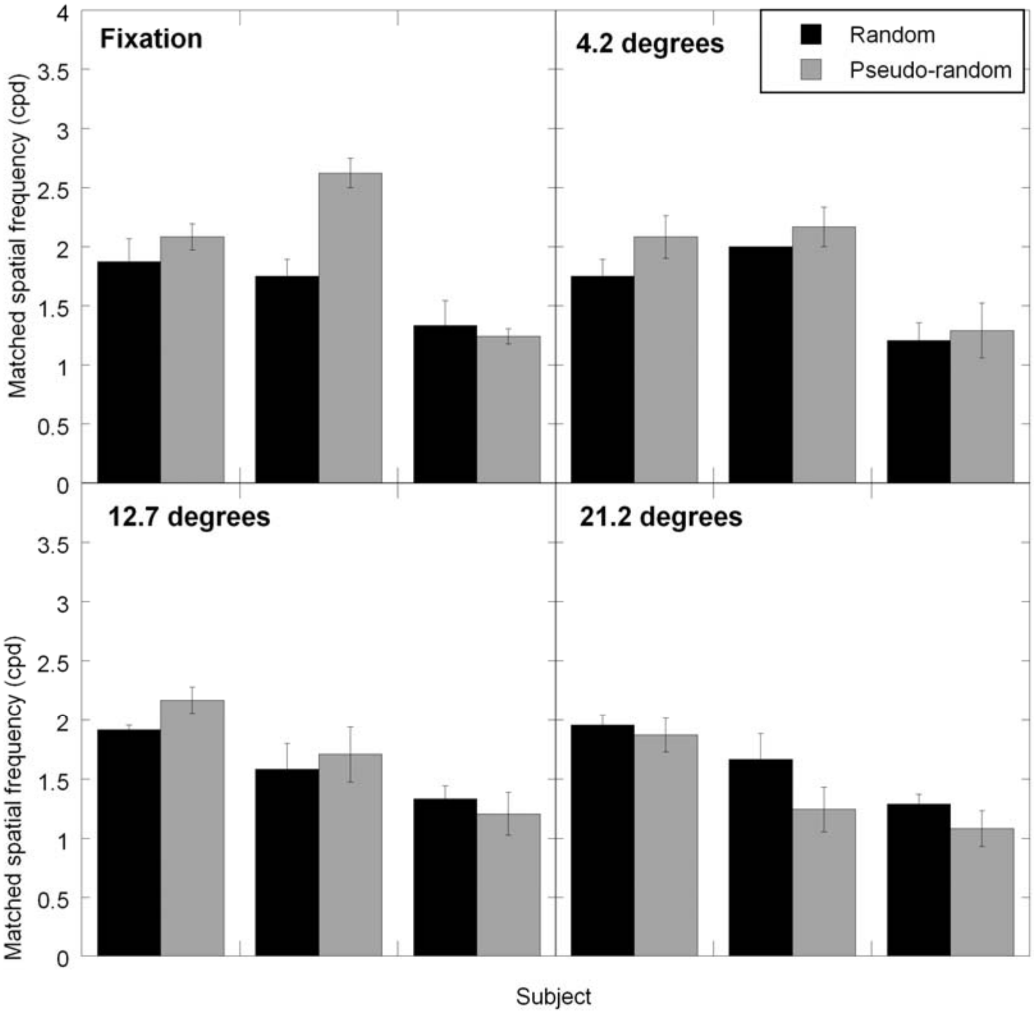

Figure 2-5. The effect of a more ‘controlled’ randomness.

Each pair of gray and black bars represents the mean and standard error of 3 runs for each subject. Black bars represent the random background element arrangements which were entirely randomly positioned. The gray bars represent the ‘pseudo random’ organizations, which are described in greater detail in Goren and Flanagan (submitted).

2.5 Discussion

These results showed that the matched spatial frequency of the illusory contour generated in FDF was independent of the density of random dots used to generate the illusion, and the eccentricity at which it was presented. The contrast of the illusory contour also had no significant effect on the perceived spatial frequency of FDF.

According to results found by Dakin and Hess for contour linking (Dakin & Hess, 1998), the range of perceived spatial frequencies at fixation found in our current study (within one octave) was within the tolerable bandwidth for contour completion (1.3 octaves). Although the Dakin and Hess study created contours composed of elements of different spatial frequencies, there was relevance to the current study, which did not manipulate spatial frequencies of individual elements. The amount of tolerance to variation in spatial frequencies within a pattern implies how much convergence of early cortical cells occurs during contour linking in later stages of processing. The small range of spatial frequencies found in the current study suggests that all of these frequencies can be processed by the same set of contour linking cells. The spatial frequencies perceived in the current study were also within the known bandwidths of cells in V1 (De Valois et al., 1982; Wilson et al., 1983).

2.5.1 Effects of eccentricity

FDF perception is significantly different from static, non-illusory stimuli such as figure ground contour completion tasks (Quaid & Flanagan, 2005a). Spatial frequency perception is affected by the location of the target. Spatial frequencies below the Nyquist limit are perceived to be relatively higher in the periphery than at fixation (Davis et al., 1987). Spatial frequencies above the Nyquist limit appear lower in the periphery due to aliasing and undersampling (Thibos & Walsh, 1985). The frequencies that subjects reported at fixation in these experiments (1-3 cpd) were well below the

Nyquist limit suggesting that as the eccentricity was increased, the perceived spatial frequency of the illusion should increase. No difference was seen in perceived spatial frequency as eccentricity was increased. This difference between static stimuli and FDF suggests that the mechanisms responsible for FDF perception differ from many static stimuli.

Contour completion is different in peripheral versus central vision (Hess et al., 2000). According to one study the mechanisms of contour linkage are different within versus beyond 10˚. When the phases of Gabor patches are shifted, centrally presented targets can still be detected, whereas peripherally located targets cannot (Hess & Dakin., 1997). The authors suggest that this difference is due to the presence of connections between cells in the fovea that are missing in the periphery which allow cells with different phases to be perceptually linked. Again, FDF is different . The importance of temporal synchrony to the FDF stimulus means that the mechanisms processing peripherally presented stimuli cannot use spatial phase information.

If the hypothesis of magnocellular dominance holds (Quaid & Flanagan., 2005a; Rogers-Ramachandran & Ramachandran, 1998), then the estimated ratio of parvocellular to magnocellular projecting ganglion cells of 35:1 at 0^{o} eccentricity vs. 5:1 at 15^{o} eccentricity within the LGN (Azzopardi et al., 1999) may have an influence on the perceived spatial frequency. The results suggest that even if a shift in mechanism was occurring, it does not influence the perceived spatial frequency.

2.5.2 Contrast

The most important factor in detecting the illusion is contrast. The current study showed that the perceived spatial frequency of the illusion did not change with change in contrast even with changes in eccentricity. This finding suggests that when the metric of contrast threshold is used, these variations in contrast do not change the way in which FDF is perceived. This means that when testing the effects of different variables on FDF perception, the illusion is perceived in a consistent way.

2.5.3 Dot density

The density of dots is a large determining factor for the saliency of the FDF illusion. In particular, increasing the density of random dots increases the visibility of the illusion at all eccentricities (Quaid & Flanagan, 2005a). The current study showed that increasing the density of dots change the perceived spatial frequency.

At first glance, more dots means that the density of dots constituting the edges increases, which should make the edge appear more defined, and cause subjects to match the illusory line to a higher perceived spatial frequency. An increase in dot density may also change perception as a greater area will be out of phase. This would explain an improvement in performance, without a shift in mechanism. However, there was no change in perceived spatial frequency.

Contrast detection thresholds were affected by the interaction between dot density and eccentricity. Specifically, very low and high dot densities have very high and low thresholds, respectively. These thresholds were unaffected by the eccentricity of the target. The current study found no interaction between dot density and eccentricity as an influence for spatial frequency.

2.5.4 Detection and perceived spatial frequency

The hypothesis that improved performance is due to the ability to rely more on the magnocellular system would mean that better performance, reflected by lower detection thresholds, would also relate to lower spatial frequencies since magnocellular cells respond best to lower spatial frequencies. Parvocellular cells also respond to low spatial frequencies, so this evidence does not point conclusively to one particular pathway.

Typically, increasing eccentricity, dot density and contrast improves detection. However, none of these factors affected the perceived spatial frequency. Thus, even though these factors influence detection of the illusion, they have no clear effect on the perceived spatial frequency.

Results from this study fell within the limits for contour completion. Namely, in spite of changes in contrast, dot density and eccentricity, subjects perceived the spatial frequency variation to be less than 1.3 octaves (Dakin & Hess, 1998). This value is also known as the bandwidth for channels in V1. It could be that in spite of all of the changes to the FDF stimulus, the same V1 channels were activated, creating the perception of similar spatial frequencies.

2.6 Acknowledgements

Jim Cassidy (Microsystem Technology) for software used to generate and display the FDF stimulus. Thanks to Patrick Quaid for suggestions on the manuscript.

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Chapter 3

The importance of background structure to perception of a temporally-defined illusion, flicker defined form

3.1 Abstract

Flicker defined form (FDF) is an illusory contour based stimulus, which is created by the high temporal frequency with which individual dot elements are modulated in luminance according to a square-wave flicker profile. The aim of this study was to determine how the placement of individual dot elements would affect contrast detection thresholds. Randomness was added by moving dots according to a defined vector length for which direction was defined randomly and dot pitch (*i.e.* distance between the dots) was used to define the quantity of randomness. Results show that adding underlying structure, using either a grid-like or circular pattern, significantly improves performance. This improvement is most pronounced close to fixation. Whether these findings point to cortical feedback or a shift in the mechanisms used to process this stimulus remains unclear.

Keywords: Illusion; Contour; Detection; Contrast; Background organization

3.2 Introduction

The human visual system is known to be sensitive to global structure, both as a stimulus and as a distractor. Detecting global structure, when presented in a noisy stimulus, is still possible. Glass patterns, which are detectable as linear, radial and circular patterns can be detected with a high level of noise (Glass, 1969), particularly when the stimulus is circular (Wilson & Wilkinson., 1998). The fact that the visual system is highly sensitive to these global patterns also affects our ability to recognize other stimuli. In visual search tasks, it is much easier to identify one aberrant element, when the remaining elements are organized and similar to each other in some ways (*e.g.* orientation, Hegde & Felleman, 1999).

Temporal dynamics such as temporal synchrony and structure have been shown to aid in the perception of form within arrays that lack spatial structure (Usher & Donnelly, 1998; Lee & Blake, 1999b; Guttman et al., 2007). Stimuli with correlated temporal structure benefit from the addition of spatial structure (Lee & Blake., 1999a). Does FDF behave in a similar manner to Lee and Blake's stimulus, which uses stochastic temporal structure, translational motion and elements with randomly defined luminance? Or does it suffer from the addition of background structure? The importance of temporal cues to FDF perception is likely to make detection thresholds independent of background structure. An effect of background structure may have implications for the role of global shape processing regions, such as V4.

Flicker defined form (FDF) is a stimulus which is defined primarily by temporal cues. Dots that flicker in counterphase to adjacent dots, reversing their luminance values, create illusory contours between the patches of flickering dots (Rogers-Ramachandran & Ramachandran, 1998). The visibility of this stimulus has been shown to be dependent on luminance, flicker rate and increasing eccentricity (Quaid & Flanagan, 2005a). The dependence on high temporal resolution and improvement in the periphery is indicative of magnocellular processing. Other results show that FDF can be matched to sine wave gratings of low spatial frequencies (<4cpd). This matching is affected by some of the same properties that affect our ability to perceive the illusion, specifically eccentricity and dot number (Quaid & Flanagan, 2005a). Data also suggests that the amount of area which flickers out of phase with the background is important in the determination of whether the stimulus can be perceived (Goren & Flanagan, 2008)

FDF is different than both real contours and static illusory contours. It is believed that the majority of its illusory saliency comes from the temporal synchrony of its elements. The current study attempts to determine if the organization of background elements affects perception of the FDF illusion. There are three possible outcomes. If the temporal synchrony is sufficient to elicit perception, then there should be no changes with background organization. If temporal synchrony is insufficient, then organization may facilitate perception of the illusion by helping it to stand out from the background. The last possibility is that the background organization may be distracting, making the illusion more difficult to see. Based on research on other temporally-dependent stimuli spatial structure should benefit perception of the illusion (Lee & Blake, 1999a). The spatial structure used in Lee and Blake's (1999) paper is different than the structure used here. If both are affected by the addition of a greater amount of structure, it suggests that flicker-defined and translationally-defined forms share some similar interactions between processing within dorsal and ventral pathways.

3.3 Methods

3.3.1 Subjects

Three students, 2 male and 1 female, aged of 23, 23 and 32 years served as observers for this task. Subjects had normal or corrected to normal vision (6/6 or better) and no known ocular diseases or surgery.

3.3.2 Experimental setup

Subjects were seated 0.32m from a Sony Trinitron Multiscan CPD-G500 monitor subtending 61.8 x 48.3 degrees. The resolution of the monitor was 1024 x 768 pixels and pixel pitch was

0.37mm. Refresh rate was 100Hz. Luminance was determined using a look up table which varied from 0cd/m^2 to 100cd/m^2.

3.3.3 Stimulus

For all experiments, dot elements of 0.34 degrees diameter were placed at random locations. These background dots were flickered at 16.67Hz (square wave). The illusory stimulus was a circular patch of dots (5 degrees in diameter) which flickered 180 degrees out of phase with the background dots. This creates the illusion of a contour, which is defined by temporal luminance modulation. The illusory contour was ramped up to the desired contrast for 160ms, followed by 400ms of sustained contrast and then ramped back to the next contrast value for 160ms. Thus, the entire stimulus was presented for 720ms.

3.3.3.1 Randomness

FDF dot fields are normally comprised of randomly positioned dots. Here we investigate the effect of randomness. All of the randomness manipulations are performed on the dots before the experiment begins and are maintained throughout the experimental run.

For all experiments randomness was defined determining a new position for each dot, which was maintained throughout the experiment. Dots were moved away from an organized structure in random directions. The two organized structures from which the dots were moved were a grid and a concentric circle pattern (Fig 3-1, A and B). For these ‘baseline’ structures, the distances between dots were kept constant (and equal for grid and circle) to ensure an equal density of dots in both paradigms. When randomness was added, the distance each dot was moved was defined as a fraction of the maximum distance between dots defined by the grid (Fig 3-1, C).

In experiments where randomness was varied, randomness was defined as:

$$R = D_R/D_{max} \qquad (1)$$

Where R is the percent randomness, D_R is the distance moved (degrees) at that particular percent randomness and D_{max} is the distance (degrees) between the dots in the completely organized case.

This distance moved was equal for all dots, although the direction (360 possibilities) was randomly assigned. The direction applied to each dot was the same across all levels of randomness. Only the amount of randomness was varied in these experiments. Thus, the vector defining the movement of each dot was only varied in length, not angle.

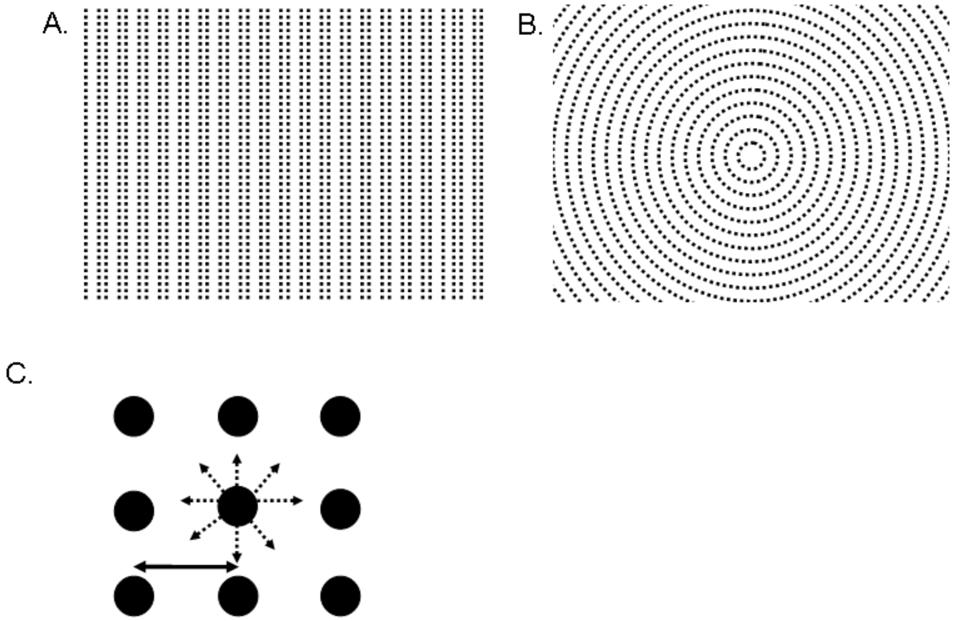

Figure 3-1. Random dot background generation.

A schematic of an organized grid-like background (A), and circle-like background (B). The third panel shows how the backgrounds were generated. The solid arrow indicates Dmax (the maximum distance the dots can be moved). The broken arrows indicate that the dot can be moved in a number of different directions, the magnitude of which determines the amount of randomness for the particular background. Note that this movement is applied to each dot individually.

3.3.3.2 Different, but equal randomness

For this first set of control experiments the amount of randomness used was kept constant for all conditions, with the direction of individual dots being different between screens. The amount of randomness was defined as the maximum distance a dot could travel. This distance was the same for all five of the random screens (Seed A-E). The differences between screens originate from the direction which each dot moves, which varies between screens. This means that although each dot moves to a maximum distance, which is the same for all of the different randomly defined screens, the direction each dot moves, varies. The randomness of the screens is equal because the maximum distance the dots moved from the organized structure is the same.

3.3.4 Task

A yes-no detection task was used to assess a log-Michelson percentage contrast threshold using a modified rapid estimation by binary search (REBS). A staircase procedure (4-2-1) was used to determine the threshold, which was defined as the average contrast value for the smallest contrast reversal steps. Two reversals were required to end the thresholding procedure.

All experiments were performed monocularly using the right eye. Stimuli were presented in the inferior temporal quadrant at four eccentricities (0º, 4.2º, 12.7º, 21.2º).

3.3.5 Analysis

Three threshold values were recorded for each subject and for each experimental condition. Mean and standard errors were calculated. Repeated measures ANOVAs were then used for statistical testing, followed by Tukey's post-hoc analysis.

Post-hoc analyses were performed on significant effects. Tukey's HSD results are reported for p-levels of 0.05, 0.01 and 0.001.

3.4 Results

3.4.1 Is there an optimal randomness?

The control experiment was intended to test whether screens with an equal level of randomness are treated similarly. Five equally random screens were used as the backgrounds for these trials. Randomness was defined by moving individual dots away from their positions in a grid structure. Figure 3-2 shows that there are no significant differences between results for the different randomly organized dots (screen), suggesting that the different orientations of the dot movements are all affecting FDF perception equally. There is neither an effect of screen ($F_{(4,8)}=1.21$, $p=0.38$, observed power=0.23), nor an interaction between the effect of screen and eccentricity ($F_{(12,24}=1.27$, $p=0.3$, observed power=0.53).

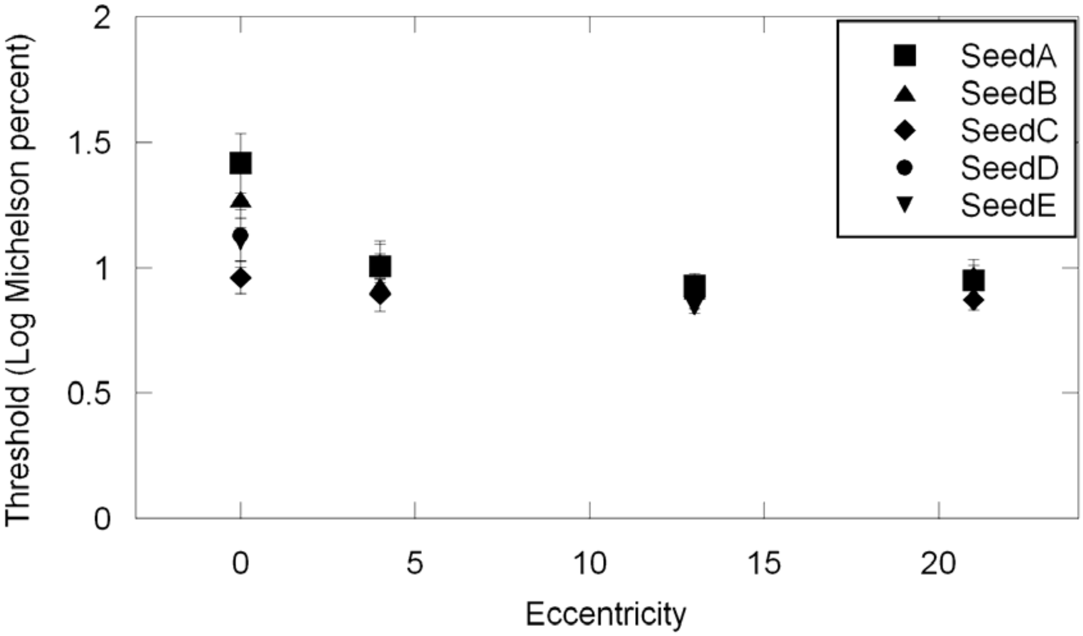

Figure 3-2. The effect of ‘different’ randomness at four eccentricities.

Seed values represent the different random screens. The amount of randomness is equal for all screens. Mean and standard errors for four eccentricities are shown.

3.4.2 Effect of size

In order to ensure that randomness effects are not simply due to a greater variability in the number of dots within the pattern, an experiment was undertaken in which the size of the stimulus was modified. Although a previous study showed that target size has a significant effect on FDF thresholds, diameters of 4º, 5º and 6º were shown to have a minimal difference (Quaid & Flanagan, 2005a).

Size had a significant effect on threshold in this study however ($F_{(2,4)}=22.81$, $p<0.01$, Fig. 3-2). Specifically, thresholds were significantly higher for targets of 4º and 5 º diameter as compared to the 6º diameter targets ($p<0.05$). Although the effects are statistically significant, they are not large in magnitude. Averaged thresholds of target sizes of 6º are only slightly lower than target sizes of 4º (1.01±0.02 vs. 1.22±0.02). The most important consideration for this control experiment was the interaction between size and randomness.

The reason for conducting this control experiment was to determine if different sizes show different effects with varying randomness. Namely, can randomness effects be attributed to variation in dot number within a target size. A larger target would have greater variability, but also greater area, which might compensate for this variability. Results of this experiment showed that size effects do not interact with eccentricity or randomness (respectively, $p>0.48$; $p>0.54$, observed power=0.25 and 0.33). This confirms that although larger targets are easier to perceive, the variability of the location of dots did not influence the effects of randomness. Due to the lack of significant interactions between size and randomness, all remaining effects of randomness were calculated using thresholds for all three sizes.

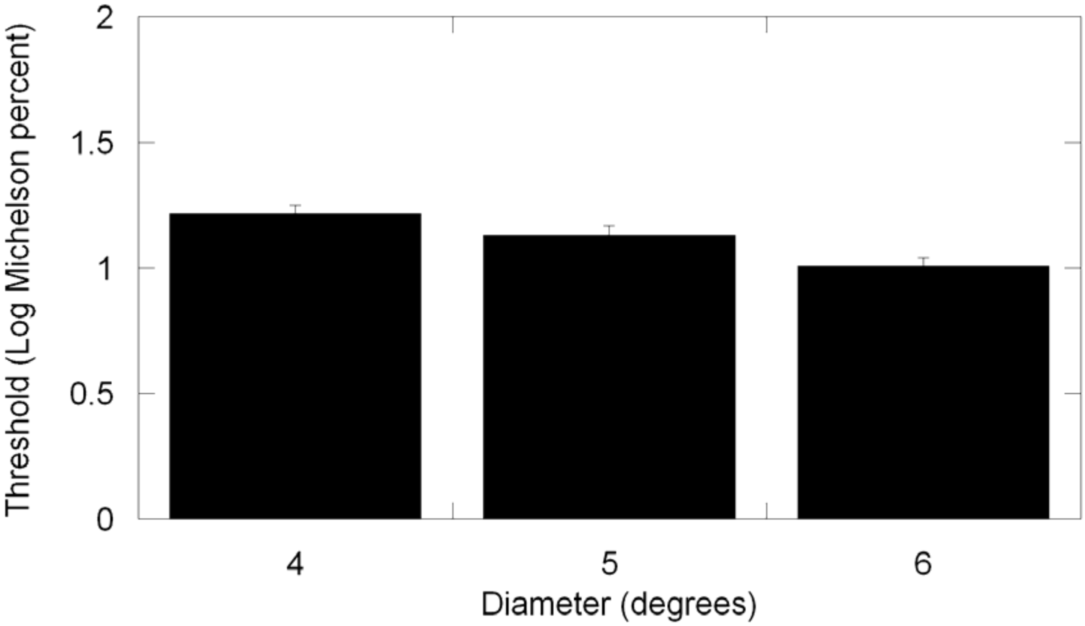

Figure 3-3. The effect of size on FDF detection.

Data averaged for 3 subjects. Mean and standard errors collapsed across randomness and eccentricity are shown.

3.4.3 Effect of randomness- Grid

This set of experiments was designed to asses the importance of randomness by quantifying the amount of deviation from a highly ordered background. Whereas many experimental paradigms (Glass, 1969) add elements to the display to increase randomness, thus maintaining the underlying signal, it has been shown that the density of dots within FDF displays can greatly affect the strength of the signal (Quaid & Flanagan, 2005a). All randomness deviated from a grid structure, containing both local and global structure, by moving the dots a set distance from their original position.

Increasing the amount of randomness in the background had a significant effect on performance ($F_{(5,10)}= 8.48$, $p<0.01$). In general, thresholds are higher for stimuli with more randomly organized dots. The magnitude of these increases in contrast threshold varied somewhat between subjects, but in some cases, thresholds doubled from the least random paradigm to the most random paradigm. However, randomness alone does not explain the variation of thresholds.

The effect of randomness is also affected by the eccentricity of the stimulus. The interaction between eccentricity and randomness is significant ($F_{(15,30)}=4.18$, $p<0.001$). At lower eccentricities, thresholds are affected by randomness with greater strength (Fig 3-4).

Post-hoc analysis shows significant differences between performance for smaller amounts of randomness (0%, 20%, 40%) and higher amounts of randomness (80%, and 100%), at fixation ($p<0.01$) and 4.2 ($p<0.01$, Fig 3-3). The effect of randomness is less robust at further eccentricities (Fig 3-4). Thresholds for higher levels of randomness (60%, 80% and 100%) are significantly smaller at 12.7º and 21.2º than 0º and 4.2º ($p<0.01$). Thresholds for lower levels of randomness (*i.e.* 20% and 40%) are also affected by eccentricity. Thresholds for these more organized stimuli presented at fixation are significantly larger than for stimuli presented at 12.7 and 21.2 ($p<0.01$).

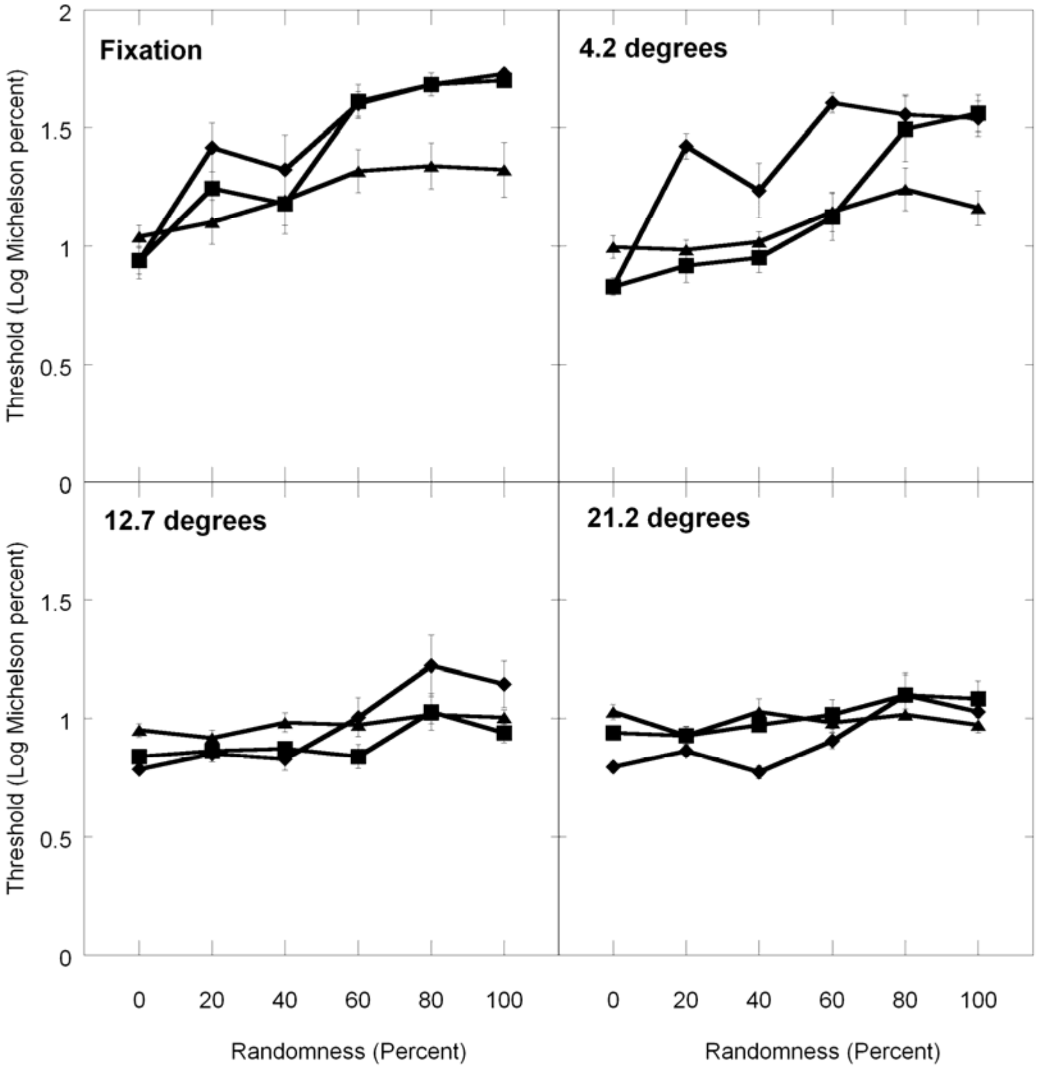

Figure 3-4. The effect of randomness on FDF detection at various eccentricities (variation from grid) collapsed across target size.

Eccentricities are given in the upper left corner of each panel. Data shown for 3 subjects. Mean and standard errors for each subject collapsed across target size are shown.

3.4.4 Effect of Randomness- Circle

The purpose of this experiment was to determine if the benefits found previously with circle detection in noise (Wilson & Wilkinson, 1998) extend to detection of FDF. Namely, if we are sensitive to circles and deviation from circles, the presence of underlying concentric structure may be able to affect perception of FDF more than a grid like pattern.

Circle and grid backgrounds affected FDF performance differently. Statistically significant differences were seen between performance with circle versus grid backgrounds ($F_{(1,2)}=34.64$, $p<0.05$). Although the effects are significant, the differences between the patterns were relatively small. Thresholds collapsed across eccentricity and randomness are similar (circle: 1.00±0.02 vs. grid: 1.13±0.02).

Another significant effect was the interaction between shape and eccentricity (Fig. 3-5, $F_{(3,6)}=7.91$, $p<0.05$). Post hoc analysis showed that differences in threshold between circles and grids can be seen at 0° and 4.2° ($p<0.05$). Thresholds at 0° were significantly higher for both grids and circles than for further eccentricities (*e.g.* 12.7° and 21°, $p<0.01$). At 4.2°, thresholds for FDF detection with underlying circular organization had similar thresholds to further eccentricities, whereas grid pattern thresholds were still significantly higher ($p<0.01$).

Circles and grid detection thresholds vary differently with randomness ($F_{(5,10)}=3.93$, $p=0.047$). This effect is only borderline significant. Both grids and circle data show differences between low and high levels of randomness. The only difference arises at 40% randomness where circles are still significantly better than the more random patterns, but grids are not ($p<0.05$). Although the absolute cutoff varies between the two patterns, thresholds seem to vary in a similar manner.

Although these effects are important, they do not reflect the goal of this study, namely to determine the effects of randomness. Both circles and grids are subject to effects of randomness, and the interactions found between randomness and eccentricity. Although differences were found between circles and squares at various eccentricities, no interaction between eccentricity, shape and randomness were found ($F_{(15,30)}$=1.23, p=0.30, observed power=0.59). Thus, thresholds can be affected by shape, eccentricity and randomness, although, the factors do not necessarily interact.

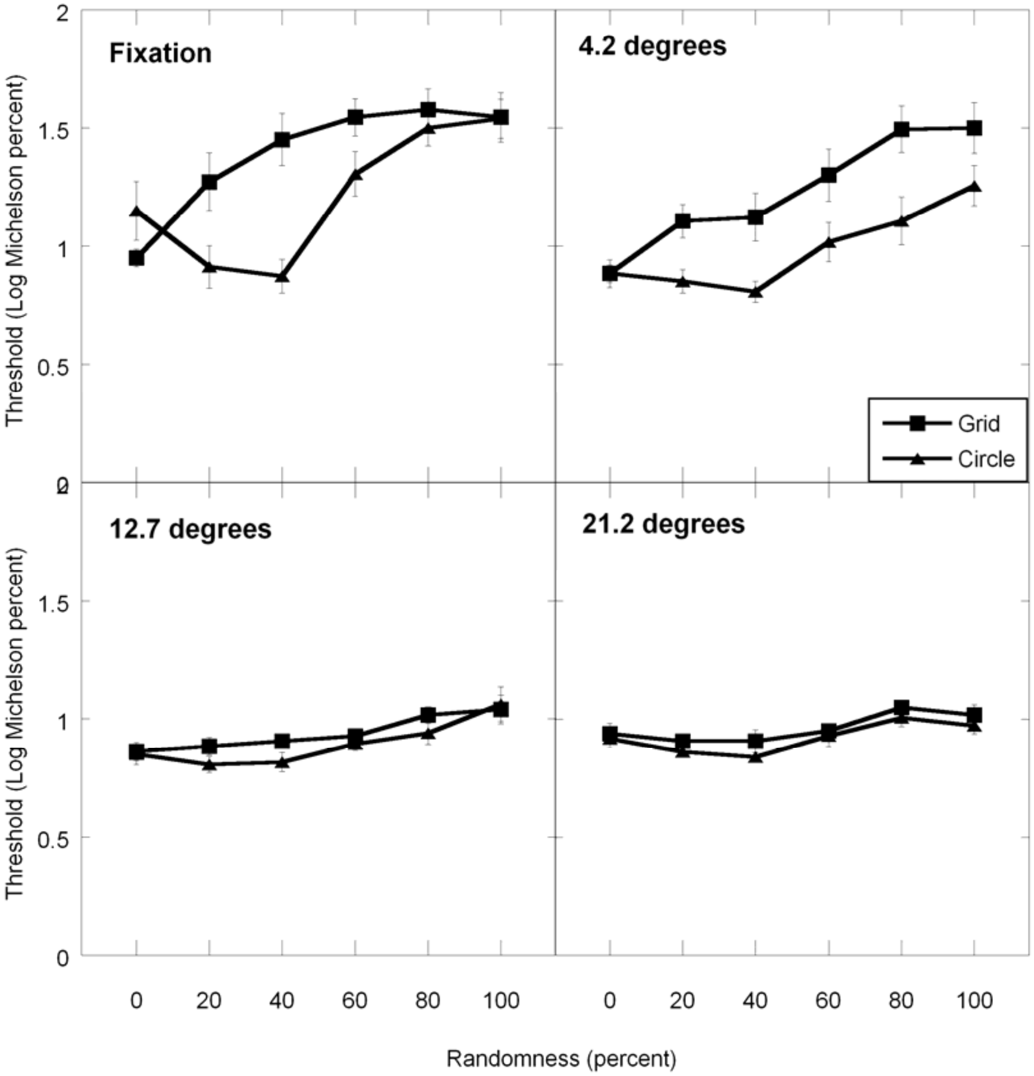

Figure 3-5. Comparison of grid and circle randomness effects on detection thresholds.

Eccentricities are given in the upper left corner of each panel. Data are averaged across subjects for 5 degree target sizes.

3.5 Discussion

FDF perception is highly dependent on the amount of structure in the background. The more structured the background, the easier it is to perceive the illusory contour even when the stimulus does not conform with background structure. This is true at all eccentricities, although more pronounced closer to fixation. Results suggest that this effect is not due to a difference in the amount of area of the stimulus, but rather an effect of the organization. The potential reasons for this, including implications for designing future stimuli will be discussed.

FDF research thus far has assumed a dominance of the magnocellular pathway in processing the illusion (Quaid & Flanagan, 2005a; Quaid & Flanagan, 2005b), but little is known about what regions are involved beyond the ganglion cell layer. Static illusory contours are believed to be processed primarily in V2 (von der Heydt et al., 1984) later than non-illusory stimuli (Imber et al., 2005). It may be that FDF is processed similarly. Although, the importance of temporal dynamics on this illusion makes it similar to other illusory motion-defined stimuli.

Form-from-motion is one type of stimulus in which shapes are defined by movement of the elements within or surrounding the shape. A clinical study showed that form-from-motion stimuli are processed differently than static shapes and simple motion (Cowey & Vaina, 2000). Although the patient's motion perception system was intact, she was unable to identify shapes. She was also unable to detect form-from-motion stimuli, suggesting that dysfunction in the form perception system disrupt the connection between -motion and form perception regions, preventing perception of motion-dependent form perception. FDF is different from form-from-motion stimuli because the FDF elements do not move, but are instead changing luminance at a high temporal frequency. Although different, the reliance on both motion and form perception is probably common to both form-from-motion stimuli and FDF.

Organization of the elements may affect high or low level mechanisms responsible for perception of the illusion. The perceived low spatial frequency of the stimulus, resistance to blur and improved performance with increasing eccentricity (Goren et al., 2005; Quaid & Flanagan, 2005b) point to magnocellular dominance in perception of the FDF illusion. This low level mechanism may be affected by the organization of the elements used to generate the illusion itself. Closer to fixation, the parvocellular pathway constitutes a larger portion of retinal ganglion cells than in the periphery (Azzopardi et al., 1999), allowing perception of spatial information (*e.g.* fine details). The shift in dominant pathway with eccentricity may explain why there is so much variation in performance. This pattern was also found by Quaid & Flanagan (2005) when mapping the spatiotemporal characteristics of the illusory contour. The parvocellular pathway's ability to respond to higher spatial frequencies than the magnocellular pathway means that it is more sensitivity to fine detail than the magnocellular pathway. The sensitivity of the parvocellular pathway to detail may make the parvocellular pathway more sensitive to background structure than the magnocellular pathway. Thus, within the macular region, where the parvocellular to magnocellular ratio is larger than at further eccentricities (Azzopardi et al., 1999), the parvocellular pathway may make the illusion more sensitive to structure.

The most likely mechanism for the benefit of structure is involvement of higher cortical areas. According to many studies, illusory contours rely on involvement from areas beyond V1. Where this feedback originates is dependent on the type of stimulus. Masking studies show the most effective masking effects at longer stimulus onset latencies, suggesting that the most effective masking occurs in later cortical areas, such as LOC (Imber et al., 2005). fMRI studies have found activation of the parietal cortex for static illusory contours (Stanley & Rubin, 2003) along with V4 (Mendola et al., 1999). The removal of dorsal extrastriate regions was shown to impair figure-ground perception in the lesioned hemifield, suggesting that feedback is important to the linkage of disconnected elements (Super & Lamme, 2007). It is also believed that pre-frontal cortex is involved with such complicated tasks (Ciaramelli et al., 2007). FDF is similar to a static illusory contour and figure-ground task, because it relies on the ability to perceptually link elements which are physically separated. The involvement of higher order dorsal and ventral stream areas in the processing of these illusory stimuli make it likely that FDF relies on similar mechanisms. The ability of parietal cortex and V4/LOC to link spatially separated elements is an ability which may affect FDF perception. A preference for highly ordered stimuli in these areas, with larger receptive fields and more global preferences, may allow a change in perception for FDF, similar to that seen in the current results.

The effect of the interaction between FDF perception and background structure is positive, facilitating perception of the stimulus. These effects were found for both the co-linear and the concentric patterns. A small overall preference for circular stimuli was seen in the current study, similar to results from other studies (Wilson & Wilkinson, 1998) This preference for circular structure found in other studies, is often attributed to higher cortical areas. Circles are easier to detect than parallel structures on a global level (Aspell et al., 2006).

Structure may change performance by stimulating the same parts of the visual system, or by changing the proportion of each of the pathways employed. It is possible that the presence of structure changes the stimulus sufficiently that it is treated as a different stimulus, thus processing may differ. One possibility is that structure creates a pop-out effect. Pop-out tasks often involve elements which vary in one dimension and thus the 'different elements' (*i.e.* FDF elements) are special. According to one study, pop-out is mediated by grouping mechanisms (Hegde et al., 1999). FDF, which groups elements based on their luminances at various times, maybe be employing pop-out mechanisms even when structure isn't present in background elements. When structure is present, the fact that the elements vary from the background structure due to the luminance differences (which all ready have grouping effects), may be an additional dimension for grouping purposes. Whether pop-out is mediated by grouping is still under debate (Lamme & Spekreijse, 1998). Although pop-out may seem to be a likely explanation for changes in FDF perception, this is still unclear.

The large divide in performance between 40% and 60% randomness suggest that 40-60% random is an ideal range for this stimulus. The fact that additional degradation in performance beyond 60% is minimal suggests that there is no perceptual difference between 60% and 100% randomness. At lower randomness values, the organization of elements may mean that the ability to perceive the illusion is similar to a pop-out task, which is different than baseline conditions for FDF. This finding is in keeping with some other results, which suggest that dot displacements of approximately 21 arc min are preferred by monkey neurons which respond to coherent motion (Peterhans et al., 2005). Randomness values of 40-60% are equivalent to vector lengths of between 0.27˚ and 0.40˚, similar to the preferred distance between the neurons. In order to keep the stimulus as similar to previous experiments as possible, the randomness should be maintained above 40%, but ideally closer to 60%.

The effect of size on perception of the illusion suggests that a larger target improves performance. Although, if the effect of the larger target was due to a greater likelihood of dots being within the circle at higher randomness values, then there would be an interaction effect between randomness and the size of the target. The lack of such an effect suggests that randomness did not affect the likelihood of there being fewer dots within the stimulus with higher levels of randomness.

Given that all of the stimuli studied here had both global and local structure, it is unclear which of these two components caused the facilitatory effects seen in this study. Further studies, which focus on the presence of either global or local information may help to clarify this. One of the possible manipulations is the use of Glass patterns (Glass, 1969) which have global, but not local information.

In summary, FDF is easier to perceive when the elements in the background are organized. These effects are more pronounced closer to fixation, probably because this is the region of the visual field where the illusion is most fragile because of parvocellular dominance. No differences between the types of underlying structure are found, suggesting that although there are different mechanisms interfering, it is likely not a higher cortical region with preferences for particular structure.

3.6 Acknowledgements

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Chapter 4

Is flicker defined form (FDF) dependent on the contour?

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4.1 Abstract

Flicker defined form (FDF) is a temporally driven illusion within which randomly positioned background elements, are flickered in counterphase to stimulus elements, creating the illusion of a contour in the region between the background and stimulus dots. It has been proposed that FDF is dependent on the boundary region between the counterphase flickering dots. Is the stimulus area or the illusory contour itself (region between stimulus and background) paramount to the FDF percept? Circular stimuli were compared to ring stimuli to determine the relative importance of area and contour. The rings were tested in the following configurations: constant maximum diameter/variable area; constant area /variable contour; and constant contour /variable area. For rings with constant diameter no effect of ring thickness was found. No effect of contour was found for rings of a constant area. For rings of constant contour, the smaller the area the greater the threshold. These results suggest a greater dependence on the area of a stimulus rather than its contour. Area dependence suggests that the theory of contour-dependence by a fast extraction system is unlikely. This temporally-defined magnocellular-dependent illusion, is influenced by slow surface perception mechanisms of the parvocellular system.

Keywords: Illusion; Contour; Detection; Contrast; Area

4.2 Introduction

Do edges define figure versus ground when the edge itself is illusory? The phantom contour illusion, more recently referred to as Flicker Defined Form (FDF) (Quaid & Flanagan, 2005a), has been shown to rely heavily on the border between two regions of dots flickering in counterphase in order to create the percept of a figure (Rogers-Ramachandran & Ramachandran, 1998). Other studies have found that form-extraction information can be perceived with delays of 5ms between figure and ground. This delay is consistent even when temporal frequencies are modified between 1.3 Hz and 30Hz (Fahle, 1993).Temporal synchrony, without spatial cues, is sufficient to elicit perception of a salient edge (Lee & Blake, 1999; Usher & Donnelly., 1998).

Although temporal characteristics are enough to elicit perception, spatial characteristics can affect perception of temporally defined stimuli. The number of random dots per degree of visual space, which define the FDF illusion, affects the perception of the illusion (Quaid & Flanagan, 2005a). More specifically, the spatial content percentage (k) has been related to FDF perception. Spatial content percentage is the product of the area of individual dots, the number of dots within a given stimulus and the area of the stimulus. Thus, k, accounts for the area within the stimulus boundary which is flickering out of phase. This spatial content dependent effect has been found in other temporally-defined stimuli (Lee & Blake, 1999). This may be due to a completion of the border creating a higher spatial frequency illusory edge, or it may simply be an area dependent effect, *i.e.* due to spatial summation. A greater number of random dots within the stimulus would give a higher spatial content for the stimulus, which gives an increased area of flicker, even though the area of the stimulus remains constant. This would still mean that more receptors would be activated.

Although the spatial content percentage is important to FDF perception, a plateau for target size was previously reported (Quaid & Flanagan, 2005a). This is similar to the results found for temporally driven stimuli other than FDF, with a number of studies having shown that only small target sizes affect contrast thresholds (Makela et al., 1994; Tyler & Silverman., 1983). Medium and larger target sizes show no effect on contrast thresholds at eccentricities away from fixation. These results suggest that flickering stimuli are processed differently than static luminance defined targets which are subject to principles of spatial summation at all eccentricities.

We can compare FDF to other stimuli that share specific characteristics such as flicker (Makela et al., 1994; Tyler & Silverman, 1983) for the similar temporal dynamics; and form-from-motion, for the ability to perceive a shape due to dynamic elements (Schoenfeld et al., 2003). Recent studies have shown that the visual system is sensitive to temporal synchrony (Lee & Blake, 1999; Usher & Donnelly., 1998), and temporal structure (Guttman et al., 2007), particularly for contour binding (Bex et al., 2001), but whether these systems use similar mechanisms, is still unknown. Although some of these stimuli seem to rely on magnocellular and/or dorsal stream mechanisms, form-from-motion stimuli seem to be reliant on the interaction between the two streams, and can be imperceivable even when motion and form perception are intact (Cowey & Vaina., 2000; Schenk & Zihl, 1997). In contrast, flicker perception is primarily dependent on the magnocellular system (Livingstone & Hubel., 1987). We believe that FDF is distinct from these stimuli because of the lack of perceivable temporal dynamics, as exemplified in the inability to perceive the surface phases when the border between the patches is covered (Rogers-Ramachandran & Ramachandran, 1998).

The most similar stimulus to FDF is Lee and Blake's stimulus which has no discernable temporal structure, but allows perception of shapes (Lee & Blake, 1999). According to Blake and Lee and others (Usher & Donnelly., 1998) stochastic (lacking structure) temporal structure is processed very efficiently by the human visual system. Thus, even this stimulus which provides no obvious cues to temporal structure, is significantly different from FDF.

Flicker defined form is believed to be a predominantly magnocellular based stimulus due to its dependence on high temporal frequencies, its perceived low spatial frequency (Goren et al., 2005) and its resistance to optical blur (Quaid & Flanagan, 2005b). The illusion can tolerate decreases in stimulus size and is enhanced by peripheral viewing (Quaid & Flanagan, 2005a; Rogers-Ramachandran & Ramachandran, 1998). Flicker defined form thresholds have been shown to be determined both by the number of dots within the stimulus and the stimulus diameter (Quaid & Flanagan, 2005a). However, it is not understood whether the stimulus area or the border of the stimulus itself is the most important component of the illusion. Previous findings showed that when the region between the phase shifted random dots was covered, the two surfaces could not be distinguished, which is why the region in between the dots, referred to here as the contour, is believed to be the most important component. The importance of this contour was the basis for Rogers-Ramachandran's theory that this illusion is controlled by a fast acting contour extraction system. This system was believed to be the magnocellular system. The current study aims to determine whether the contour is the most important component for perception of the illusion. If area is found to be equally or even more important, this would suggest that the fast acting contour perception would not be the mechanism to explain FDF perception.

4.3 Methods

The sample consisted of two sets of 3 subjects. The first set was aged 23, 23 and 31 years old, one female and two males. The second set consisted of two females (aged 24 and 27) and one male (aged 24). All subjects were naïve to the purpose of the experiment. All subjects had normal, corrected vision (6/6 or better) and no known ocular abnormalities. Subjects viewed the stimulus with their right eye.

Subjects were seated 32cm from a Sony Trinitron monitor 20″ (Multiscan CPD-G500) using a resolution of 1024 x 768 pixels and a pixel pitch of 0.37mm. At this distance the monitor subtended 61.8 x 48.3 degrees. The refresh rate was 100Hz. Luminance values ranged from 0cd/m2 to 100cd/m2. Twenty-three contrast values were presented, using this range of luminance values. Stimuli were generated on a PC running custom software in a LINUX based environment.

Stimuli's contrast values were measured in log Michelson units.

$$\frac{\mathrm{Lmax}-\mathrm{Lmin}}{\mathrm{Lmax}+\mathrm{Lmin}}$$

4.3.1 Stimulus

Dots subtending 0.34° were generated at random locations throughout the screen and were flickered at a temporal frequency of 16.67Hz. Background elements were flickered in counterphase to stimulus elements, creating the illusion of a contour in the region between background and stimulus (Quaid & Flanagan., 2005a; Rogers-Ramachandran & Ramachandran, 1998). Stimulus dots were defined as those that fell within the boundary of the stimulus area. If a dot was overlapping this boundary, the percentage of area that fell within the boundary determined whether the dot was classified as stimulus or background. A dot that was 50% or more within the stimulus area, was determined to be a stimulus dot. All dots were defined as either stimulus or background. This means that the boundary itself could potentially contain a portion of the background and/or stimulus dots.

The current study, was designed to determine the relative importance of the boundary between stimulus and background, as opposed to the amount of stimulus area. Circles and rings were used in all of the following experiments in order to ensure that all areas of the stimulus were equally salient. Using squares, gratings or other shapes with obvious corners would have created particular regions that were more salient, particularly for the illusory contour. A second reason for choosing circles was a greater ease of manipulation of contour versus area. Using more complex stimuli, such as gratings would make manipulation of contour, independent of area, significantly more difficult.

Stimulus size, amount of contour and area were modified, along with ring thickness in order to determine FDF's dependence on spatial characteristics. Stimulus size is defined by the outer diameter of the stimulus. Stimulus size is not affected by increasing contour within its diameter. For example, Figure 4-1 shows the manipulations for experiment 1 in which the stimulus size was not altered. Stimulus area was defined as the area between the inner and outer diameters of the rings. This area encompasses the locations where the stimulus random dots were found. During these experiments, the density of the dots was not manipulated, so the spatial content percentage did not change. The amount of contour in the stimulus was defined as the sum of the inner and outer contour that defined the ring.

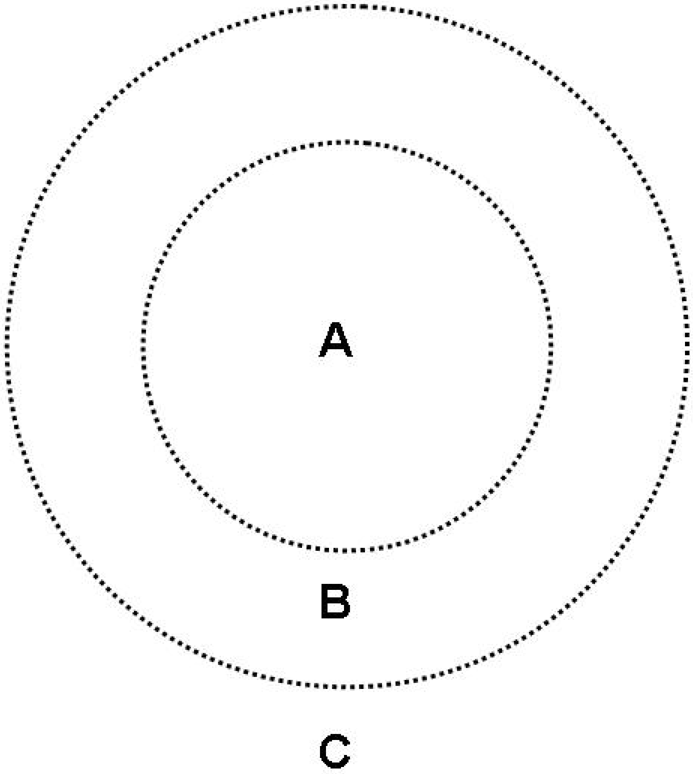

Figure 4-1. Stimulus structure

This figure shows the difference between stimulus and background elements. Note that the entire image would be covered with randomly located dots. A and C are the background regions. The elements bounded by these regions are in phase with each other and are in counterphase to elements within the B region (the stimulus region). Stimulus area is the area of B. Contour is the length of the dashed line (*i.e.* the sum of the inner and outer contour).

4.3.1.1 Constant stimulus diameter- varying ring thickness

The first set of experiments used a set of ring stimuli within which stimulus size was kept at a constant 5º diameter, but the inner diameter was varied to give ring thicknesses of Ring I (2º), Ring II (1.5º), Ring III (1º) and Ring VI (0.5º) (Fig. 4-2). The stimulus size and spatial content percentage were kept constant while the area of the stimulus was modulated. Overall contour length of the stimulus increased as the diameter of the inner ring was increased, as even though the outer portion of the contour was unchanged, the inner portion was being modified. Thus, contour and area were negatively related in this experiment.

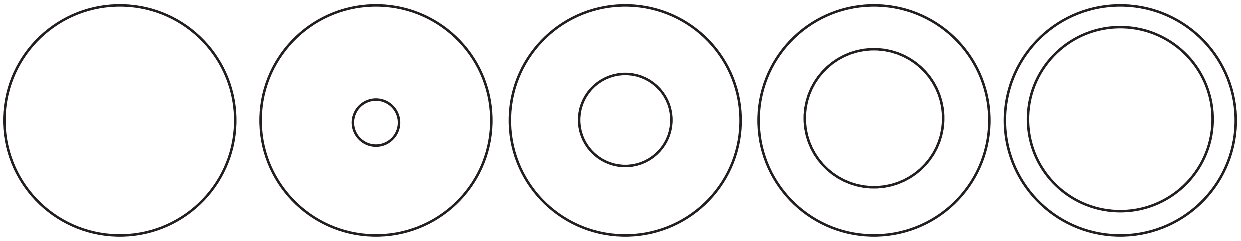

Figure 4-2. Ring stimuli for experiment 1.

Stimuli were of a 5º diameter, the inner circle was of diameter 0º, 1º, 2º, 3º, and 4º with corresponding ring thicknesses of 0º, Ring I (2º), Ring II (1.5º), Ring III (1º), and Ring IV (0.5º). Inner circle flickered in phase with background elements and in counterphase to elements within the ring.

4.3.1.2 Constant ring area- varying stimulus contour

The second set of experiments involved using a constant area equivalent to a 5° diameter circle (19.6 degrees2), while modifying the amount of contour (Fig. 3). Five different stimuli were created with contours: Contour I (29.3°), Contour II (44.8°), Contour III (58.6°), Contour IV (72°) and Contour V (85.1°). These contours had the same areas and spatial content percentage, but varied in their stimulus size. The outer diameters, defining stimulus size were: 6°, 8°, 10°, 12° and 14°.

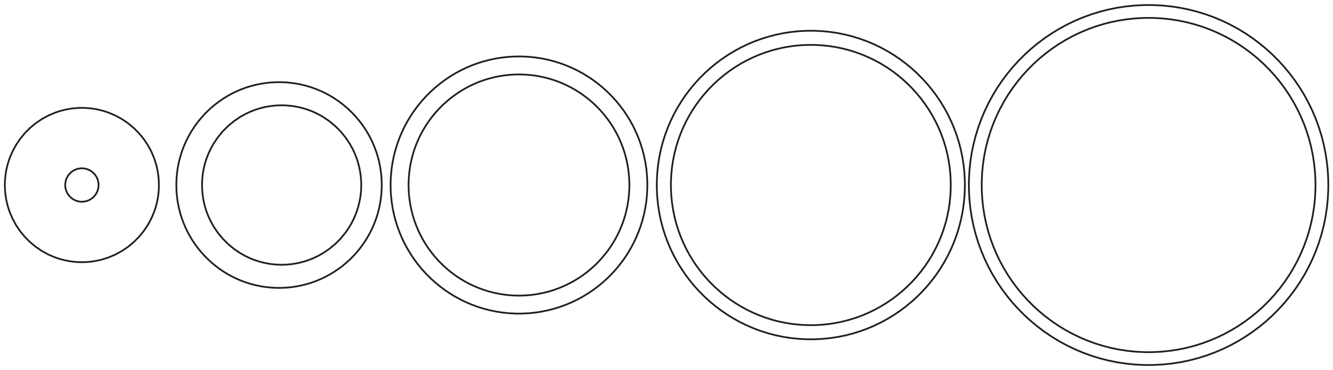

Figure 4-3. Constant area stimuli, variable contour.

Constant area stimuli, variable contour. Stimuli were of variable diameter, but the amount of area (within the ring) was constant. Five different stimuli were created with contours: Contour I (29.3°), Contour II (44.8°), Contour III (58.6°), Contour IV (72°) and Contour V (85.1°). Inner circle flickers in phase with background elements and in counterphase to elements within the ring.

4.3.1.3 Constant ring contour- varying stimulus area

The third set of experiments involved keeping the amount of contour constant and varying the area (Figure 4). For this condition, the amount of contour was matched to the contour of the 5° diameter circular stimulus (15.7°). Four different areas were tested: Area I (3.1 degrees2), Area II (6.3 degrees2), Area III (9.4 degrees2). Area IV (12.6 degrees2),. In order for the contour to remain constant and the area to change, the overall stimulus size, defined by the overall diameter of the stimulus, was modified. For this experiment the outer stimulus diameters were: 2.9°, 3.3°, 3.7°, 4.1°.

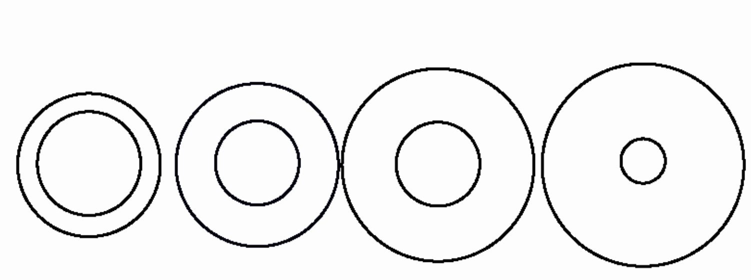

Figure 4-4. Constant contour stimuli, variable area.

Figure 4. Constant contour stimuli, variable area. Stimuli were of variable total size and ring area, but the amount of contour (outer and inner circle combined) was constant. Four different areas were tested: Area I (3.1 degrees^2), Area II (6.3 degrees^2), Area III (9.4 degrees^2) and Area IV (12.6 degrees^2). Inner circle flickers in phase with background elements and in counterphase to elements within the ring.

4.3.2 Protocol

Subjects were instructed to fixate on a red dot at the centre of the screen which was present at all times during experiments. Stimuli were presented for 720ms (160ms ramp up, 400ms constant contrast, 160ms ramp down). In a yes/no detection task, subjects indicated with a button press their ability to perceive the stimulus. In order to improve the variability of results, false positives were recorded. False positives were measured as responses that occurred within 180ms of the stimulus ramp onset or for within the final 1 second of the interstimulus interval. Most subjects indicated a response while the stimulus was being presented, so a delayed response would typically indicate a response where there was no stimulus (*i.e.* before a presentation). For false positives, any trials with more than 20% false positives were excluded (Bayer & Erb, 2002). The exclusion of trials was very rare, as subjects were practiced observers.

Contrast thresholds were estimated using a 4-2-1 staircase procedure with 2 reversals at the final crossing, and recorded using log Michelson contrast units. Twenty-three log steps of contrast values ranged from -0.3 to 2.0. In most cases where thresholds of 1.70 or greater are reported, they reflect an inability to perceive the stimulus due to upper limit constraints. Specifically, the contrast difference between the stimulus and background dots was unperceivable above a contrast of 1.70 log Michelson units. For all experiments, the effect of ring thickness was tested at each of four eccentricities (0º, 4.2º, 12.7º, 21.2º) within the inferior temporal quadrant along the 45° meridian, which correspond to stimulus locations of 3° x 3°, 9° x 9° and 15° x 15°. All subjects were tested three times for each stimulus condition (ring thickness, location).

4.3.3 Analysis

Mean and standard errors were calculated. Repeated measures ANOVA was used to determine the effect of different eccentricities, ring thickness (related to area of the stimulus), contour and size, and for any interaction between the variables. Tukey's honest significant difference (HSD) post hoc analysis was performed where significant effects of ANOVA were found.

4.4 Results

4.4.1 Constant stimulus diameter- varying ring thickness

For this experiment, the stimulus size was kept constant (*i.e.* 5º diameter) while thickness of the ring was varied. Effects of ring thickness were not statistically significant ($F_{(4,8)}$=1.16, p=0.40, power=0.22, Fig.4-5). No significant eccentricity-dependent effects were found, although trends suggest that thresholds decreased with increasing eccentricity ($F_{(3,6)}$=2.62, p=0.15, power=0.38). These trends could be seen in all three subjects with thresholds for 12.7° and 21.2° being lower than those found at 0° and 4.2°. The magnitude of this change varied by thickness of the ring and by subject. However, the interaction effects of ring thickness and eccentricity were not statistically significant ($F_{(12,24)}$=0.95, p=0.52, power=0.39). The apparent trends revealed increasing thresholds with decreasing ring thickness, which were more pronounced at fixation.

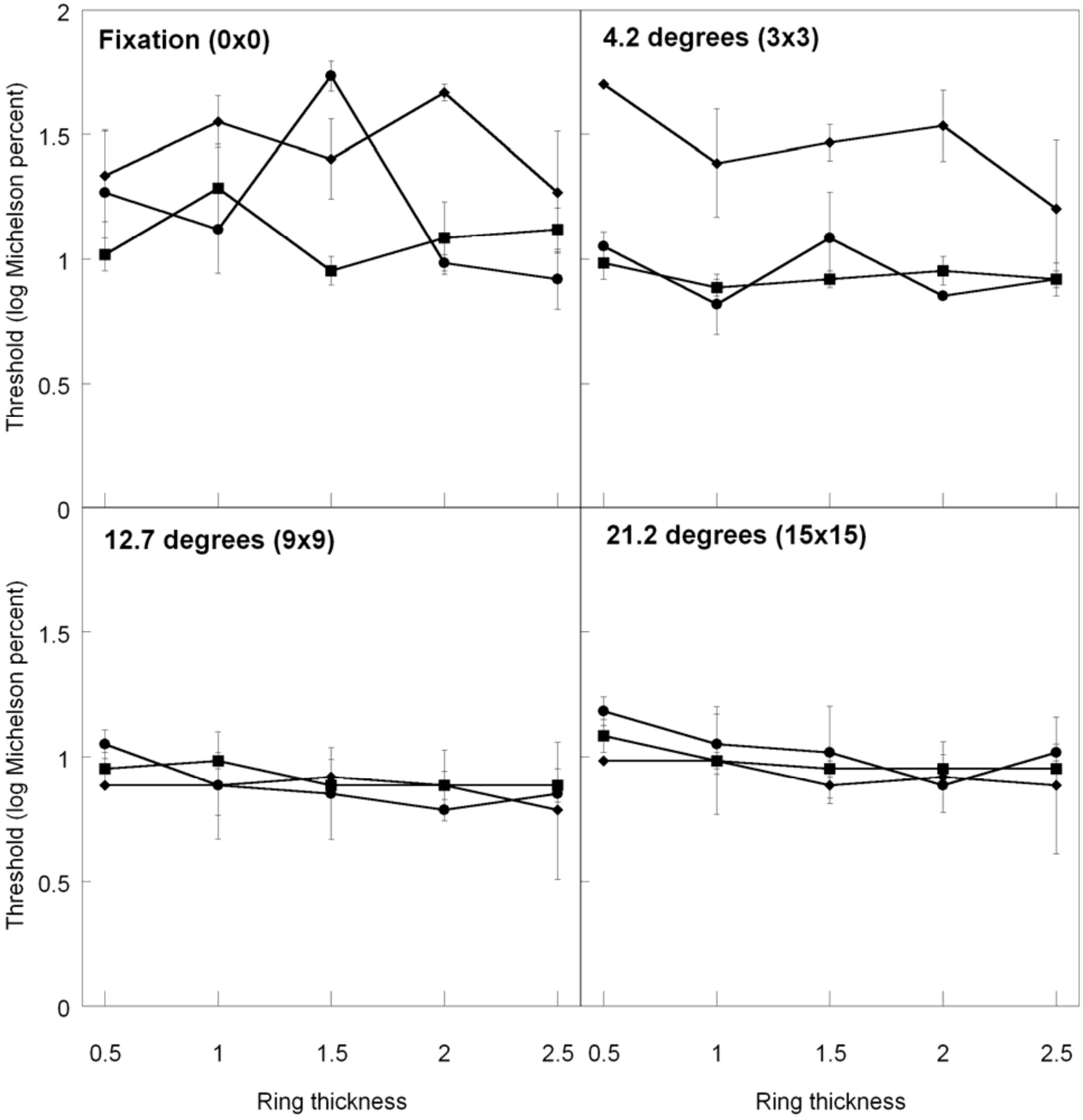

Figure 4-5. Effect of ring thickness on detection thresholds.

Figure 5. Effect of ring thickness on detection thresholds. Stimulus size of 5° for all stimuli, with ring thicknesses of Ring I (2°), Ring II (1.5°), Ring III (1°), Ring IV (0.5°) and solid circle (thickness of 2.5°) at various eccentricities (indicated in upper left corner). Mean and standard error for each of 3 individual subjects is shown. Different symbols indicate the 3 subjects.

4.4.2 Constant ring area- varying ring contour

In this experiment, the amount of area (*i.e.* of the ring) was kept constant while the amount of contour (the sum of the outside and inside of the ring) was varied. The stimulus diameter changed. No significant variation in threshold was found for the effect of modified contour (Fig. 4-6, $F_{(4,8)}=1.65$, $p=0.25$, power=0.31), or the interaction between contour and eccentricity ($F_{(12,24)}=2.02$, $p=0.069$, power=0.78).

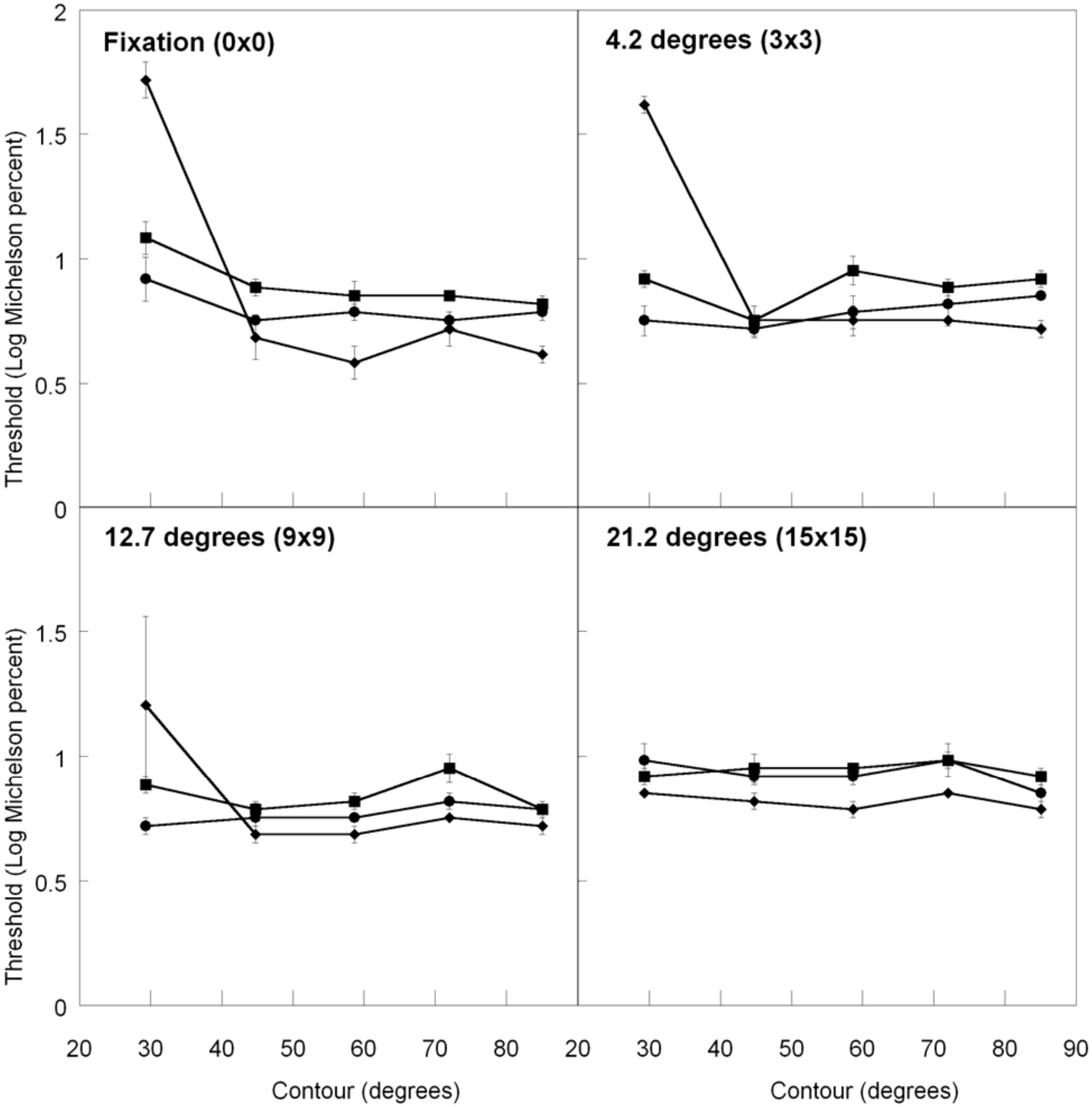

Figure 4-6. Effect of ring contour on detection thresholds.

Stimulus size and area of the stimulus (area flickering in counterphase to background) was constant. Amount of contour created by the counterphase flickering dots was varied. Five different stimuli were created with contours: Contour I (29.3°), Contour II (44.8°), Contour III (58.6°), Contour IV (72°) and Contour V (85.1°). Mean and standard error for 3 subjects are shown. Different symbols indicate the 3 subjects.

4.4.3 Constant ring contour- varying ring area

In this experiment, the amount of contour (*i.e.* the sum of the outside and inside of the ring) was kept constant while the area of the stimulus was varied. Four areas were tested, which will further be referred to by their ranking: Area I (3.1°), Area II (6.3°), Area III (9.4°), and Area IV (12.6°). Due to a large amount of variability, between subjects at fixation, this data was excluded from the statistical analysis. When it is included, similar effects of area and area-eccentricity interactions are found. Changes in area were found to affect thresholds, in an eccentricity-dependent manner (Fig. 4-7). Significant differences were found between stimuli of different areas ($F_{(3,6)}$=211.97, $p<0.001$). The interaction between area and eccentricity was also significant ($F_{(6,12)}$=15.04, $p<0.001$) meaning that the effect of area was significantly dependent upon the eccentricity in question. In particular, variation was most prominent for further eccentricities.

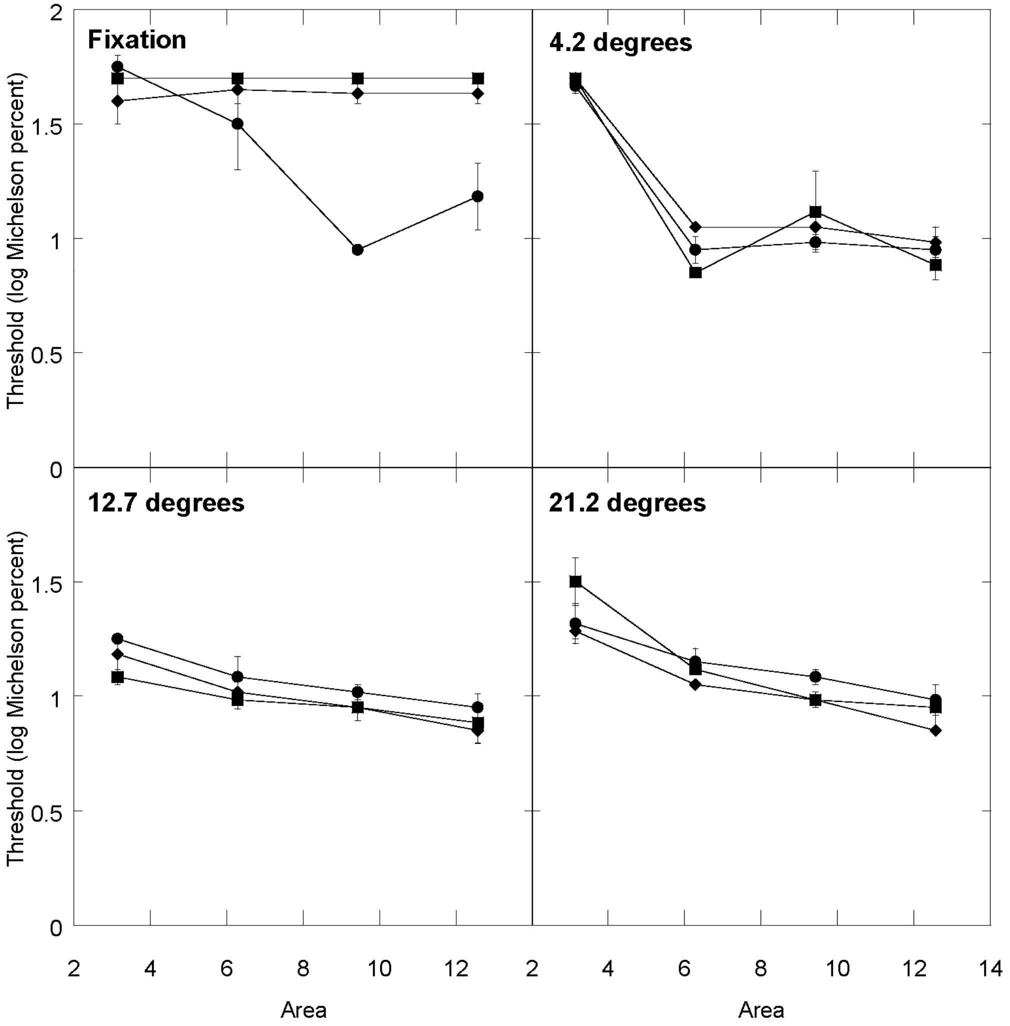

Figure 4-7. Effect of ring area on detection thresholds.

Effect of ring area on detection thresholds. Stimulus size and amount of area created by the counterphase flickering dots were constant. Area of the stimulus (area flickering in counterphase to background) was varied. Four different areas were tested: Area I (3.1 degrees^2), Area II (6.3 degrees^2), Area III (9.4 degrees^2) and Area IV (12.6 degrees^2). Mean and standard error for each of 3 individual subjects are shown. Eccentricity is indicated in the upper left corner.

Larger stimuli had lower thresholds (as one might expect). All 3 subjects showed decreases in threshold with increasing area of the stimulus. Post hoc analysis showed that smaller stimuli have higher thresholds than larger stimuli. Area I had significantly higher thresholds (mean: 1.69±0.01) than Area II (0.95±0.06), Area III (1.05±0.04) and Area IV (0.94±0.03) at 4.2º ($p<0.001$). At 12.7º Area I still had significantly higher thresholds than the two largest rings ($p<0.05$). This effect is also seen at 21.2º ($p<0.01$).

Thresholds decreased with increasing eccentricity, which is in agreement with the observation that the contour's visibility improves with increasing eccentricity (Quaid & Flanagan, 2005a; Rogers-Ramachandran & Ramachandran., 1998). The Area I stimulus thresholds were significantly lower at 12.7º (mean:1.17±0.05) and 21.2º (mean: 1.37±0.07) versus 4.2º (mean: 1.69±0.01, $p<0.01$). Area I showed higher thresholds than Area III and IV at 4.2˚, 12.7˚, and 21.2˚ ($p<0.05$). Area II, III and IV showed no improvements with increasing eccentricity. In summary, smaller target sizes give improved sensitivity with increasing eccentricity, in some cases making centrally imperceptible stimuli, perceptible.

4.4.4 Interaction between ring thickness and overall diameter

An analysis of the data was performed to determine the role of overall diameter in the perception of thin rings. Figure 8 shows a comparison of the thinnest ring in the first experiment to the thinnest ring in the second experiment. Both rings had thicknesses of approximately 0.5˚. One of the circles (from experiment 1) had an overall diameter of 5˚, whereas the second had an overall diameter of 14˚. Thresholds are lower for the larger stimulus, although this difference is small with large variability (average difference of <0.33±0.08) and not statistically significant ($F_{(1,2)}=9.66$, p=0.09, power=0.41).The majority of significant findings concerning FDF have pointed to the eccentricity-dependence of different effects (*e.g.* area, contour). In this study, area manipulations have effects, which depend on the eccentricity of the target. Specifically, if effects of overall diameter were found that might influence the lack of contour manipulation effects, then we would expect them to also be affected by eccentricity, which they are not ($F_{(3,6)}$=0.83, p=0.52, power=0.15).

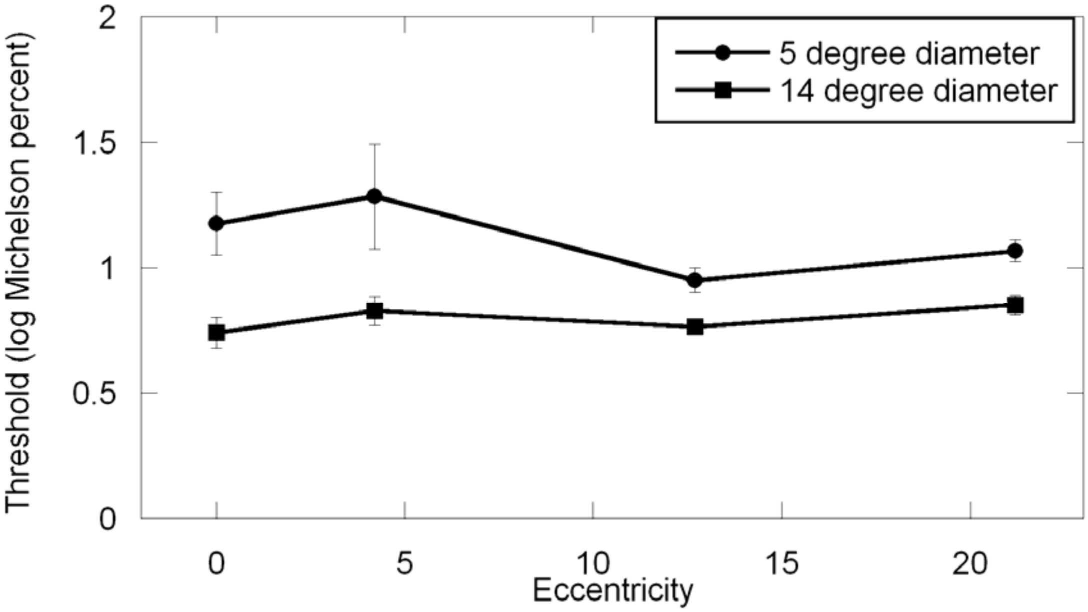

Figure 4-8. Effect of increasing ring diameter, while maintaining ring thickness.

This graph shows averaged results across 3 subjects for rings of 0.5 degrees. The smaller ring has an overall diameter of 5 degrees, whereas the larger has a diameter of 14 degrees.

4.5 Discussion

In order to perceive the phantom contour illusion (*i.e.* Flicker Defined Form), it has been proposed that the dominant feature is the boundary between the counterphase flickering dot regions.

Previous work suggested that the density of dots, and the spatial content percentage affect perception of the illusion (Quaid & Flanagan, 2005a). This study aimed to determine whether the boundary is the most important component of the stimulus. The importance of the contour to FDF perception was used to support the fast contour extracting system theory, which is most likely the magnocellular system (Rogers-Ramachandran & Ramachandran, 1998). A dependence on the area of the target would suggest that although the surfaces cannot be distinguished, they play an important role in perception. Inability to distinguish phases means that if the surface plays a role in extracting the FDF contour, it alone, is insufficient. This means that the boundary, relying on the contour extraction system must add additional cues. The first experiment, intended to show how reducing the area of the stimulus, while maintaining equal stimulus size, affects perception. The second experiment maintained a constant area, while the amount of contour was modified. The third experiment maintained a constant amount of contour while the amount of area was modified.

4.5.1 Importance of area

To determine whether the lower thresholds that were found for solid circles, as compared to a ring, were simply due to the presence of a greater out-of-phase signal, an experiment was conducted in which the amount of contour was kept constant. This experiment showed that changing the amount of area had a significant effect, even though the total amount of stimulus contour was kept constant. As area was decreased, performance degraded.

The effects of area were dependent on eccentricity. At further eccentricities the effect of area was more pronounced, *i.e.* improvements were greater farther from fixation. This was due to the illusion being more difficult to perceive at fixation (Quaid & Flanagan, 2005a), which meant that none of the sizes produced large improvements in thresholds. As mentioned in the methods section, the current study limited the area and/or contour to that of the baseline circle. Further into the periphery, where the illusion is easier to perceive, the addition of area was initially (at small sizes) beneficial. Although, this improvement soon plateaus because the additional area was not as beneficial, similar to findings of other studies (Makela et al., 1994; Tyler & Silverman, 1983).

4.5.2 Importance of contour

The finding that the thinner the ring, the worse the perception was surprising if one espouses the view that FDF is dependent on the presence of a boundary between the counterphase flickering dots. If the boundary is important, then creating more 'contour', should also improve performance. The data suggests, that the presence of additional contour, while keeping the entire stimulus size constant, had no benefit to the perception of the illusion

A number of explanations can be postulated for this finding. First, it is possible that contour is less important than area in order to perceive FDF. Results show that when the area is decreased, the stimulus was harder to see, in spite of the presence of equivalent contour.

A second, more likely explanation is that either sufficient contour or area, once suprathreshold, allows perception of the stimulus. The presence of either sufficient contour (*e.g.* a very thin ring which contains minimal area, but large amounts of contour) or area (*e.g.* a solid circle with high amounts of area but less contour than a ring which contains both internal and external contour), even if the other is below threshold, would still signal the FDF percept. The amount of contour may not be important, provided there was sufficient area flickering out of phase. Thus, even if the amount of contour was insufficient, the presence of a supra-threshold area, may have allowed the stimulus to be seen. If the area was insufficient, adding additional contour maybe meaningless.

This concept is in keeping with other studies which find that temporal cues can allow a stimulus to be perceived with greater ease than spatial summation alone can predict (Lee & Nguyen, 2001).

The third possibility is that the stimuli used for contour manipulations in the current study were all suprathreshold. All of the experiments in which contour was manipulated gave very low contrast thresholds. This means that in the most difficult viewing conditions (small amounts of contour at low contrast) subjects were still able to detect the stimulus with ease. Thus, adding additional contour had no benefit as the smallest amount of contour was sufficient to allow perception.

The fourth possibility is that aliasing between the inner and outer contour may eliminate the benefit of additional contour. Previous unpublished data suggests that the illusory contour can be perceptually matched to a 2cpd grating (Goren et al.,, 2005). Some of the contour-manipulated stimuli were less than half of a degree thick, which means that the inner and outer contour of approximately 2cpd perceptually overlap and combine into one contour, removing the benefit of inner and outer contour.

4.5.3 The interaction between area, contour and overall stimulus size

The current study aimed to determine which was more important to FDF perception: area or contour. It seemed that threshold changed with area, but not with contour. But could the changes in overall stimulus size (*i.e.* outer diameter) have affected results?

A confounding factor to be considered in the second and third set of experiments was the changing size of the stimulus. According to an earlier FDF study (Quaid & Flanagan, 2005a), circular stimuli of area 12.6º-28.3º (diameters 4º-6º) do not vary significantly in performance between fixation and 21.2º. Stimuli of diameter 4º-6º were easily detectible, when a standard density of background random dots was used. According to the Quaid & Flanagan (2005a) study, the most important determining factor for FDF perception was a constant "k", which was dependent on the area of the stimulus and the density of the dots.

Area-manipulated stimuli in the current study were smaller in stimulus diameter and area than the circular stimuli cited by Quaid and Flanagan (2005a). Some of the differences in performance may be due to problems of spatial summation (Barlow, 1958). Comparing stimulus sizes within the current study, the overall stimulus sizes were smaller for the third experiment (diameter: 2.9º-4.1º) than the other experiments (experiment 1: 5º, experiment 2: 6º-14º). In contrast, contour-manipulated stimuli were all larger in overall diameter than the baseline 5º. The increasing size of the contour-manipulated stimuli have a number of implications.

Differences between contour-modifying and area-modifying experiments represent a trade off between the distribution of area (clustered or dispersed) and overall stimulus size. In the case of area-modifying experiments, size and area act in the same way. It is unclear whether the decrease in size or area of the stimulus was the reason for the degradation of performance. In contour-modifying experiments, the increase in size of the stimulus acts in opposition to the distribution of the area. Namely, in this set of experiments, although the overall stimulus size increased, the area was distributed as a thin ring, which is harder to perceive. It is possible that the overall increase in size, compensates for the thinning of the ring.

The benefit of increasing overall size is unclear, but there are a number of possibilities. Larger stimuli, although thinner, mean that the stimulus falls further into the periphery. Contour–modified experiments vary in size from 6º to 14º. A 14º stimulus will extend 7º into the periphery. This is important because, as the stimulus moves further into the periphery, the stimulus is much less dependent on area and size, as established in this and other studies (Quaid & Flanagan, 2005a).

Variability effects are also in keeping with previous studies that suggested perception of the illusion was more robust at greater eccentricities (Quaid & Flanagan, 2005a; Quaid & Flanagan, 2005b). The fragility of the illusion at fixation, found in both this and other studies of FDF, increases variability in thresholds both between and within subjects (Quaid & Flanagan, 2005a).

A comparison of two rings of equal thinness (0.5º) shows that there was an advantage to larger overall size. This effect was most pronounced close to fixation. The improvements with increasing area in the second set of experiments were too large to be explained by the change in overall target size. An almost 3-fold increase in target size caused a maximum difference of less than 0.5log Michelson percent contrast units (fig. 4-8). A much larger effect can be seen from area manipulations, according to experiment two. It is possible that for the contour-manipulation experiments the addition of greater overall stimulus size counteracted the effects of contour manipulation. Although, the effects of contour manipulation were still significantly smaller than those for area, if the overall diameter size was able to compensate. This still suggests that although overall target size can compensate somewhat for decreases in area, or contour, the limitation imposed by area is much larger and cannot be compensated for by overall target sizes. Obviously, the area maintained in the contour experiments was sufficient for the illusion to be perceived. In the third experiment, in which area was manipulated, performance degraded significantly with decreasing area. Also to be considered is that increasing overall target size, with equal ring thinness, means an increase in area. Some of the effects of the increase in overall target size are potentially due to the increase in area.

This study showed that there was an area-dependent component to perception of FDF, and that the boundary region alone could not model stimulus perception. These findings suggest that perception of FDF is based on a combination of stimulus size (*i.e.* the outer diameter) and stimulus area (*i.e.* the difference between the outer and inner diameter), which compensate for the thinning of rings and decreasing area. These findings support previous data which place emphasis on the relationship between the size of the stimulus and the amount of area within that stimulus that flickers out of phase that has previously been labeled as the percentage spatial content (Quaid & Flanagan, 2005a). Rogers-Ramachandran's original theory that FDF-like stimuli use only the fast contour extraction system suggests that the characteristics of the surface, such as area, should not affect perception. The current study showed, along with the importance of spatial content percentage, that the fast contour pathway is insufficient to explain the percept. This indicates that FDF perception, a predominantly magnocellular phenomenon, is influenced by the interaction with the parvocellular mechanisms, which in turn is affected by stimulus eccentricity.

At all eccentricities, greater stimulus area means that more receptive fields can be activated. As area is decreased, thresholds increase and performance degrades. Stimuli which were modulated in contour, but maintained the baseline area had low thresholds. Thus, even though the rings were thinner, thresholds remained low. This is either due to the importance of area, or to the compensatory benefit of increasing stimulus size. The first experiment in which stimulus size was maintained, but area was manipulated by thinning rings showed that overall stimulus size can compensate for decreasing area.

The importance of area was eccentricity-dependent. For smaller stimulus sizes (<5˚ in diameter) performance improved faster further from fixation, but then stopped improving, in contrast to the principles of spatial summation. Similar results were reported for FDF by Quaid and Flanagan (Quaid & Flanagan., 2005a), for other flickering stimuli (Makela et al., 1994; Tyler & Silverman, 1983) and on other temporally defined stimuli by Lee and Blake (Lee & Blake, 1999).

In summary, FDF is a temporally driven illusion, which benefits from temporal synchrony, but remains subject to the rules of other luminance-defined stimuli, close to fixation. Although FDF detection is subject to area and stimulus size thresholds, it is still easier to detect further from fixation, similar to other findings and in keeping with a typical magnocellular response (Quaid & Flanagan, 2005a). Thus, although FDF shares many properties with other first order stimuli, such as a dependence on area close to fixation, its ability to compensate by a greater amount of contour, makes it distinct in its mechanisms and properties. According to a recent study, it is unlikely that this stimulus is entirely dependent on the magnocellular system (Skottun & Skoyles., 2006). The current study suggests that although there is a dependence on the fast acting contour extraction system, which we believe to be the magnocellular system, FDF is still dependent on a slow surface system, which is most likely the parvocellular system and the ventral pathway.

4.6 Acknowledgements

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Chapter 5

The importance of contour completion in a broken temporally driven illusion

5.1 Abstract

The percept of Flicker Defined Form (FDF) is achieved when two dots regions are flickered in anti-phase at a relatively high temporal frequency (Rogers-Ramachandran & Ramachandran, 1998; Quaid & Flanagan, 2005). However, the importance of contour closure in FDF has not been explored. The current study manipulated a ring shape by adding breaks of various orientations, sizes and numbers. Subjects performed contrast threshold detection task. Some effect was found for the number of breaks, although these effects were variable and small in magnitude. No effect of orientation or break size was found. The temporal modulation of FDF's elements was sufficient to ensure detection and override the benefit of contour closure seen in luminance defined stimuli.

5.2 Introduction

According to Gestalt rules of psychology, the whole is greater than the sum of the parts (Koffka, 1935). Two important gestalt principles are relevant to the current stimulus. The first, common fate, potentially the most important for this stimulus, uses temporal synchrony and motion coherence to bind elements (Spillman & Ehrenstein, 2004). Temporal structure alone is capable of creating spatial percepts (Lee & Blake, 1999). Some studies have found that temporal structure is better than temporal synchrony (Guttman et al., 2007). The second, good continuation is a principle which binds elements that are both in close proximity and collinear (Spillman & Ehrenstein, 2004). Good continuation can bind elements which are spaced, which may contribute to a filling-in between elements in the FDF array. Lee and Blake have found that when both spatial and temporal cues are present for contour linking, they act together to improve perception (Lee & Blake, 2001). Good continuation may also be important in terms of closure. Closure makes identifying a contour significantly easier when the elements form a closed shape (Kovacs & Julesz, 1993). It is obvious that FDF relies on common fate (Quaid & Flanagan., 2005a), but do principles of closure apply to Flicker defined form? FDF's dependence on area and organization of background elements suggest that FDF is dependent on spatial properties of the stimulus. A dependence on spatial properties suggests that FDF detection thresholds are likely to be lower in closed FDF contours than in open contours.

Flicker defined form (FDF) is an illusory contour stimulus that is believed to be created by the preferential processing of high temporal and low spatial frequencies by the magnocellular pathway (Rogers-Ramachandran & Ramachandran., 1998). The illusory edge is created by the high temporal counterphase flicker of two regions of neighbouring dots. The illusion can only be created when there are luminance differences between the dots (Rogers-Ramachandran & Ramachandran, 1998). More recent research suggests that the illusion improves with increasing contrast of dot elements and increasing density of dot elements in addition to increasing eccentricity when using a low number of dots (Quaid & Flanagan, 2005a). Unpublished data from our lab also suggest that increasing organization of dot elements increases the salience of the illusion, particularly at lower eccentricities.

The most compelling evidence for the dominance of the magnocellular pathway in processing this illusion is the change in detectability across the visual field. Similar to flicker stimuli and different from luminance-defined static stimuli, the illusion is more robust when presented in the periphery (Quaid & Flanagan., 2005a), where the magnocellular system dominates (Azzopardi et al., 1999). Perception of FDF also degrades when the temporal modulation is lower than 7Hz (Rogers-Ramachandran & Ramachandran, 1998). This study also found that perception of the illusion is best above 15Hz, implying that a relatively high temporal frequency is key to the FDF percept. Perception of FDF is also robust to dioptric blur. The addition of 6 dioptres of blur does not change detectability of an FDF target (Quaid & Flanagan, 2005b). This observation implies a dependence on lower spatial frequencies. In addition, unpublished data from our lab shows that during a matching experiment comparing FDF to a grating FDF was perceived to be approximately 1.5cpd. The preference of both the magnocellular system and FDF for high temporal and low spatial frequencies (Livingstone & Hubel, 1987) suggests a reliance on the magnocellular system in order to perceive the phantom contour used to generate FDF.

According to Kovacs and Julesz (Kovacs & Julesz, 1993), the addition of breaks is disruptive enough to the perception of an entire contour that a small break is capable of preventing perception. Other studies have found that even when elements defining the shape are orthogonal, improvements with closure are still seen (Saarinen & Levi, 1999). Therefore, not only orientation information contributes to the benefit of closed contours. According to Lee and Blake, the presence of temporal synchrony or structure is capable of overcoming the lack of spatial structure (Lee & Blake, 1999).

Benefits of contour closure have been shown in static stimuli. FDF, which has neither orientation information, nor discriminable luminance boundary information, is dependent on temporal cues to group elements. This study aimed to determine if the illusory edge created by temporal cues benefits from contour closure. A dependence on closed contour would show that FDF, in spite of the lack of orientation information, shares certain mechanisms with orientation-defined stimuli.

5.3 Methods

5.3.1 Subjects

Six subjects were (3 male, 3 female) between the ages of 23 and 33. Three of these subjects were tested on orientation effects. Three were tested on the remaining conditions including break size and number. Subjects had normal or corrected to normal vision (6/6 or better) with no known ocular or neurological abnormality. All subjects, except one, were naïve to the purpose of the experiment.

5.3.2 Experimental setup

Subjects were seated 0.32m from a Sony Trinitron Multiscan CPD-G500 monitor with resolution of 1024 x 768 pixels and pixel pitch of 0.37mm. The refresh rate was 100Hz. The monitor subtended 61.8 x 48.3 degrees. Luminance ranged from 0cdm^{-2} to 100cdm^{-2} with a mean luminance of 50cdm^{-2}. These luminance values were used to create 23 log Michelson percentage steps of contrast ranging from -0.3 to 2.

5.3.3 Stimulus

The screen was covered with circular dots (0.34 degrees diameter) positioned at random locations. The dots were modulated in luminance as a square wave at 16.7Hz. Stimulus area was defined by dots within the stimulus being modulated in counterphase to background dots (Fig. 5-1). This counterphase modulation was present for 160ms of ramping to a desired contrast level (to prevent a sudden change in contrast), 400ms at a stable contrast value and 160ms of ramping back to baseline contrast.

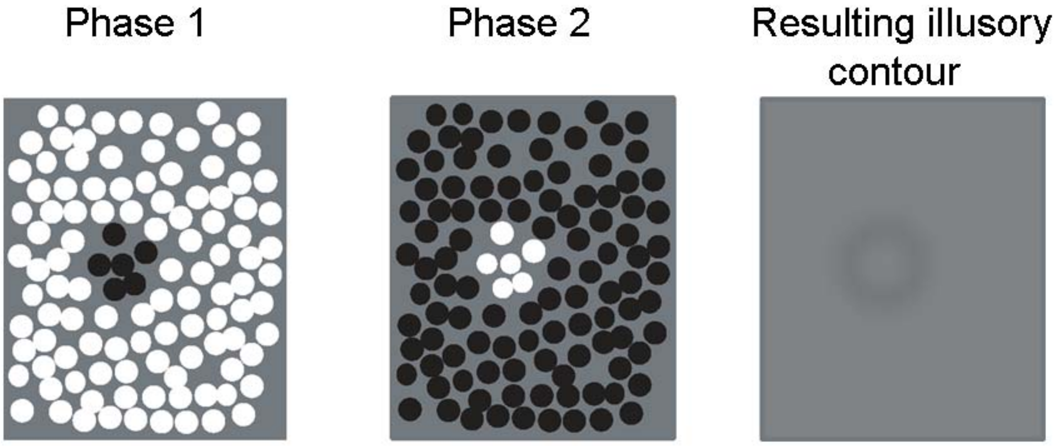

Figure 5-1. Flicker defined form stimuli.

The first and second panels show the two phases which are alternated at 16.67Hz. The third panel is a schematic of the resultant illusory edge.

After the stimulus presentation a response time of 1 second was allowed. As soon as a response was given, whether correct or incorrect, the trial was ended in order to prevent stimulus presentations from being predictable. If a response was not given during the stimulus presentation or response time, 1 second of interstimulus time was presented. The interstimulus time, along with the first 180ms of the trial, were used to record false positive catch trials. False positives were very rare (most trials produce 0 false positives) in the cohort tested.

All targets had a maximum diameter of 5° and an inner diameter of 3°, making the ring structure 1° thick. According to previous research (Goren & Flanagan, 2008), this ring structure is harder to detect than a solid circle, but still reliably perceptible.

Targets were all presented in the inferior temporal quadrant. Four eccentricities were tested: Fixation; 4.2º (corresponding to 3ºx3º); 12.7º (corresponding to 9ºx9º) and 21.2 (corresponding to 15ºx15º). Each trial consisted of only one break-type condition, but all four, randomly presented eccentricities. Each condition was repeated three times for each subject. Mean and standard errors for each subject were calculated and used for analysis.

5.3.4 Orientation Effects

Four orientations were tested as a control to ensure that the position of the break had minimal effects on performance. Orientations of 0, 90, 180 and 270 degrees were used, with a break size of 90° (in polar angle), eliminating a quarter of the ring structure. All breaks were centered around the orientation at which it was being tested.

5.3.5 Break size

Three break sizes (33°, 50°, and 100°, polar angle) were tested and compared to rings without any breaks. All breaks were centered at 0° (vertical). These break sizes were chosen in order to correspond to the different break sizes seen in the third part of this study (Fig. 5-2).

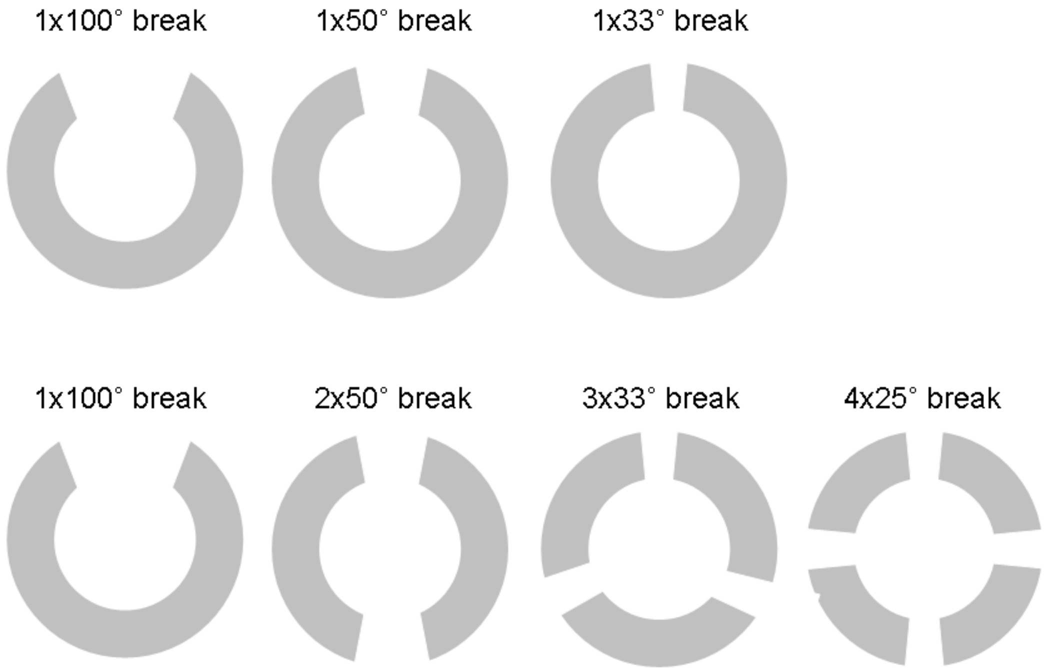

Figure 5-2. Broken ring stimuli.

The first panel show stimuli used in the break size conditions. The second panel shows stimuli in the break number conditions. Note that 25º and 33º breaks are physically similar due to dot density limitations. Note that break sizes are not to scale.

5.3.6 Number of breaks

In order to understand the importance of completion, adding multiple breaks to a ring can show whether the absolute loss of area is the important factor, or simply the breaks in the contour. All breaks added to a total of 100° to ensure that differences between two, three and four breaks were not simply due to an area loss. At least one of the breaks was placed at 0° and the remaining breaks were placed at equal distances from each other. The number of breaks tested varied from 1 to 4 (Fig. 5-2). The stimulus with two breaks was composed of 2-50° breaks, one at 0° (top of the ring) and one at 180° (bottom of the ring). The stimulus with three breaks was composed of 3-33° breaks, one at 0°, one at 120° (lower right hand corner) and one at 240° (lower left hand corner). The fourth stimulus with four breaks was composed of 4-25° breaks at 0°, 90°, 180° and 270°.

To determine the effects of multiple breaks, comparisons were made between these three conditions, and between the single break condition and the multiple break condition of equal size.

5.3.7 Protocol

A detection task was performed in which subjects were expected to indicate that they detected a shape by pushing a button upon detecting the stimulus. A 4-2-1 staircase procedure (with two final reversals) was used to assess a contrast threshold measured in percentage log Michelson contrast. Twenty three contrast levels of 0.1 log units were used which varied between -0.3 to 2.0 log Michelson percent contrast units.

False positives were recorded as all responses given 180ms after stimulus onset and 1 second following stimulus presentation (and response time). All trials consisting of greater than 20% false positives were excluded.

5.3.8 Analysis

Mean and standard errors of three thresholds were calculated for each subject. Mauchley’s test for sphericity was conducted, and violations were corrected using Huynh Feldt corrections. Repeated measures ANOVA was used to determine significant effects, after which post hoc analyses using Tukey’s Honest Significant Difference were conducted. Statistics were performed using Statistica 7.0 and graphs were prepared using Kaleidagraph 3.6.

5.4 Results

5.4.1 Break orientation

The orientation of the break did not affect contrast thresholds (Fig. 5-3). No significant effects of orientation were found ($F_{(3,6)}$=0.84, p=0.52, observed power= 0.15) or for the interaction between orientation and eccentricity ($F_{(9,18)}$=0.40, p=0.92, observed power=0.15). All of the subjects showed trends toward increasing thresholds close to fixation. The average increase in threshold between 21° and fixation was 0.57. The decrease in threshold with increasing eccentricity was found for all orientations and all subjects.

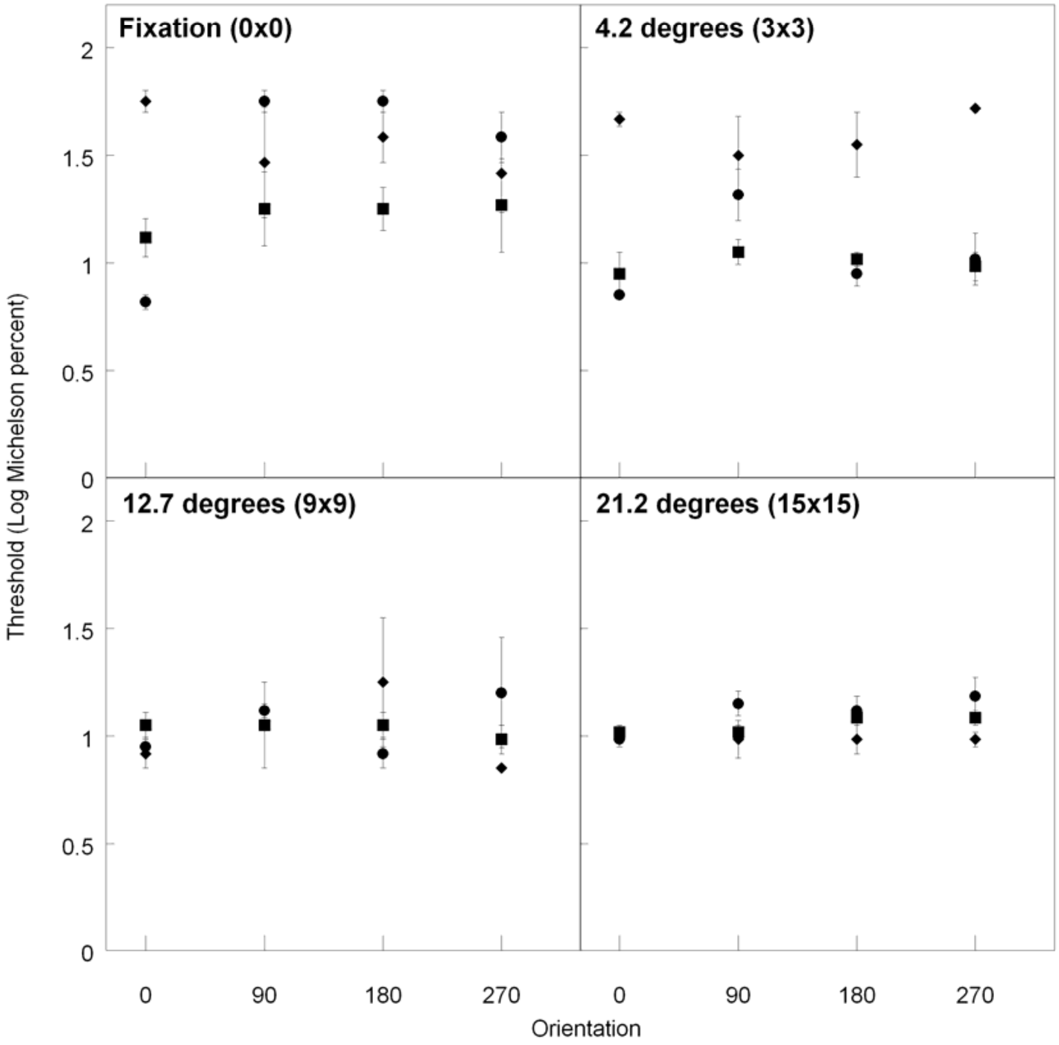

Figure 5-3. The effect of break orientation on FDF detection thresholds.

Data shown are for 3 individual subjects, at different eccentricities with mean and standard errors shown.

5.4.2 Break size

Data from fixation were excluded from analyses because the task was very difficult and a number of subjects were unable to detect the stimulus under all break conditions at fixation. No significant effect of break size were found ($F_{(3,6)}$=0.76, p=0.55, observed power= 0.14, Fig. 5-4) or interaction effects between break size and eccentricity ($F_{(6,12)}$ =1.23, p=0.36, observed power=0.31). Even with variations in break size that spanned less than 1° to almost 4° (in degrees of visual angle, versus polar angle), no difference in thresholds was seen.

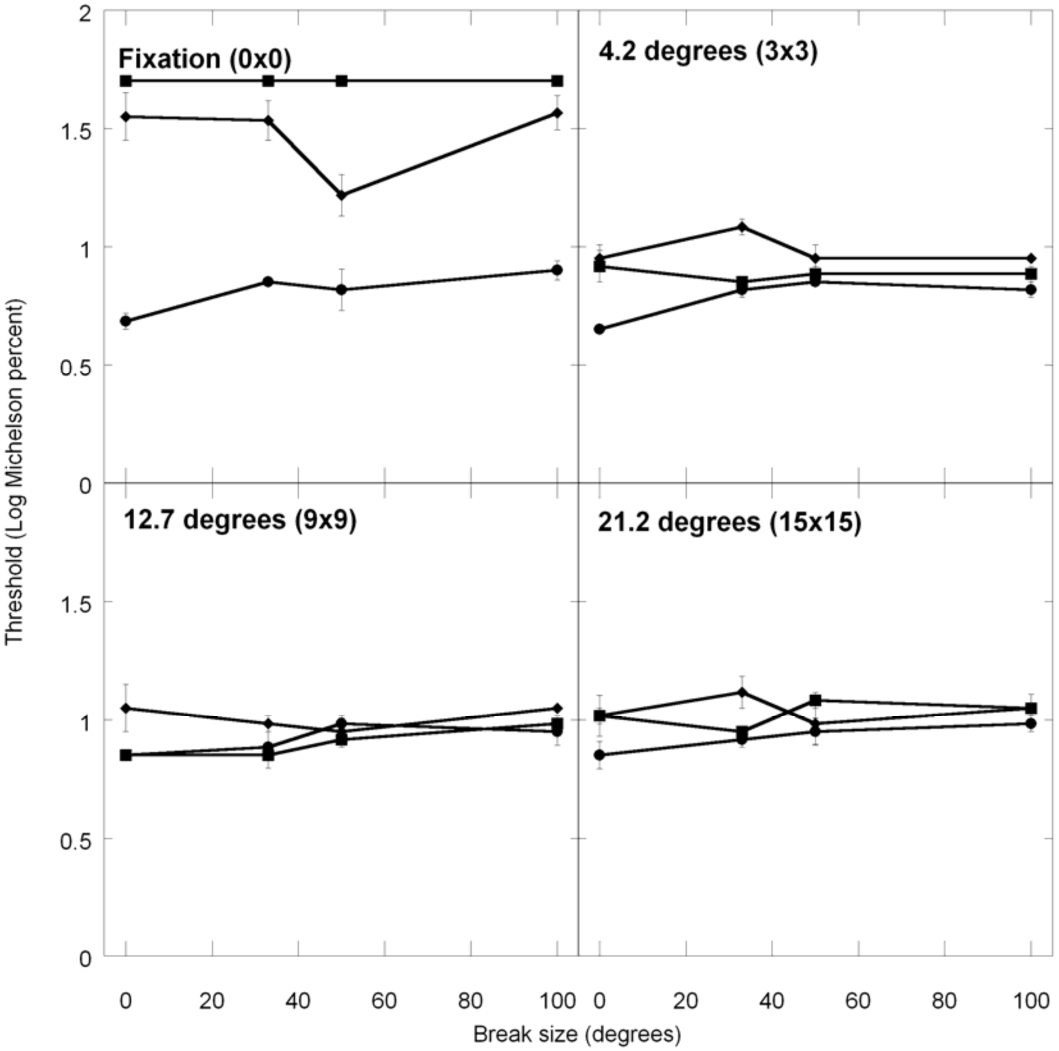

Figure 5-4. The effect of break size on FDF detection thresholds at various eccentricities.

Data shown are for 3 subjects with mean and standard errors shown.

5.4.3 Number of Breaks

This experiment intended to determine whether the addition of multiple, smaller breaks behaves more like figure-ground stimuli in which the addition of any breaks impairs perception of the illusion. To ensure that the differences were not due to absolute area losses, all of the breaks added to approximately 100°. As an additional comparison, one break of 100° was compared to the multiple break conditions. The second experiment showed no difference for significant differences in break size between small breaks (*e.g.* 33°) and large breaks (*e.g.* 100°). It is highly unlikely, therefore, that any potential differences between a single 100° break and multiple breaks adding to 100° are due to area differences.

Data from fixation were excluded from the analysis due to the difficulty encountered while performing these tasks. As can be seen from the figures, one subject was unable to see the stimulus under any of the conditions when the stimuli were presented at fixation. A significant effect of the number of breaks was found ($F_{(4,8)}=4.1361$, $p=0.04$, Fig. 5-5). A significant difference was found between solid rings and rings with 4 breaks ($p<0.05$). When a separate analysis was performed, which excluded the 4.2˚ location no effect of break number was found ($F_{(4,8)}=3.23$, $p=0.07$, observed power=0.56). At 4.2º there was also no significant difference between solid rings and rings with 4 breaks ($F_{(4,8)}=3.23$, $p=0.07$, observed power=0.57). Beyond 4.2˚ the largest differences in threshold were less than 0.3 log Michelson percent units. Although a significant difference was found overall between 4 breaks and solid rings, these effects were not found at each eccentricity separately or for lesser numbers of breaks. The analysis is likely confounded by the results of one subject, who showed a large threshold increase for rings with 4 breaks.

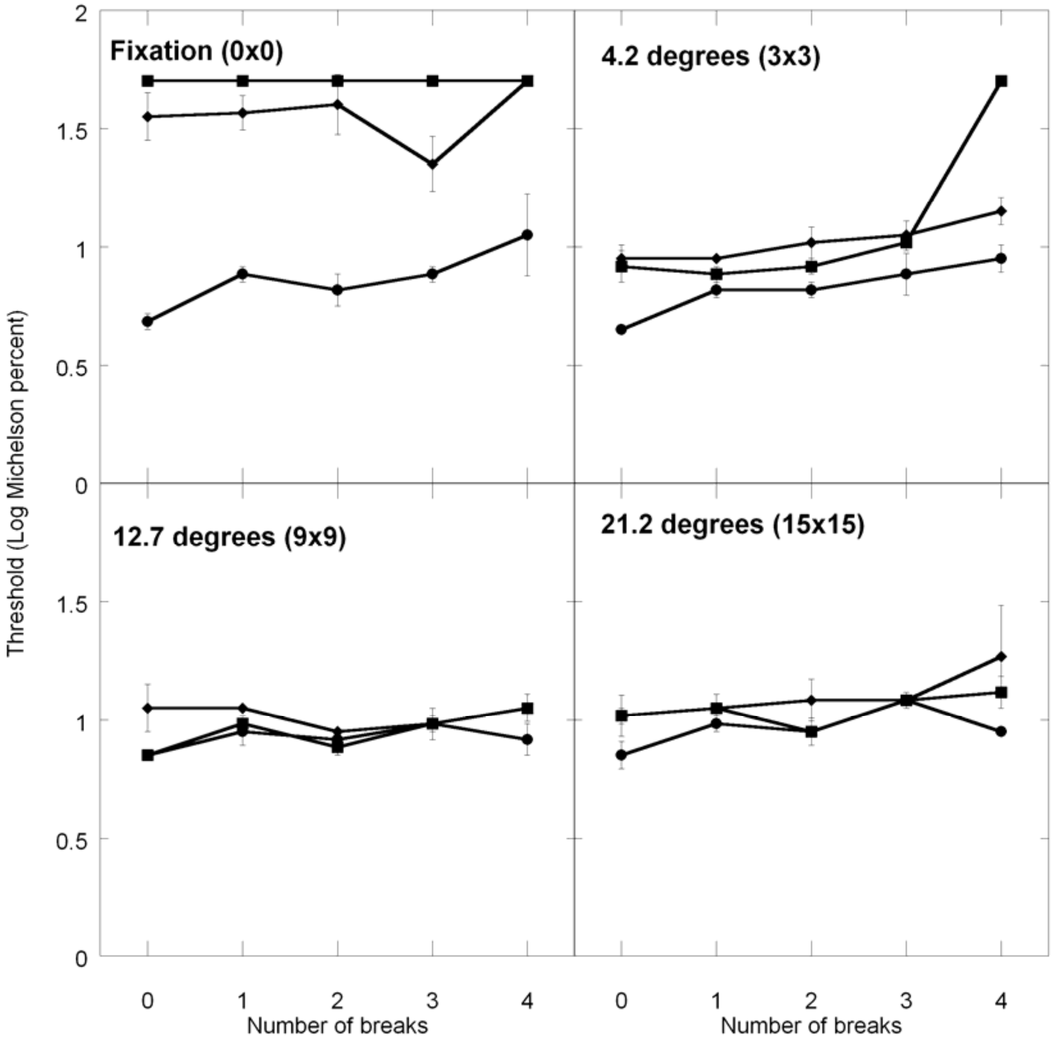

Figure 5-5. The effect of number of breaks on FDF detection thresholds.

Data shown are 3 subjects with mean and standard errors shown.

5.4.4 Comparing number of Breaks with equal break sizes

Data collected at fixation were excluded in this analysis as well, because of the inability of two subjects to see the multiple break stimuli at this location. No effect of single vs. multiple breaks was found ($F_{(1,2)}$=4.425, p=0.17, observed power=0.23, Fig. 5-6). . No significant effects were found for the interaction between single/multiple breaks and the number of breaks (for example: one 50 degree break and 2-50 degree breaks were similar to one 33 degree break and 3-33 degree breaks)($F_{(2,4)}$=1.876, p=0.27, observed power=0.21). Also, no differences in these interactions were found at different eccentricities ($F_{(4,8)}$=1.394, p=0.32, observed power=0.26).

Single breaks and multiple breaks were perceived with similar ease at multiple eccentricities. These results corroborate previous results which suggest that the area of the break did not affect detectability of the stimulus.

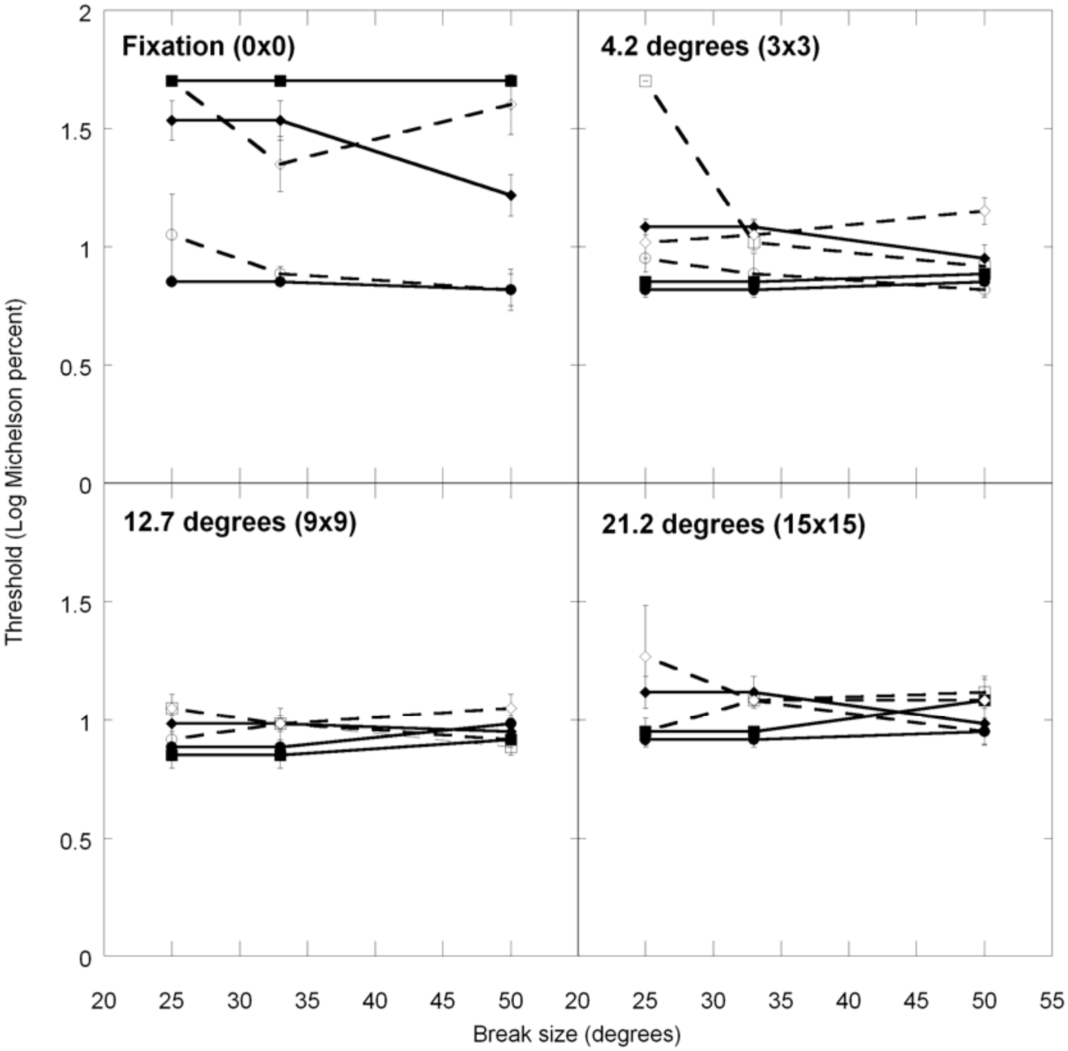

Figure 5-6. The effect of break number with equal break size.

Mean and standard errors are for individual subjects, represented as different symbol shapes. Break sizes of 25º and 33º are physically indistinguishable (due to stimulus limitations), so thresholds for 33º are used for both 25º and 33º break conditions in the single break condition. Solid shapes and lines represent single breaks. Hollow shapes and hatched lines represent the multiple break equivalent.

5.5 Discussion

FDF is an illusion which has been previously shown to be dependent on the boundary between regions that flicker out of phase (Rogers-Ramachandran & Ramachandran, 1998). Current results suggest that even when a significantly sized break (*i.e.* 100°) is added to the ring structure, there is no significant effect on detection thresholds. Breaks of varying sizes have no effect on detection thresholds, along with the location of the break. In addition, while maintaining an equal amount of area, but modifying the distribution of those breaks, no differences were seen.

The minimal effect of a single break, regardless of size and orientation is in contrast to the findings of Julesz and Kovacs (1993). Julesz and Kovacs found a decrease in detectability as soon as a small proportion of stimulus elements was removed. Thus, an even larger break would degrade performance further. The current stimulus, which lacks orientation information seems to really less on the gestalt rule of contour closure. The two studies rely on different pathways (form versus motion) and different mechanisms. Specifically, FDF cannot rely on linking between elements with common orientations due to a lack of orientation information within the individual elements.

Previous research has found that spatial cues when combined with temporal cues improve performance beyond spatial or temporal summation (Lee & Blake, 2001). Thus, since the current stimulus was produced using temporal synchrony, the temporal dynamics were able to compensate for poor spatial properties, such as the lack of contour completion. Namely, the temporal synchrony was enough to bind the elements, allowing the contour that was connected to be perceived.

Although effects of single breaks of various sizes were not found to affect detection thresholds, it does not mean that perception was entirely unaffected. The addition of a break may be affecting the way that the stimulus was perceived and the mechanisms that make it possible, some of which will be discussed further. For example, in the case of a small break (*e.g.* 33°), detection of the pattern may be unaffected, but there are a number of different possibilities that may explain the effects of breakage.

5.5.1 Break size consideration

The lack of a difference between the FDF perception with break sizes of 25˚ and 33˚ could be due to the limitations of the stimulus configuration. The most area removed by breaks in the ring was $3.5^{\circ 2}$. This means that for the multiple break condition consisting of 4 breaks, each one is less than $1^{\circ 2}$. The density of dots on the screen was approximately 2 dots/degree. The random placement of dots means that the number of dots which constitute the break can vary, depending on the site of the break, and the eccentricity of the target. This variation was not systematic. In most cases these small breaks contain between 1-3 dots, all of which were small areas. Since no differences were seen between solid rings and rings with breaks of 33°, 50° or 100°, a difference of 1 or 2 dots should make very little difference to the detectability of this stimulus.

5.5.2 Filling-in/Facilitory interactions

It is possible that the break is 'filled-in' by mechanisms such as collinear facilitation. For static stimuli, figure ground segregation uses these mechanisms to link elements which are physically separated from one another. In the case of figure ground segregation, the elements are not perceived as a connected whole, but the visual system is able to identify the elements as belonging to the same shape. In the case of FDF no orientation information is present within individual elements, and the luminance information is presented too quickly to be a cue (Rogers-Ramachandran & Ramachandran, 1998). If filling-in is occurring, the binding of individual elements is most likely due to the temporal information (Lee & Blake, 2001).

It seems likely that some filling-in is occurring because the FDF stimulus is perceived as an unbroken entity, in spite of its composition. By composition we mean that the individual elements, even in a solid circle or ring are placed at random locations, and thus spaces are present between them. Still, the illusory edge is reported by subjects to be perceived as an illusory edge. In the case of a ring with a small break (*e.g.* 33°), it is unclear if the subject's perception of the stimulus is a solid ring, or a broken one. This will be explored further in the future with discrimination experiments.

If filling-in is occurring at the sites of the breaks, then rings with large breaks cannot be filled-in due to limitations on the extent of connections. According to one study of perceptual filling-in, facilitory effects can be seen up to 12 times the wavelength of a Gabor element (Polat & Sagi, 1993). The current study is not composed of Gabor elements, which makes comparison difficult. If it is assumed that each dot element in the current stimulus is equivalent to one cycle then we can estimate the filling-in limits. The size of the break in degrees of visual angle varies from less than 1 degree to just greater than 3 degrees. Based on the size of the dot elements (0.34˚ diameter), all of the breaks would be within the facilitative range (12 times the wavelength).

According to another study, illusory percept mechanisms such as apparent motion and segregation of figure from background are subject to the importance of element separation. According to Braddick, 5-20˚ displacement degrades this segregation process (Braddick, 1974). FDF's stimulus elements are placed at an average density of 2 dots/degree, which means that most dots are separated by less than 1˚. Braddick's findings are not relevant to the 'connected' portions of FDF because individual elements are within the limits found in his study. The breaks added to rings in the current study are also within the limits found in Braddick's study. However, the implications of Braddick's study may not be applicable to the effects of breaks found in the current study.

5.5.3 Grouping

A likely explanation for both FDF perception in general, and specifically the independence from contour closure, is that grouping is likely to play a role. The addition of non-synchronous movement to elements within a contour can impair detection (Poom & Borjesson, 2004). The elements within the FDF display share luminance information at any given moment and are synchronous. Although, the temporal information is not a cue to the edge, but it allows the luminance information to be processed in a way that allows the edge to be perceived.

5.5.4 'Just enough' area effects

Most likely, rings with large breaks are processed differently than rings with small breaks. The lack of a difference between no break and small breaks (33˚) is most likely due to filling-in or facilitative effects. Two of the results in the current study suggest that for broken rings area can be decreased without a noticeable difference in thresholds. First, break size can be increased, removing up to a quarter of an already small ring has no effect on detection thresholds. Second, comparing single breaks with multiple breaks of equal size showed only a small difference in thresholds (approximately one log Michelson contrast unit), which is within standard error measures. In the most extreme case, the area loss in the multiple break condition (4x25˚) is more than 3 times larger than the single break (33˚) and yet no differences were seen. More importantly, the difference between these two conditions was no different than the differences seen for one break vs. 2 breaks, in which the area difference between single and multiple was double. The fact that a 33˚ break shows similar results to a target with four breaks of similar size suggests that the target can suffer additional area loss, without detection thresholds suffering. This suggests that once a minimum amount of area is defining FDF, the permutation of this area is much less limited than standard luminance defined contours. Specifically, whereas luminance defined contours benefit from closure, FDF does not.

In the multiple breaks experiment the same amount of area was removed, but divided over a different number of breaks. If filling in were the most important mechanism then a greater number of breaks of smaller area would allow the shape to be detected with greater ease as compared to fewer, larger breaks (*e.g.* 2x50). This means that the four break condition should have been easier to detect than the other multiple break conditions.

If filling-in was important, why are rings with large breaks equally detectable to those with small breaks? Rings with large breaks (*e.g.* 100˚) may be benefitting from facilitory interactions (Polat & Sagi, 1993), but subjects reported that the largest breaks look like broken rings, not solid rings. The break and contour are probably visible due to a large enough connected area, or 'just enough' area effects. Unlike the original study (Kovacs & Julesz, 1993) which suggests that a break can make a contour much harder to perceive, the current study had an additional advantage because of the temporal structure. According to (Lee & Blake, 1999) temporal structure is sufficient to elicit structure perception, even without spatial structure. The presence of spatial structure helps, but it is not required. The current study showed that closure of the contour was not important which explains why there was no significant change in performance between closed contours, broken contours with small breaks and contours with large breaks

5.5.5 Importance of 4 break condition

Rings with 4 breaks are significantly different than solid rings at 4.2˚. This effect was most likely due to the lack of 'connected contour'. Rings with 4 breaks were composed of 4 small segments, which are difficult to perceive due to their size, thus, the disconnect between the elements may be preventing detection due to the insufficient size of individual segments. It is important to note that this effect was found at 4.2˚, but not at other eccentricities. Thus, although this effect reflects a difference between broken and unbroken stimuli, the effect was limited by the stimulus' spatial location.

The current study found high variability near fixation both within and between subjects. Other studies have found that FDF perception was fairly stable in the periphery, but was more affected by manipulations closer to fixation (Quaid & Flanagan, 2005a).

FDF represents a special class of illusory stimuli that most likely are dependent on the interaction between ventral and dorsal streams, which are heavily involved in shape and motion perception respectively. Our results suggest that contour closure does not affect FDF detection. When orientation and collinearity are involved with contour perception in static stimuli, closure benefits detection (Kovacs & Julesz, 1993). Under other experimental paradigms, closure has been shown to improve detection of contours, even when orientation information is not helpful (*e.g.* orthogonal to the contour, Saarinen & Levi, 1999). Most likely, the presence of temporally driven perception of the illusion is sufficient to elicit perception. The stimulus relies on the temporal structure to compensate when there are insufficient structural cues.

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Chapter 6

Resolution of flicker defined form

6.1 Abstract

Flicker defined form (FDF) has been studied using detection paradigms, while this study intended to determine how well the shapes could be discriminated and recognized. Two forced choice paradigms were used to assess contrast thresholds for discrimination (2AFC) and recognition (4AFC). Discrimination paradigms involved discrimination between two shapes. Recognition involved matching a shape to a static, non-FDF defined shape. Targets included solid shapes (circle, triangle and square), rings and rings with breaks (1 or 4). Results showed that many different combinations of shapes could be discriminated. Solid shapes (triangles, squares) were easiest to discriminate from circles, when compared to rings and broken rings. Discrimination and recognition of rings, when comparing both tasks, was more difficult than for other shapes, due to confusions with both circles and rings with 4 breaks. When asked to recognize shapes, rings with four breaks were the most difficult to recognize. This was most likely due to common confusions between rings with four breaks and solid rings. No differences were seen across eccentricity, suggesting that although detection improved, shape discrimination and recognition were slightly worse further into the periphery. This study showed that not only could FDF targets be detected, as previously shown, they could also be resolved. Implications for depth perception and filling-in phenomenon within FDF stimuli are discussed.

Keywords: Contrast; Illusion; Discrimination; Shape perception

6.2 Introduction

Flicker defined form (FDF) has primarily been studied using detection paradigms. Detection of the FDF stimulus involves perception of the contour, which may or may not represent the true form of the FDF stimulus. For example, are very small gaps within an FDF contour perceptually filled-in or completed? Are they frequently confused with solid shapes or rings? Are rings easily confused with circles?

FDF is a poorly understood illusion that most likely represents a combination of motion, flicker and form perception pathways. Similar in its dependence on the linking of separated elements to figure ground tasks, it shares some common characteristics with other static stimuli. When FDF patterns are presented without temporal modulation, the illusory edge created between the two regions of dots is perceived, suggesting that the form pathway alone is insufficient for FDF perception. A high temporal modulation of the contrast of FDF elements (in counterphase to background elements) creates the percept of an edge. When the spatial characteristics of the dots are changed (*e.g.* dot density, organization, area of the target), FDF perception is affected (Quaid & Flanagan, 2005; Goren & Flanagan, 2008a; Goren & Flanagan, 2008b). Thus, FDF represents a stimulus which is distinct from but also similar to static stimuli.

This study aimed to determine whether FDF targets of different shapes can be discriminated from other, similar shapes, and whether they can be recognized as particular shapes (*i.e.* matched to a static version of themselves). The ability to resolve details within the shape has implications for the importance of the shape perception pathway. We believe that FDF shapes will be discriminable and recognizable, giving the form perception pathway a role in FDF perception.

6.3 Methods

6.3.1 Subjects

Participants in the study were one female and two males, aged 23, 23 and 31, respectively. A second set of subjects was used for recognition experiments, consisting of two females and one male, aged 23, 24 and 27. All had normal or corrected to normal vision and all, except for one, were naïve to the purpose of the experiment. Only the right eyes were tested in the current study.

6.3.2 Stimulus

All stimuli were presented on a Sony Trinitron monitor 20″ (Multiscan CPD-G500) with a pixel pitch of 0.37mm. A screen resolution of 1024 x 768 pixels, at 32cm which created a visual field of 61.8 x 48.3 degrees. The refresh rate was 100Hz. Mean luminance was 50cd/m2 with a minimum of 1.33cd/m2 and a maximum of 100cd/m2. All stimuli were presented in the inferior temporal quadrant. Four eccentricities were tested: 0˚, 4.2˚ (3˚x 3˚), 12.7˚ (9˚ x 9˚) and 21.2˚ (15˚ x 15˚).

6.3.2.1 Basic stimulus:

All stimuli for the current study were created using randomly positioned dots of 0.34˚ diameter. All dots within the stimulus patch were flickered in counterphase to elements in the background. Flicker was defined by a square wave function at 16.7 Hz. At this frequency the phases cannot be distinguished, apart from the illusion contour created between the regions (Rogers-Ramachandran & Ramachandran, 1998). The stimulus shape was modified for the purpose of this experiment in order to show differences in discrimination abilities between different shapes.

6.3.2.2 Circle shape:

The circle was a 5˚ diameter circle, similar to those used in previous FDF studies (Quaid & Flanagan, 2005). This shape was used as a target for the first set of experiments.

6.3.2.3 Triangle and square shape:

Triangle and square shapes were 5˚ in width (at base) and were used to compare shape perception for solid shapes, by comparing to the circle.

6.3.2.4 Ring shape:

Two different ring shapes were used. Both had outer diameters of 5˚, similar to the circle. An inner diameter of 2˚, which corresponded to a ring thickness of 1.5˚ was used as a distractor (the non-target presented during the same trial). The second ring had an inner diameter of 3˚, creating a corresponding ring thickness of 1˚. This third ring was used as a target for the second set of experiments.

6.3.2.5 Broken ring shape:

A number of different broken ring shapes were used in this experiment. For all broken rings, an outer diameter of 5˚ was used with an inner diameter of 3˚, creating a ring thickness of 1˚. All broken rings had gap sizes defined in polar angles. For all of these experiments, at least one of the gaps was situated at the top of the circle with the break flanking the midline. One stimulus, with a gap size of 80˚ represents the single break condition. A second broken ring condition consisted of four breaks of 25˚. One set of experiments which assessed differences in orientation used a 100˚ break, positioned at either 90˚ or 180˚.

6.3.3 Task

Subjects were seated 32cm from a monitor displaying the FDF stimulus. All stimuli were presented monocularly, to the right eye while subjects fixated on a red circle in the centre of the screen. A two interval forced choice paradigm was used to determine contrast thresholds required for discrimination. Stimuli were presented for 720ms, comprised of a 160ms period in which the contrast increased from baseline, 400ms of unchanging contrast and 160ms period of in the contrast decreased back to baseline. Following each stimulus an additional period of 250ms was given for subjects to respond. There was an interstimulus period of 500ms between the two trials in which no stimuli were presented to minimize the possibility of the two stimuli masking each other.

6.3.3.1 Shape discrimination

A two alternative forced choice (2afc) method was used in which both the target and distractor for a trial were presented at the same location, but offset temporally. The interval in which the target or distractor was presented was randomized. Subjects were instructed to indicate (using the numbers one or two) which of the two intervals contained the target. The target and distractor shape remained the same throughout a particular experiment. Subjects initiated the following trial by pushing a key.

- *Solid shape discrimination:* The reference stimulus for these experiments was a circle. Distractors were squares and triangles; a solid ring (1.5˚); and broken rings with a single break and four breaks.
- *Ring discrimination:* The reference stimulus for these experiments was a 1˚ thick ring. Distractors were a ring of 1.5˚ thickness; and broken rings with a single break and four breaks.

- *Broken ring discrimination:* The reference stimulus for these experiments was a 1° thick ring with a 100° break (oriented with the break at the top). Distractors were a broken ring with four breaks; and rings with a single 100° break at either 90° or 180° orientations.

6.3.3.2 Shape recognition

A four alternative forced choice *(4afc)* paradigm was used to assess contrast thresholds required for recognition of FDF-defined shapes. This experiment was called a recognition experiment because the targets were matched to non-FDF defined versions of the same shapes. Thus, subjects were able to identify circles, rings, and broken rings. The targets for these experiments were either a solid circle, a ring of 1° thickness, a broken ring with 100° break and a broken ring with 4 breaks of 25°. After the target was presented, a static screen with each of the four targets was presented. The four targets were presented at suprathreshold contrast (1.6 log Michelson percent units) in each of the four major quadrants. The targets were always presented in the same locations. Subjects were instructed to indicate which target they had seen by pressing number keys 1-4 which were related to each location on the screen.

6.3.4 Analysis

Method of constant stimuli was used to determine a contrast threshold. Seven levels of difficulty with five trials at each level were tested. Data were averaged across 6 runs, so that each threshold was based on 30 trials per level. A Weibull function using maximum likelihood was fit to the data to obtain a threshold at 75% correct for all discrimination data. Only one threshold was calculated for each condition for each subject, based on a total of 210 trials. No means and standard errors are reported for individual subject data.

Recognition experiments were based on the average of 3 runs, and thus, 15 trials per level. For this experiment a similar fitting was performed with thresholds for a 62% correct level. Only one threshold was calculated for each condition for each subject, based on a total of 105 trials. No means and standard errors are reported for individual subject data.

For recognition experiments confusions between shapes were recorded and analysed. A t-test in which the values were compared to a value of 33% (chance) was used to determine if the confusions represented a real bias. A Bonferroni correction was applied to the p-values to determine significant effects.

These thresholds were then analyzed using repeated measures ANOVA across 3 subjects and Tukey's HSD for significant F values.

6.4 Results

6.4.1 Circle discrimination (from solid shapes, rings and broken rings)

Discrimination of circles from squares and triangles produced statistically similar thresholds ($F_{(1,2)}$=0.06, p=0.82, observed power=0.05), with no eccentricity interactions ($F_{(3,6)}$=0.21, p=0.88, observed power=0.07, Fig 6-1). For the remainder of conditions these values were averaged as the solid shape condition.

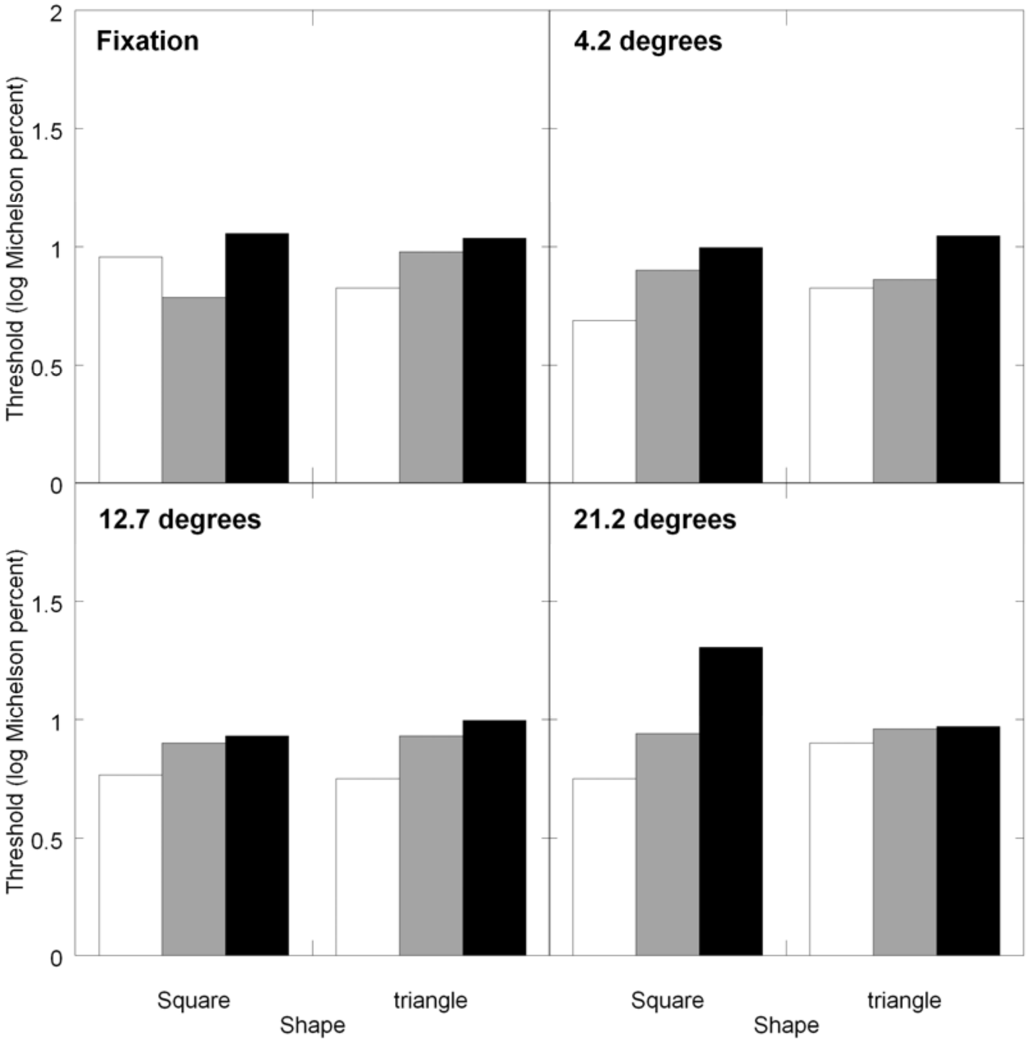

Figure 6-1. Discrimination of solid shapes.

Data are shown for contrast thresholds required for discrimination when circles are presented along with the targets shown along the x-axis. Three subjects are represented as different shades of gray. Eccentricity of the target is indicated in the upper left hand corner.

The ability to discriminate a circle was tested using solid shapes, rings and broken rings (Fig 6-2). The shape of the distractor affected thresholds ($F_{(3,6)}=5.95$, p=0.037, observed power=0.69). Post hoc analysis of this effect showed that solid shapes had much lower thresholds than thresholds for circles discriminated from solid rings ($p<0.05$). No differences were found between broken rings and solid rings or solid shapes.

No interactions between shape and eccentricity were found ($F_{(9,18)}=1.49$, p=0.22, observed power=0.51).

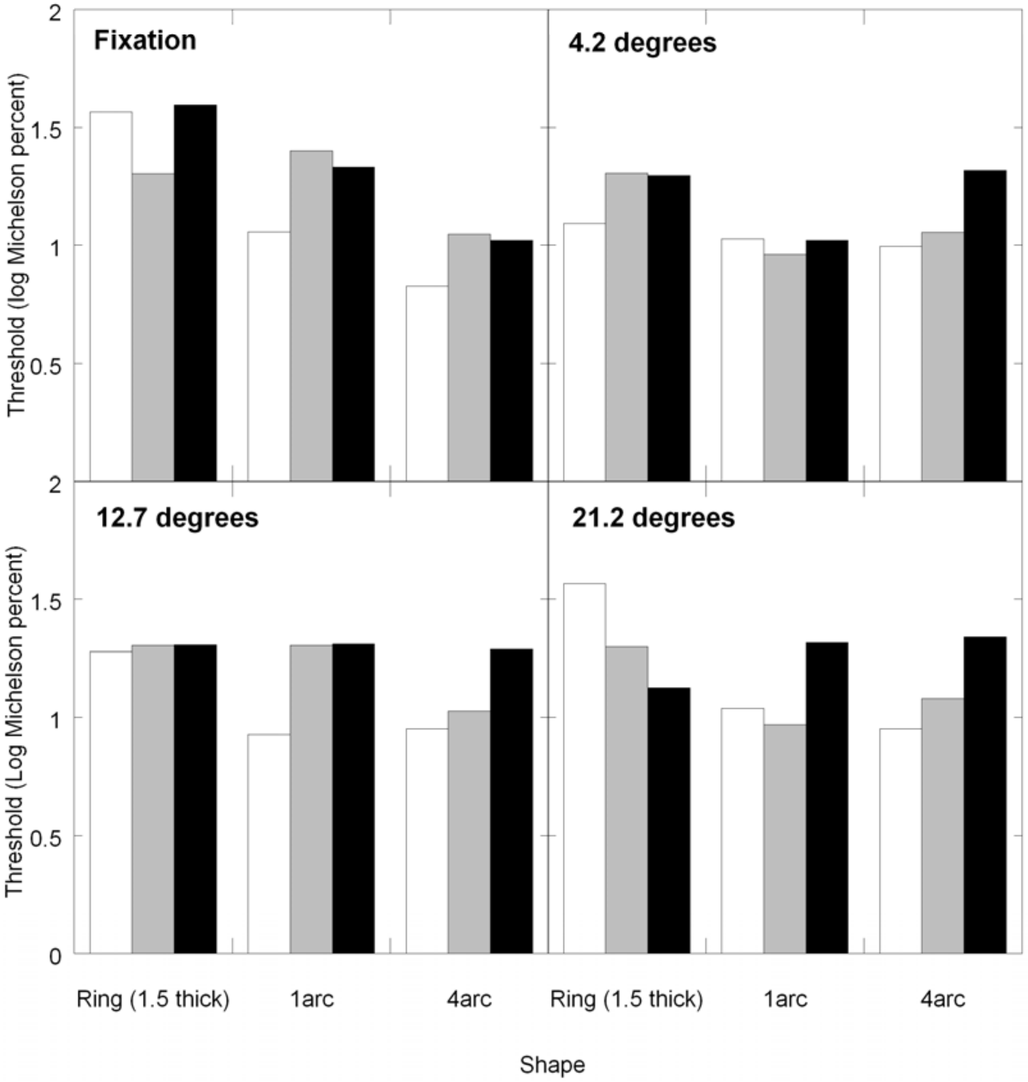

Figure 6-2. Discrimination of shapes from circles.

Data are shown for contrast thresholds required for discrimination when circles are presented. Targets are shown along the x-axis. Each subjects is represented as different shades of gray. Eccentricity is indicated in the upper left hand corner. Targets are rings (1.5º thick) and rings with breaks (1arc: 1-

80º; and 4arc: 4-25º).

6.4.2 Ring discrimination (from broken rings, and rings with different thickness)

This category of discrimination involved two types of tasks. The comparison of rings to other rings involved a judgement of thickness. The comparison of rings to broken rings involved discrimination of an entirely different shape.

No significant effects of shape were found ($F_{(1,2)}$=1.28, p=0.38, with a Huynh Felt correction for sphericity violation). No significant interaction between shape and eccentricity was found (Fig 6-3, $F_{(6,12)}$=2.16, p=0.12, observed power=0.54). One subject was unable to reach threshold under a number of different conditions. When this subject was excluded from the analysis, no significant effects of conditions ($F_{(2,2)}$=0.43, p=0.7, observed power=0.07) or interaction were found ($F_{(6,6)}$=1.45, p=0.33, observed power=0.26).

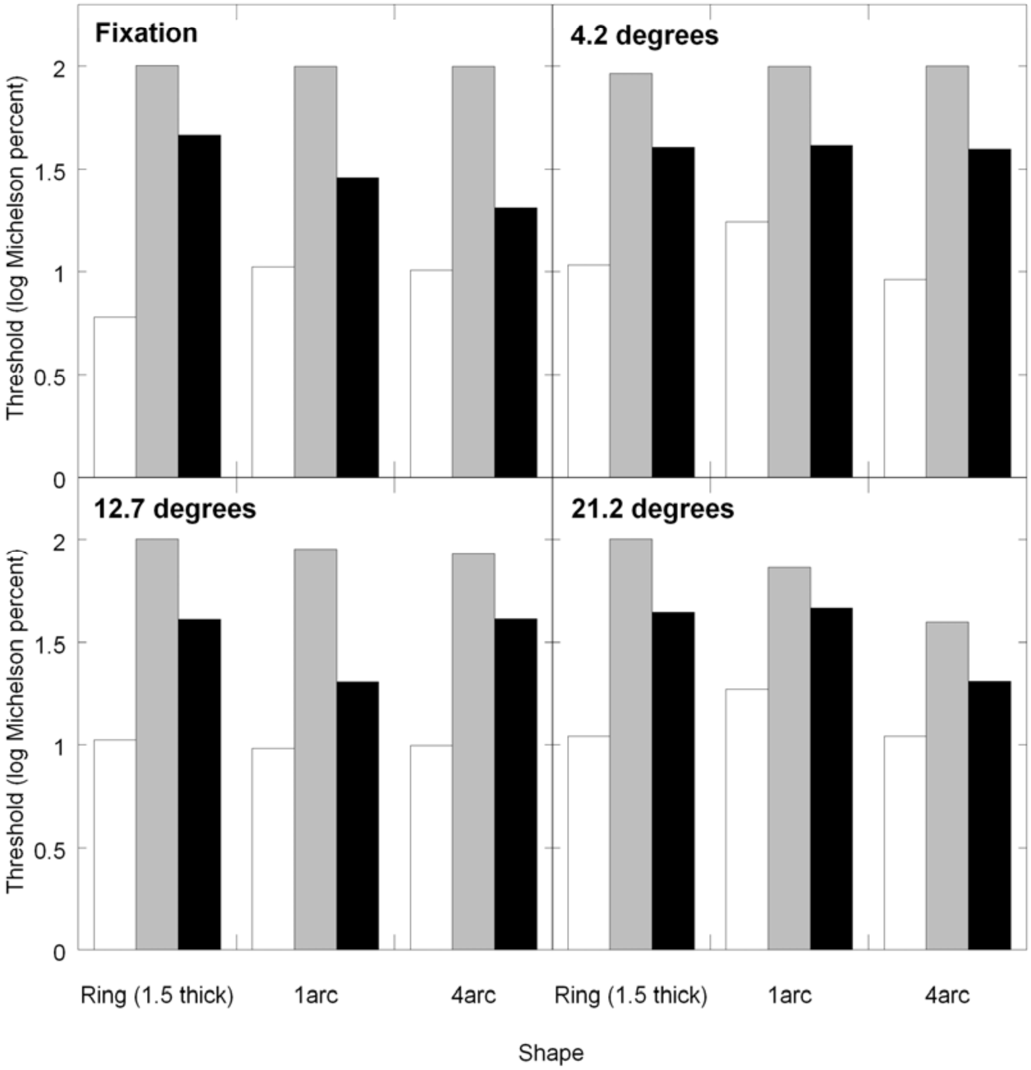

Figure 6-3. Discrimination of shapes from solid rings.

Data are shown for contrast thresholds required for discrimination when circles are presented along with the targets shown along the x-axis. Three subjects are represented as different shades of gray. Eccentricity of the target is indicated in the upper left hand corner. Targets are rings (1.5º thick) and rings with breaks (1arc: 1-80º; and 4arc: 4-25º).

6.4.3 Broken ring discrimination (from other broken rings and rings with different orientations)

This category of discrimination involved two types of tasks. The first was a comparison of rings with one large break, versus rings with four small breaks. The second was an orientation discrimination task.

No significant effects of shape were found, suggesting no difference between shape and orientation tasks ($F_{(2,4)}=3.45$, $p=0.13$, observed power=0.35, Fig 6-4). Also, no interaction between shape and eccentricity was found ($F_{(6,12)}=1.94$, $p=0.15$, observed power=0.49).

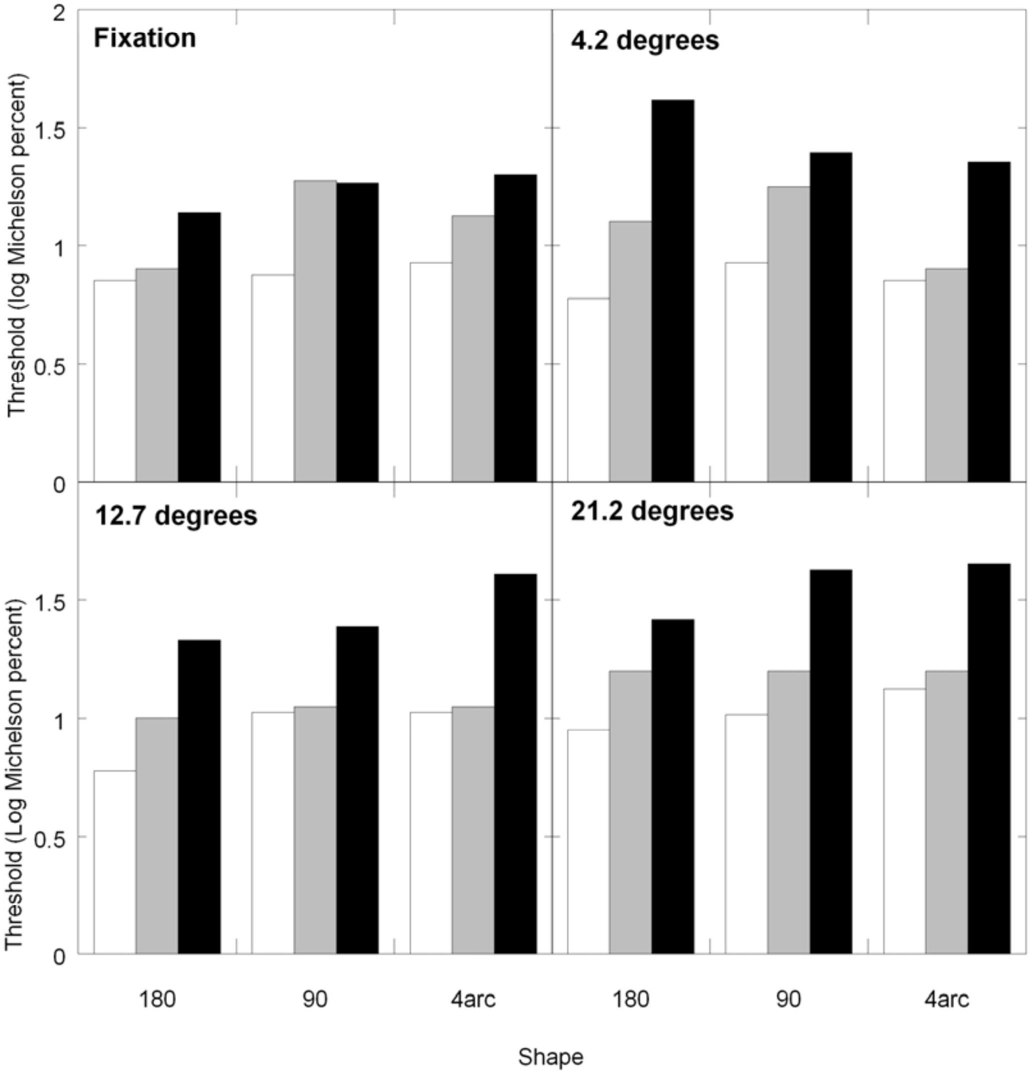

Figure 6-4. Discrimination of shapes from rings with one large break.

Data are shown for contrast thresholds required for discrimination when circles are presented along with the targets shown along the x-axis. Three subjects are represented as different shades of gray. Eccentricity of the target is indicated in the upper left hand corner. Targets with 180 and 90 are those with 100º breaks at these locations; 4arc are rings with 4-25º breaks.

6.4.4 Recognition of shapes

For this task subjects were asked to match shapes to non-flickering versions of the target (Fig 6-5). This way, subjects could identify the four static shapes clearly, without confusions. An incorrect identification of an FDF-defined shape was due to an incorrect assessment of the target, not the distractor (as in the 2 AFC).

A significant effect of shape was found (Fig 6-6, $F_{(3,6)}$=9.69, p=0.010). Post hoc analysis showed significant differences between rings with 4 breaks and circles ($p<0.01$). A significant difference was found between rings with four breaks and those with one break ($p<0.05$). No interaction was found between shape recognition and eccentricity ($F_{(9,18)}$=1.3, p=0.30, observed power=0.44). One subject was unable to see recognize rings with 4 breaks and solid rings under all conditions. When this subject was excluded from the analysis a significant effect of shape was found ($F_{(3,3)}$=26.07, p=0.01) with significant differences between rings with 4 breaks and all other shapes ($p<0.05$), including solid rings (although this effect was the least significant).

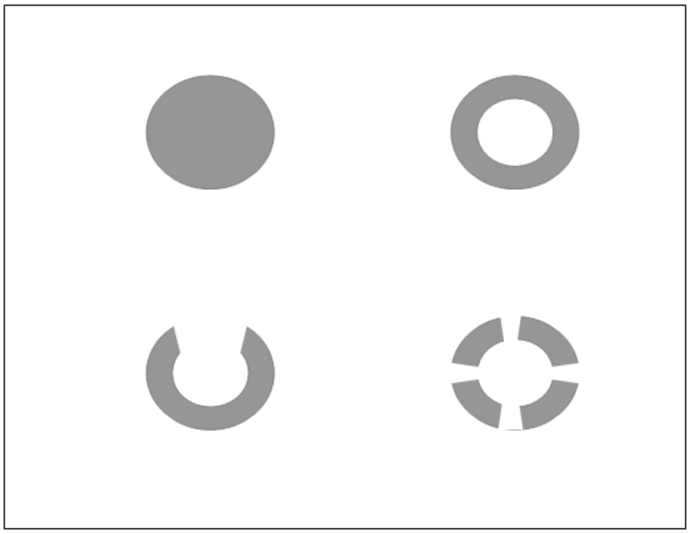

Figure 6-5. Schematic of comparison static shapes shown for 4 AFC experiment.

Shapes were presented statically at a suprathreshold contrast (1.6 log Michelson percent), defined by dots. The targets were presented at 12.7˚ from the fixation point. These locations were kept constant throughout the experiment.

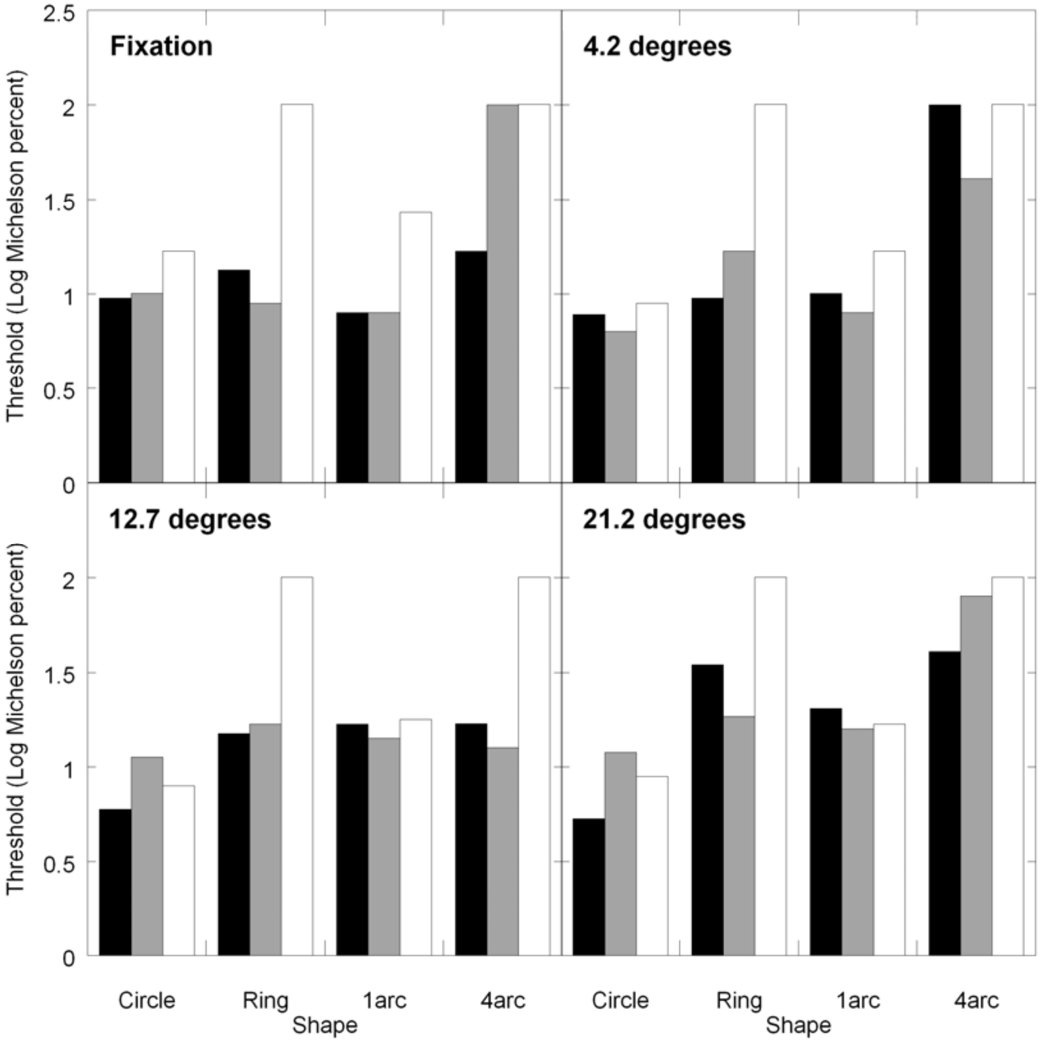

Figure 6-6. Recognition of shapes.

Data are shown for contrast thresholds required for recognition when four different shapes are presented (shown along the x-axis). Three subjects are represented as different shades of gray. Eccentricity of the target is indicated in the upper left hand corner. Circles have 5º diameter; rings have 1º thickness; 1arc are rings with one single 100º break; and 4arc are rings with 4-25º breaks.

6.4.5 Confusions between shapes

Three major confusions were found (Fig. 6-7). Circles and rings were frequently confused with a frequency of 44±2% (t(71)=6.821, p<0.001). When rings with one break were presented, subjects chose rings more frequently than chance (mean=42±2%, t(35)=4.121, p<0.001). Surprisingly, when rings were presented, subjects chose rings with one break less frequently than chance (mean=25±2%, t(35)=-4.715, p<0.001). When rings with four breaks were presented they were frequently confused with solid rings (mean=41±2%, t(35)=4.121,p<0.001). When solid rings were presented, they were confused with rings with four breaks at frequencies similar to chance.

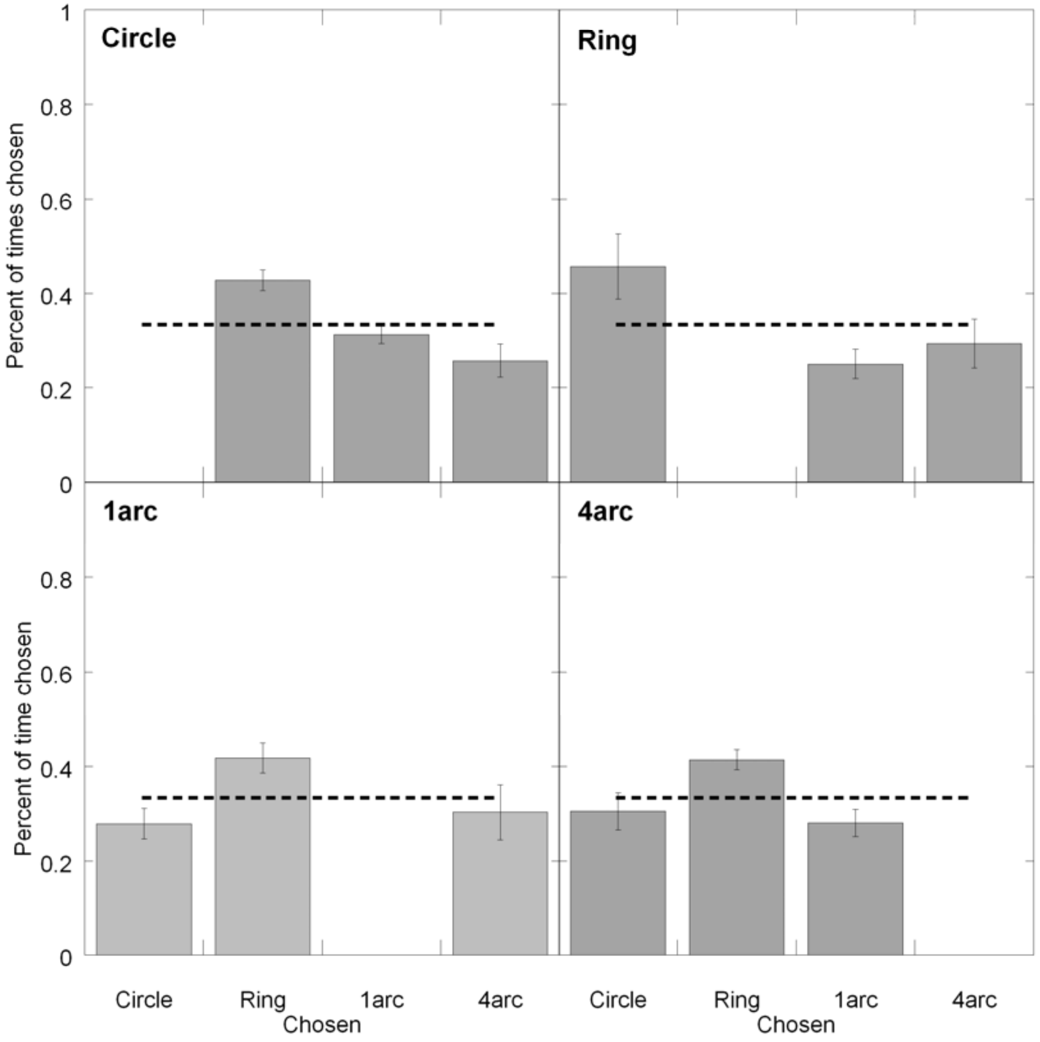

Figure 6-7. Confusions between shapes for recognition of shapes.

Shown is the distribution of incorrect responses. The shape in the upper left hand corner represents the shape presented. Values along the x-axis represent shapes chosen, excluding the correct answer. Note that when circles were presented the number of incorrect trials varied from an overall minimum of 7 to a maximum of 20 (out of 35). When rings were presented this range was 13-30. When rings with 1 break were presented this range was 9-23. When rings with 4 breaks were presented this range was 14-33. The correct response is left blank as a null category since it cannot, by definition, be incorrect. Circles have 5º diameter; rings have 1º thickness; 1arc are rings with one single 100º break; and 4arc are rings with 4-25º breaks. Means and standard errors of 3 subjects are shown for the commonly confused shapes, collapsed across eccentricity. The dotted line represents an equal distribution across shapes chosen (33%).

6.5 Discussion

This study has a number of important implications. The first is that shapes can be both discriminated and recognized. This means that not only is the FDF stimulus detectable, the shape that it defines is processed, suggesting a strong role for the shape perception pathway. Commonly confused and indiscriminable shapes have implications for the underlying mechanisms.

6.5.1 Solid shape perception

It is not surprising that discrimination of solid shapes was easier than discriminating circles from rings and broken rings. The simplicity of the solid shapes, in addition to the salience of corners suggests that resolution of these shapes should be easy. The remaining shapes tested in this study were more similar to circles.

6.5.2 Circles versus Rings

FDF-defined rings were difficult to discriminate from circles, and to recognize. Discrimination results showed that rings were more difficult to discriminate than solid shapes.

Recognition experiments showed that recognizing rings was very difficult, probably due to a large bias towards confusions with circles, in addition to confusions with other shapes.

Although rings and circles can be discriminated from each other, at low contrasts the edges of the ring were indistinguishable, making the ring look like a solid circle.

Confusions with rings and circles are likely because of two possibilities. The first is that the outer edge of the FDF stimulus is the most salient. This could be due to a depth effect. The counterphase flicker of groups of dots can produce the percept of depth, causing the smaller region to be perceived in front (Iwabuchi & Shimizu, 1997). With two similar regions in counterphase to each other, the one which is perceived in front varies between subjects. Depth perception within FDF has a number of implications. First, the entire FDF target would be perceived as in front, and thus more salient. The presence of a ring means two regions of similar area (within and inside of the ring) in counterphase. Which region was perceived in front or behind was probably variable, similar to the findings of Iwabuchi and Shimizu (1997). The potential for alternation of the perceived depth may have made the internal FDF edge less salient, making the ring difficult to distinguish from the circle.

Recently unpublished data from the lab shows that FDF edges were matched to 1.5 to 2 cycles per degree of a sine wave grating, across a large range of stimulus conditions. The ring thicknesses used in this study were less than 2˚. The ring sides would therefore have 2 edges (inner and outer contour) with thicknesses of 2cpd each. Thus, each edge is ~0.5˚ thick, for a ring of 1˚ thickness. Although this should allow the ring to be perceived, it may make rings easier to confuse with circles.

6.5.3 Solid rings versus rings with four breaks

Broken rings are equally detectable to solid rings under most conditions (Goren & Flanagan, 2008a). When asked to discriminate rings and rings with 4 breaks from circles, thresholds were very similar. When asked to discriminate solid rings from rings with four breaks this was performed at a similar performance level to discriminating solid rings from rings with one large break. All ring discriminations produced higher thresholds than the other two targets (*i.e.* circles and rings with one large break). Even though solid rings and rings with four breaks were discriminable, they were often confused. This was particularly noticeable in the recognition tasks in which rings with four breaks were often much more difficult to recognize than other shapes.

The inability to consistently discriminate solid rings from those with four breaks was most likely due to completion or filling-in effects (Polat & Sagi, 1993). FDF-defined rings with four breaks were likely perceptually filled in, resulting in the perception of a solid ring. This probably increased discrimination thresholds for the rings (which would be easily confused) and recognition thresholds for rings with four breaks (which would look like solid rings). Whether these filling in effects are synergistic with the temporal factors that contribute to the perceptual grouping of FDF elements is unclear. Other synergistic effects found between spatial and temporal structure, may also have effects on FDF (Lee & Blake., 2001).

6.5.4 Eccentricity effects

No differences in performance are seen in resolution of shapes across eccentricity. This was surprising because FDF detection thresholds improve significantly when the stimulus is presented further into the periphery (Quaid & Flanagan, 2005). The reason for improved detection in the periphery was postulated to be a dominance of the magnocellular system in the periphery. The lack of an improvement with increasing eccentricity was most likely due to the nature of the current task. In order to recognize a stimulus, one needed to have better resolution, which was not possible further into the periphery. So even though detection improved, the ability to resolve (discriminate and recognize) a shape was compromised.

This finding has implications for the classification of FDF. Past studies have shown that in some ways FDF is similar to static stimuli (*e.g.* area dependence, background organization dependence)(Goren & Flanagan, 2008b; Goren & Flanagan, 2008c). Other studies have shown that FDF is different from static stimuli (*e.g.* no benefit to good continuation, improvement into the periphery, Goren & Flanagan, 2008a; Quaid & Flanagan, 2005). The fact that resolution was impaired into the periphery suggests that FDF was similar to static stimuli, dependent on shape perception pathways.

6.5.5 What does this tell us about FDF

This study has important implications to our understanding of FDF. Showing similarities to static stimuli, such as filling-in, potential depth dependence and an ability to both discriminate and recognize shapes, suggest that FDF is not simply a flicker stimulus. It is a flickering stimulus with shape information that can be resolved, but is subject to the conditions under which it is presented (*e.g.* contrast, similarity to other shapes).

6.6 Acknowledgements

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Chapter 7

Discussion

Flicker defined form, a temporally defined illusory edge stimulus, has been previously shown to be dependent on area, location of presentation and contrast in order to be perceived. Little was known about how it was processed, although it was believed to be a magnocellular-driven mechanism. Until now, the importance of the magnocellular system has been based on the improvements seen with increasing eccentricity, and high temporal frequency of the stimulus (Quaid & Flanagan, 2005a), in contrast to other, luminance defined static stimuli. The increasing proportion of magnocellular cells in the periphery (Azzopardi et al., 1999) matched with better performance suggests that magnocellular cells are more important for FDF perception. The inability to detect FDF below 15Hz (Rogers-Ramachandran & Ramachandran, 1998) suggests that FDF is reliant on high temporal frequencies, to which the magnocellular system is more sensitive. FDF is resistant to blur, which eliminates higher spatial frequencies. Higher spatial frequencies, to which the parvocellular system is more sensitive, are not the most important range of spatial frequencies for FDF detection. Performance does not vary with up to 6 diopters of blur (Quaid & Flanagan, 2005b). A loss of higher spatial frequencies due to blur suggests that FDF perception.

To better understand the mechanisms involved with FDF perception, it is useful to compare and contrast to other, well studied, illusory stimuli. For example, does FDF perception rely on the same sorts of mechanisms as static stimuli, or does the temporal dynamic compensate for missing spatial information.

7.1 FDF and spatial vision: Similarities to static stimuli

The first study shows that subjects can match the illusory stimulus to a spatial frequency in a consistent manner. Although magnocellular and parvocellular cells overlap in their ranges for both spatial and temporal frequencies, the range of spatial frequencies which are often matched for FDF (1-2 cycles per degree) reflect a strong preference for magnocellular function, because of the magnocellular pathway's preference for low spatial frequencies. These frequencies are closer to the lower limit of the contrast sensitivity function (*i.e.* many more perceptible spatial frequencies above than below this value), but also not far from the peak of the contrast sensitivity function (*i.e.* much less contrast is required to perceive these frequencies). The absence of a shift in perceived spatial frequencies with increasing eccentricity and random dot density suggests that the mechanisms underlying FDF perception do not change when the stimulus characteristics which affect detection are modified. No other studies, to date, have looked at the subjective, perceived spatial frequency of a temporally defined illusion.

The second study shows that FDF can behave similar to a pop-out stimulus by being more salient when background elements are organized, in spite of equal organization inside and outside of the stimulus. The temporal dynamics in FDF appear to drive stimulus perception. According to studies by Lee and Blake, temporal information is enough to segregate figure from background (Lee & Blake, 1999b). Although, the addition of spatial structure can enhance perception, similar to FDF (Lee & Blake, 1999a). Spatial structure on a local scale (*e.g.* less than 1 degree of visual angle) is in a range of perceptual space that would normally be processed by the parvocellular system. If the benefit of organization is local, then this suggests that the parvocellular system, which contains smaller receptive fields and responds to higher spatial frequencies, is important to FDF. This ability of the parvocellular system to resolve fine detail, may be important for the local organization available in an organized version of the FDF stimulus. If the benefit is over the entire area of the stimulus (~5 degrees), then the larger receptive fields and low spatial resolution of the magnocellular system may be important. The very small difference between circular and grid structure, in which circular structure is preferred by area V4, suggests that the benefit of structure may involve some feedback from areas like V4. The benefit of structure probably means that higher order cortical areas responsible for shape processing are probably involved. The integration of both motion and shape perception suggests that under these conditions (*i.e.* with background structure) FDF is being processed in a more complicated way than a simple figure ground task which may only rely on areas such as V1.

The third study shows that FDF is dependent on the amount of area of the stimulus, in a manner that cannot be compensated for by the amount of contour or the overall size of the stimulus. Early studies of FDF have shown a benefit to area. Quaid found that detection of FDF is dependent on a spatial constant K which is related to the size of the target and the density of the elements within the target (Quaid & Flanagan, 2005a). The third study shows that even when the overall target size is modified, it does not influence perception as much as the increase in area, although the effect of gap sizes suggests that large variations in area can be tolerated. The benefits of target area are known for static stimuli. Greater target size means a greater likelihood of spatial summation.

This third study was particularly surprising because of the lack of importance of contour. Until now, FDF perception has been believed to be dependent on the border region between the stimulus and background dots. The factor that defined FDF perception, according to this study, was the area within the stimulus only.

7.2 FDF is unlike static stimuli

In contrast, FDF perception has also been found to be different from static stimuli. The first study showed that even though the physical properties of the illusion are changing (*e.g.* the density of the dots which compose the illusion), the spatial frequency perceived is unaffected by these changes in physical properties. Most luminance-defined stimuli, which are positioned more eccentrically, or are more densely defined (*e.g.* density of elements), appear different in their detectability and their physical attributes (*e.g.* spatial frequency). Under sampling in the peripheral retina and V1 make spatial frequencies above the nyquist limit appear as lower spatial frequencies. Those below the nyquist limit look like higher spatial frequencies (Davis et al., 1987). More elements defining a stimulus give the perception of higher spatial frequencies. The lack of changes for FDF, in spite of changes seen for luminance defined stimuli, suggests that the temporal component of FDF makes it behave differently than static stimuli.

The second study shows that although an improvement in detectability is seen with increasing background structure, no large benefit is seen for circular structure in spite of evidence in the literature of the visual system's circular sensitivity (Wilson & Wilkinson., 1998). A difference is seen for Glass patterns with circular structure than grid like structure (Glass, 1969). Although Glass patterns are very similar in their structure (*i.e.* individual elements widely spaced with overall structure), no difference is seen between circle and grid structures for FDF.

The fourth study shows that the Gestalt law of good completion does not influence FDF perception. Luminance defined static tasks benefit from completion of patterns. Contours which are incomplete are difficult to detect, even when only a small component of the contour is removed (Kovacs & Julesz, 1993). The current study removed only a few elements (1-3); multiple elements in multiple locations and multiple locations in a single location. None of these conditions made detection consistently more difficult. Even though luminance defined static stimuli are greatly affected by closure, FDF was not, suggesting that the temporal dynamics are sufficient to allow detection.

7.3 FDF detection reflects shape perception

The fifth study shows first, that the illusion is discriminable in most cases. That means that subjects are not merely responding to flicker. Even the most complicated stimuli, such as rings with multiple breaks can be discriminated from circles, rings and rings with large breaks. Although thresholds do vary, most of these stimuli are discriminable from each other. For some of the more complex stimuli (*e.g.* rings and broken ring) higher contrast thresholds were required for discrimination.

When asked to recognize shapes by matching FDF-defined shapes to static versions of the same shapes, subjects were able to match circles and rings with one break with greater ease than remaining shapes. An analysis of confusions showed that when rings with four breaks are presented they are frequently confused with solid rings. Circles and rings were also frequently confused. These two effects suggest that filling-in is occurring when FDF is presented, affecting our ability to resolve certain, more complex stimuli.

7.4 Role of end stopping

Although the third study showed that contour is not a deciding factor in FDF perception, the regions between the dots form an important component of this stimulus. Original research in this illusion showed that when the region between the dots is covered the two phases cannot be discriminated (Rogers-Ramachandran & Ramachandran, 1998). No work to date had looked at spatially bounded stimuli (such as the circles and rings used in the current studies).

End stopping relies on regions outside of the classical receptive field. End stopping represents a suppression of the response after the stimulus is beyond a particular length. The extra-classical receptive field can extend to 13˚, allowing stimuli outside of the classical receptive field to affect the neuron's response to a stimulus within the centre of the classical receptive field (Angelucci & Bullier, 2003). In some cases, neurons can respond when there is no stimulus within the classical receptive field (Rossi et al., 2001). A classical receptive field would probably not respond to the FDF stimulus. A receptive field which falls between the counterphase regions would produce a minimal signal. The involvement of surround effects from outside of the classical receptive field can increase the response of the neuron. A series of aligned extra-classical receptive fields may signal the presence of the illusory edge, because of the difference between the classical and extra-classical receptive fields. Feedback from other cortical regions like V2, V3 and MT to receptive fields within V1 may be particularly important for FDF which is highly dependent on temporal modulation (Angelucci & Bullier, 2003)

7.5 The lack of TRUE M and P input

FDF is a unique illusory stimulus which shares some properties of static, and kinetic stimuli. In this way, no one illusory stimulus can be used as a model for FDF perception. It is most likely, from the data, that FDF involves both static (ventral) and kinetic (dorsal) pathways similar to stimuli such as form from motion (Cowey & Vaina, 2000). Some other illusory stimuli, such as those by Lee and Blake, show that elements which lack spatial structure (and information) can still produce shape percepts based on temporal structure (Lee & Blake, 1999b). However, the addition of structure (*e.g.* spatial phases), can still benefit such an illusion (Lee & Blake, 1999a).

Physiologically, the spatial overlap of magno and parvocellular cells suggests that even if the stimulus is *better* suited for one particular type of cell, the other cell type will inevitably be activated and contribute to perception of the stimulus. Higher order cortical areas also receive significant amounts of input from both types of cells. As early as V1, information from V1 cells is crossed. Many V1 cells receive input from both types of cells (Nealey & Maunsell, 1994). Magnocellular cells contribute ~40% to V4 cells (Ferrera et al., 1994), which is believed to be an entirely form perception region. MT, a primarily motion perception region, receives most of its input from magnocellular cells, but some from parvocellular cells (Maunsell et al., 1990). A blockage in magnocellular input affects flicker more than drift suggesting that the parvocellular system must be present to allow drift when no input is being received from magnocellular cells.

7.6 Summary

FDF is a stimulus, defined by temporal dynamics, and sometimes affected by spatial structure. This study has shown that FDF can be matched to spatial stimuli (*i.e.* spatial frequency), is easier to perceive with increasing background structure, and area (not just the contour) and can be discriminated and recognized, for certain shapes. These results suggest that FDF relies on motion pathways, but also benefits from overlap in function of shape recognition pathways.

FDF is a stimulus, defined by temporal dynamics, and sometimes unaffected by spatial structure. This study also showed that FDF does not benefit from Gestalt rules of contour closure, unlike some static stimuli. Other studies have shown that FDF can still be detected in spite of blur. These results suggest that FDF relies on motion pathways, which sometimes do not benefit by their interactions with spatial pathways.

According to a recent study of individual MT neurons, more selectivity for particular shapes was found when the shape was defined by motion, as compared to luminance cues (Handa et al., 2008). Again, although FDF is very different from motion defined shapes, it is likely that the temporal dependence both show is processed in MT. The differences in shapes displayed in the current studies, coupled with the results of Handa et al., imply a role for MT in the differences in detection between shapes and/or shape discrimination ability.

FDF is a stimulus, which is, due to its dynamic nature, dependent on dorsal stream function, and most likely areas such as MT. Our hypothesis that FDF uses motion perception pathways, is partially due to the seeming dependence of FDF perception on magnocellular input. It has been shown that neural response to flicker in MT is dependent on magnocellular function, even more than drift (Maunsell et al., 1990). The likely involvement of MT in FDF perception implies that FDF shares some common pathways with motion perception.

A recent review by Kourtzi et. al (2008) of primate form and motion integration suggests that even though low level cortical areas, such as V1 are likely to play a role in the binding of orientation-based contours, regions such as the higher cortical areas, like MT, are involved with this process (Kourtzi et al., 2008). They hypothesize that the integration of the static and dynamic cues probably involve both higher and lower level mechanisms, both ventral and dorsal, both feedforward and feedback.

Motion perception regions are likely to be innervated by shape perception pathways, requiring parvocellular input, which leads to ventral stream function. The cues present in the stimulus (*e.g.* background structure, contour closure, eccentricity, blur) most likely affect the strength of the role that can be played by each of these two pathways. The interconnectedness of both higher order motion and shape perception pathways, through input from both magnocellular and parvocellular, suggests that FDF represents a stimulus which is dependent on both pathways.

7.7 References

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