Scotopic contour and shape discrimination using radial frequency patterns

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Radial frequency (RF) patterns are valuable tools for investigations of contour integration and shape discrimination. Under photopic conditions, healthy observers can detect deformations from circularity in RF patterns as small as 3 seconds of arc. Such fine discrimination may be facilitated by cortical curvature detectors or global shape-detecting mechanisms that favor a closed contour. Rods make up 95% of photoreceptors in the retina, but we know very little about how spatial information is processed by rod-mediated pathways. We measured scotopic radial deformation discrimination using both full and partly occluded RF pattern stimuli. We found radial deformation thresholds of around 2–3 minutes of arc for stimuli with a wide range of radii and RFs. When parts of the stimulus were occluded, scotopic thresholds improved up to the point that three or four cycles of modulation were visible; no further improvement occurred with the addition of more visible cycles. When only one to three cycles were visible, an increase in curvature per cycle became important, allowing observers to detect smaller deformations from circularity. Our results indicate that the scotopic radial deformation thresholds for the stimuli tested are not dependent on global circularity cues but are instead mediated by local curvature cues.

Introduction

Area V4 of the visual cortex is an intermediate processing stage for shape, contour, color, orientation, depth, and motion information (Roe et al., 2012), and it serves as a link between local and global representations (Webb, Roach, & Peirce, 2008). A growing body of fMRI and electrophysiology evidence from macaques shows that areas of V4 preferentially respond to curves over straight lines and to closed circular shapes over open ones (Dumoulin & Hess, 2007; Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Pasupathy & Connor, 2002; Wilkinson et al., 2000).

Radial frequency (RF) patterns (Figure 1) are valuable tools for psychophysical studies of shape and contour processing and discrimination (Wilkinson, Wilson, & Habak, 1998). Deformations from circularity in RF patterns as small as 3 seconds of arc (arcsec) are detectable by healthy observers when measured under photopic (cone-mediated) conditions. There is a large body of evidence that global shape processing mechanisms (Dumoulin & Hess, 2007; Green, Dickinson, & Badcock, 2018; Hancock & Peirce, 2008; Wang, Wilson, Locke, & Edwards, 2002) contribute to this remarkable deformation sensitivity. For example, radial deformation thresholds are elevated beyond expected levels when small parts of the RF pattern are occluded or nonuniformly deformed (Loffler, 2008; Schmidtmann, Kennedy, Orbach, & Loffler, 2012), and curvature discrimination thresholds are lower for closed contours than for line segments (Hess, Wang, & Dakin, 1999; Wilkinson et al., 1998). Random orientation of stimuli forces observers to use global processes rather than local processes due to the random location of salient cues such as the curvature maxima, or convex peaks of the stimuli (Green, Dickinson, & Badcock, 2017; Loffler, Wilson, & Wilkinson, 2003; Pasupathy & Connor, 2002). Analysis of BOLD responses further supports the presence of midlevel visual areas that respond to RF of closed contours (Salmela, Henriksson, & Vanni, 2016).

However, the presence of global mechanisms for RF discrimination is disputed and may hold for only a subset of RF configurations (Jeffrey, Wang, & Birch, 2002; Loffler, 2015; Mullen, Beaudot, & Ivanov, 2011;...
Schmidtmann et al., 2012), Schmidtmann and Kingdom (2017) used a new model (Curve Frequency Sensitivity Function) to account for the effect of RF on discrimination thresholds in both RF and line stimuli. Because their model predicts responses to both lines and RF patterns, they suggested that local processing accounts for observer responses in both cases, since the closed contour RF patterns are not processed differently (i.e., as shapes) from the line patterns.

All the research described above was conducted under photopic conditions. To our knowledge, scotopic (rod-mediated) shape discrimination has not been defined. Rods comprise 95% of photoreceptors in the retina and 90% of photoreceptors in the macula (Curcio, Sloan, Kalina, & Hendrickson, 1990; Dubra et al., 2011), but we know very little about how spatial information is processed by rod-mediated pathways. The few studies that have investigated spatial vision under scotopic conditions (Duffy & Hubel, 2007; Livingstone & Hubel, 1994; Mandelbaum & Sloan, 1947; Yap, Levi, & Klein, 1989; Zele & Cao, 2014) reveal that rods signal the brain on the same or parallel pathways to cones, but that they have larger receptive fields and operate on a larger spatial scale. Some retinal ganglion cells may even adjust their receptive field tunings depending on light level (Yao et al., 2018). These large receptive fields provide the means for detecting small quanta of light necessary for night vision, but increased sensitivity comes at the cost of shifting spatial vision to a larger scale. How does scotopic spatial vision operate across a large spatial scale? We posited that scotopic spatial vision is not merely a scaled version of photopic spatial vision. RF patterns are ideal stimuli for rod-mediated testing because the radius of the ring can be set to greater than the radius of the rod-free zone around the fovea (Curcio, Millican, Allen, & Kalina, 1993) and rod spacing is relatively constant in the retina between 4° and 20° (Curcio et al., 1990; Merino, Duncan, Tivueedhula, & Roorda, 2011).

The first aim of the current study was to describe scotopic shape discrimination, the spatial scale that the scotopic visual system operates on when processing these RF stimuli, and the stimulus parameters that affect performance on a scotopic shape discrimination task. We do not know if parametric manipulation affects discrimination performance for scotopic stimuli the same way as for photopic stimuli. For example, based on previous research under photopic conditions, we might expect to find that higher RFs result in lower thresholds (Schmidtmann & Kingdom, 2017; Wilkinson et al., 1998) and that increasing circular contour frequency reduces thresholds (Jeffrey et al., 2002). We test parametric manipulation of RF patterns on discrimination thresholds across two experiments.

Adding small masks or asymmetries to photopic RF patterns has been demonstrated to cause a large jump in discrimination threshold, consistent with global pooling (Dickinson, McGinty, Webster, & Badcock, 2012; Schmidtmann et al., 2012). The upper limit of global pooling has been estimated to lie between five and 10 modulation cycles (Loffler, 2008; Loffler et al., 2003; Mullen et al., 2011; Schmidtmann et al., 2012), though Schmidtmann and Kingdom’s (2017) recent

Figure 1. Examples of RF pattern stimuli. The stimulus is a ring with a luminance profile defined by a fourth-derivative Gaussian and a radius deformed by a sine wave. (A) A nondeformed ring. (B) An RF pattern with a radial frequency of 8 (RF8), meaning that it is radially deformed by eight cycles of a sine wave. (C) An RF pattern with a higher radial frequency of 16 cycles (RF16). (D) An RF8 pattern with a smaller radius than the pattern in (B). Note that (C) and (D) have the same circular contour frequency (see Experiment 2). (E) An RF8 pattern with a lower spatial frequency, which results in a thicker ring. (F) An RF8 pattern with one-fourth of the stimulus masked, like those used in Experiment 3.
model based on curvature theorizes that this apparent “cutoff” is actually an effect of diminishing returns from curvature information on discrimination threshold. Curvature may account for RF discrimination thresholds by trading off RF pattern radius against RF (Jeffrey et al., 2002).

Given that rod vision operates on a large spatial scale, is global pooling possible? The second aim of the study was to test if rod-mediated shape discrimination is mediated by local or global processing over a range of RF conditions. Further, we sought to determine whether curvature plays a role in mediating scotopic shape discrimination.

### Methods

#### Stimulus

The RF pattern used in the following experiments is a ring with a luminance profile defined by a fourth-derivative (D4) Gaussian and a radius deformed by a sine wave, as described by Wilkinson and colleagues (1998). The RF pattern is described by the following parameters: radius (°) from center of the ring to the peak of the D4; RF (number of sine wave cycles per 360°); spatial frequency (cycles per degree [CPD] of visual angle), which defines the thickness of the D4 Gaussian; contrast; and deformation amplitude, defined by the height of the deforming sine wave as a proportion of the mean radius (on a scale from 0 to 1). The radial deformation threshold (arcsec) is measured as the smallest noticeable difference between the radius of a nondeformed (i.e., perfectly circular) RF pattern and the radius at the peak (curvature maxima) of the deforming sine wave in the deformed RF pattern.

#### Participants

Eight healthy volunteer (HV) observers aged 19–54 years were recruited in total, but not all observers completed all experiments. All observers had visual acuity of 20/20 or better and were deemed healthy by a full ophthalmic exam. The authors (HV1 and HV2) are experienced psychophysical testers; the remaining six observers (HV3–HV8) were naive to psychophysical testing. All testing was completed using the observers’ dominant eyes. This study was approved by the Institutional Review Board of the National Institutes of Health, is HIPAA-compliant, and adheres to the tenets of the Declaration of Helsinki.

### Apparatus

The tests were programmed in MATLAB (MathWorks, Natick, MA), using the Psychtoolbox 3 toolbox (Brainard, 1997; Pelli, 1997). The stimuli were presented on a 36-in. CRS Display++ LCD monitor (Cambridge Research Systems, Rochester, UK) running at 1920 × 1080 resolution. The LCD panel has a fixed contrast ratio on the order of 1400:1 and the grayscale resolution is 10-bit RGB extended to 16-bit RGB with temporal dithering. For scotopic tests, the monitor was calibrated by setting the maximum luminance of the display to 1 cd/m² and placing three neutral density filters (0.9121, 0.9410, and 0.8452 log unit reductions) in front of the monitor, which reduced the maximum luminance to 0.002003 cd/m². For photopic tests, the filters were removed, and the maximum luminance of the monitor was set to 120 cd/m². In both cases, the monitor was linearized, and outputs were tracked in real time by built-in systems within the Display++. Observer responses were registered using a Cedrus RB-540 response box (Cedrus Corporation, San Pedro, CA). All testing was conducted in a dark room with no light sources other than the stimulus monitor. Observers sat 1 m from the monitor with an eye patch over the untested eye.

### Testing procedure

The task in all experiments was a two-alternative temporal forced choice shape discrimination; deformed and nondeformed RF patterns were presented sequentially (in random order), and the stimulus that contained radial deformation from circularity was selected (Hess et al., 1999; Jeffrey et al., 2002; Mullen et al., 2011; Schmidtmann et al., 2012; Wang, He, Mitzel, Zhang, & Bartlett, 2013; Wang et al., 2002; Wilkinson et al., 1998). Figure 2 illustrates the trial sequence. All stimuli and fixation crosses were oriented randomly at every presentation. A large (4.2°) white fixation cross with a black border was presented to maintain observers’ fixation in the center of the display. This large size was chosen to prevent the cross from disappearing during scotopic fixation, as the tails of the cross could be seen scotopically, even if the center disappeared. In photopic tests, a small (0.23°) black fixation cross appeared on the display throughout the test. The background of the display (i.e., the entire monitor) was set to mean luminance gray to match the edges of the RF pattern stimulus. For scotopic tests, observers adapted to the dark for 30 min prior to testing. For photopic tests, there was no adaptation period.

The test followed an accelerated stochastic approximation staircase procedure (Faes et al., 2007) to
estimate a 75% radial deformation discrimination threshold. The test ran for 12 reversals, and the step size shrank after each reversal. The threshold estimate was the deformation amplitude presented on the final trial (Swanson & Birch, 1992) converted to arcsec. The full staircase was run three times for every stimulus configuration, and each staircase took about 4 min to complete. To avoid possible learning or adaptation effects, conditions were presented in a pseudorandom order, meaning that after a staircase for one condition was completed, the next staircase tested a new condition.

Data analysis

Data analysis and graph creation were conducted in GraphPad Prism 7.04 (GraphPad Software, La Jolla, CA) using built-in functions. For each condition, the mean threshold from each of the three staircases was calculated.

### Experiment 1

The first experiment investigated the effects of manipulating the stimulus parameters—radius, RF, and spatial frequency—on scotopic radial deformation thresholds. Table 1 shows the range of parameter values for each of the three tests.

### Results and discussion for Experiment 1

Figure 3 displays the radial deformation thresholds from the three parametric investigations of RF patterns under scotopic conditions for four observers. Colored data points represent the mean of three thresholds per condition for each observer. The bold black line represents the linear fit of all threshold measures from all observers. In Tests A (effect of radius) and B (effect of RF), there was not a significant relationship between the independent variable and radial deformation thresholds (p = 0.94 and p = 0.46, respectively). In Test A, thresholds averaged 154 arcsec (SD = 64), and in Test B thresholds averaged 159 arcsec (SD = 54). In Test C (spatial frequency of the luminance profile), radial deformation thresholds for scotopic RF patterns remained relatively constant from 1–4 CPD. Higher radial deformation thresholds were observed at 0.5 CPD. Only HV1 could see the 6 CPD stimuli; no observers could see the 8 CPD stimuli. These patterns of results resemble those from photopic tests, where radial deformation thresholds do not change significantly over a range of radii, RFs, and spatial frequencies (Wilkinson et al., 1998). However, our scotopic radial deformation thresholds are well above the ≈3 arcsec radial deformation thresholds recorded.

<table>
<thead>
<tr>
<th>Test</th>
<th>Radius (°)</th>
<th>Radial frequency (cycles/360°)</th>
<th>Spatial frequency (CPD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2–6</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>B</td>
<td>5</td>
<td>5–13</td>
<td>4</td>
</tr>
<tr>
<td>C</td>
<td>3</td>
<td>5</td>
<td>0.5–8.0</td>
</tr>
</tbody>
</table>

Table 1. The parameters tested in Tests A, B, and C of Experiment 1. The manipulated parameters and their ranges are in boldface type. In Test A, five radii were tested. In Test B, five radial frequencies were tested. In Test C, six spatial frequencies were tested. CPD = cycles per degree.
under photopic testing (Schmidtmann et al., 2012; Wang et al., 2002; Wilkinson et al., 1998).

Experiment 2

In photopic testing, radial deformation thresholds remain constant when circular contour frequency (CCF) is held constant (Jeffrey et al., 2002; Jeffrey, Wang, & Birch, 2004). CCF—represented as cycles per contour length degree (cycles/cl-deg)—is a measure of the physical length of one cycle of modulation around the circumference of an RF pattern. CCF is dependent on both the radius (more specifically the circumference) and the RF of the pattern. For example, in an RF pattern with a radius of 2° and four radial cycles, each cycle of modulation covers 3.14° of viewing angle: CCF = 0.32 cycles/cl-deg. In a stimulus of radius 4° and eight radial cycles, each cycle also covers 3.14° (CCF = 0.32 cycles/cl-deg), but there are twice as many cycles in the stimulus (higher RF). Photopic radial deformation thresholds are closely matched for a given CCF regardless of RF or radius, and are inversely correlated with CCF over a wide range of CCF values (0.08–2.6 cycles/cl-deg; Jeffrey et al., 2002). CCF is a measure of curvature information in an RF pattern: An increase in the curvature of each cycle (by increasing the RF of the pattern or by reducing the radius) results in higher CCF.

The aim of the second experiment was to investigate the relationship between scotopic radial deformation thresholds and CCF. The parameters used are listed in Table 2. All combinations of radius and RF were tested. Therefore, multiple stimulus configurations had the same CCF. One observer (HV1) was tested photopically to confirm that the pattern of data observed by Jeffrey and colleagues (2002) could be replicated on our equipment. Four observers were then tested scotopically.

Results and discussion for Experiment 2

Radial deformation thresholds were constant for a given CCF in photopic conditions (Figure 4A). The photopic data closely resembles those of Jeffrey et al. (2002) and shows that radial deformation thresholds decrease as a function of increasing CCF (Figure 4A) from an average 48.4 ± 9.4 arcsec at 0.159 cycles/cl-deg to an average 3.4 ± 0.28 arcsec at 5.093 cycles/cl-deg. Under scotopic conditions, radial deformation thresholds did not decrease as CCF increased (Figure 4B through E) and instead remained relatively constant across the conditions tested. All observers showed a trend toward higher thresholds at the highest CCFs.

<table>
<thead>
<tr>
<th>Photopic</th>
<th>Scotopic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radii</td>
<td>0.5°, 1°, 2°</td>
</tr>
<tr>
<td>Radial frequencies</td>
<td>2, 4, 8, 16 cycles</td>
</tr>
<tr>
<td>Spatial frequency</td>
<td>19.2 CPD</td>
</tr>
<tr>
<td>CCF values</td>
<td>0.159 to 5.093 cycles/cl-deg</td>
</tr>
</tbody>
</table>

Table 2. The parameters tested in Experiment 2. All combinations of radius and radial frequency were tested. Therefore, multiple stimulus configurations had the same CCF.
tested, contrary to what is observed photopically (Jeffrey et al., 2002).

**Experiment 3**

The results of Experiment 2 prompted us to investigate whether differences in global pooling or local computations were responsible for the contrasting relationship between radial deformation thresholds and CCF when recorded under photopic or scotopic conditions. Under photopic conditions, partial occlusion of an RF stimulus greatly elevates thresholds in stimuli with low RFs but does not in stimuli with high RFs (Schmidtmann et al., 2012). One explanation posited for this result is that at low RFs, global shape detection is the critical cue for discrimination, and occlusion breaks the circular shape. At higher RFs, however, sensitivity is limited by local computations, so partial occlusion does not significantly elevate thresholds (Loffler, 2015). This explanation is disputed (Mullen et al., 2011). An alternative explanation is that there is a nonlinear relationship between the curvature information in an RF pattern and the discrimination threshold. Each added cycle corresponds with a diminishing reduction in threshold. Removing one cycle of an RF16 may result in a negligible increase in threshold, but removing one cycle of an RF4 would have a large effect (Schmidtmann & Kingdom, 2017).

We examined whether global pooling was evident in scotopic radial deformation thresholds by measuring the dependence of radial deformation threshold on the number of cycles of modulation visible to the dark-adapted observer. We measured thresholds using RF4 stimuli where four, three, two, or one cycle was visible; RF8 stimuli where eight, four, three, two, or one cycle was visible; and RF16 stimuli where 16, eight, four, three, two, or one cycle was visible. Masks began and ended at inflection points between cycles of modulation to preserve the “curvature maxima” or peaks of modulation, which have been shown to be the most important cues for the task (Loffler et al., 2003; Pasupathy & Connor, 2002; Schmidtmann & Kingdom, 2017). Masks were “hard edges” like those used by Dickinson and colleagues (2012) rather than contrast windows used by Mullen et al. (2011). Though others have preferred to use stimuli where the full ring is present but only partly deformed, instead of masking the nondeformed part of the ring, Dickinson and colleagues show that both options are equally valid (Dickinson et al., 2012).

**Results and discussion for Experiment 3**

Figure 5 shows scotopic radial deformation thresholds as a function of the number of visible cycles of...
modulation. HV1 and HV2 were tested on RF4, RF8, and RF16 stimuli at both 4\(^\circ\) and 8\(^\circ\) radii. HV3 was tested on RF4 and RF8 stimuli that were 8\(^\circ\) in radius. All results show the same pattern: Scotopic radial deformation thresholds decrease as cycles are added to the stimuli, but each additional cycle produces diminishing returns. The result is that for the RF8 and RF16 stimuli, there appears to be little to no difference in threshold between the full stimulus and half-occluded stimulus.

To further confirm the pattern that we observed in Experiment 3, we recruited two more observers and tested them on only the 8\(^\circ\) radius, RF8 pattern. Their results, along with the results from HV1, HV2, and HV3, are plotted in Figure 6. The nonlinear relationship between visible cycles and threshold is the same for all observers, though there are individual differences in the threshold measures themselves. These differences cannot be explained by observer age or experience with the testing procedure. No observer had higher thresholds when half the stimulus was masked than when the full stimulus was visible.

The results of Experiment 3 suggest that, for the scotopic stimuli tested, the visual system integrates...
only up to three or four cycles of modulation when discriminating between a deformed stimulus and a circular stimulus, regardless of radius or RF. Adding cycles beyond this limit does not appear to lower radial deformation thresholds further. The results indicate that the visual system, under dark-adapted conditions, uses curvature information from only an arc of the RF pattern stimulus to make a judgment of circularity. The results for all conditions suggest that the thresholds are not dependent on global circularity cues but are instead dependent on a critical amount of local curvature information. While others have shown a gradual decrease in threshold as visible cycles are added, sometimes with a marked decrease for fully closed or symmetrical stimuli (Dickinson et al., 2012; Schmidtmann et al., 2012), we instead show a decrease as up to three or four cycles are added, followed by a flattening where adding further cycles does not measurably decrease thresholds. We display these results a different way in Supplementary Data Figure S1. Here we replot data from HV1 and HV2 on a log-log scale and fit a probability summation model to the first three data points (one to three visible cycles). The data for one to four cycles fit the model, indicating that local processing explains the thresholds. For RF8 stimuli, the data point for eight visible cycles (i.e., the full ring) falls at a higher threshold than predicted by probability summation. This confirms both that the full stimulus is not needed for observers to reach their lowest discrimination threshold, and that we fail to detect an effect of global processing.

Further analysis

As we confirmed in Experiment 2, thresholds decreased with increasing CCF for photopic stimuli but not for scotopic stimuli. However, we know from Experiment 3 that not all the contour information contained in the RF pattern is used in the radial deformation discrimination task under scotopic conditions. We sought to separate the relative effects of CCF and occlusion on scotopic radial deformation thresholds. Here we present a subset of the data from HV1 and HV2 in Experiment 3—data from conditions where only one, two, or three cycles of modulation are displayed—in terms of threshold as a function of CCF. Figure 7 illustrates the further analysis. When one cycle is visible (red data points), radial deformation thresholds decrease as CCF increases. Adding a second cycle to the stimulus (green data points) decreases deformation thresholds for all CCFs. The decrease in scotopic radial deformation thresholds as a function of CCF, when most of the scotopic RF stimulus is occluded and only one or two cycles of modulation are visible—in terms of threshold as a function of CCF. Adding a third cycle decreases deformation thresholds further, down to the levels observed in Experiments 1 and 2 (average = 128.8 ± 38.5 arcsec for HV1 and 166.7 ± 60.0 for HV2). Here, the relationship between threshold and CCF becomes less clear but more closely resembles the relationship between scotopic thresholds and CCF for full scotopic patterns (Figure 4B through E).
There are two ways to increase the amount of curvature information in an RF pattern: (a) increase the CCF of the pattern to increase the curvature of each cycle by reducing the radius (Figure 8B) or increasing the RF; and (b) adding visible cycles back to the stimulus (Figure 8C). The above data show that when only one or two cycles of modulation are visible in an RF pattern, scotopic radial deformation threshold is dependent on CCF. When more cycles are visible, the effect of CCF becomes secondary.

Discussion

A major finding from the current study is that scotopic radial deformation threshold, expressed in seconds of arc, is not dependent on the radius of the stimulus—that is, scotopic thresholds do not follow Weber’s law with respect to the radius of the stimulus. Remarkably, scotopic radial deformation thresholds remain relatively constant at around 2–3 arcmin across a wide retinal area, spanning 2–8° retinal eccentricity. This finding mirrors the investigation of scotopic visual acuity as a function of retinal eccentricity (Mandellbaum & Sloan, 1947). Our scotopic radial deformation thresholds, too, are consistent with results from tests of scotopic position and stereo acuity (Livingstone & Hubel, 1994). The consistency of our scotopic shape discrimination findings—and scotopic visual acuity across a wide range of retinal eccentricities—can be explained by relatively constant rod spacing in the retina between 4° and 20° (Curcio et al., 1990; Merino et al., 2011).

We have shown that scotopic radial deformation thresholds remain at about the same level for both the full stimulus and half-occluded stimulus and elevate only when fewer than three or four cycles of modulation are visible. We have also shown that when only one or two cycles of modulation are visible, thresholds decrease as CCF, a measure of local curvature, increases. How do we unify these two findings under one explanation?

Current theories agree that detection of curvature is essential for shape discrimination examined under photopic conditions (Jeffrey et al., 2002; Schmidtmann & Kingdom, 2017). The most salient features of the RF pattern are the points where the curvature is the highest—the convex and concave peaks of the modulation. As Schmidtmann and Kingdom’s (2017) model demonstrates, curvature information can be added to an RF pattern by increasing the RF, which results in lower discrimination thresholds (their figure 5). We achieve the same effect by adding visible cycles back to our occluded ring stimuli (our Figures 5 and 6) with diminishing returns from increasing RF. Our Figure 6 strongly resembles Schmidtmann and Kingdom’s figure 2 but at a larger spatial scale and with curvature described in terms of visible cycles rather than RF (Schmidtmann & Kingdom, 2017). Schmidtmann and...
Kingdom also show that their model predicts observations for both RF rings and modulated line patterns. Our masked stimuli, which we used to measure the effect of adding cycles, more closely resemble short arcs than closed RF ring patterns when the lowest numbers of cycles are presented. The fact that we do not find lower thresholds for complete ring stimuli than for partly masked stimuli (Experiment 3) and that when only one or two cycles of modulation are visible, thresholds decrease as CCF increases (Further Analysis), indicates that, for the stimuli we presented, local cues, not global ones, are the most critical for our scotopic shape discrimination task.

Although we do not observe the effect of global processing in the study, we cannot rule out that global processing may be found to occur for other scotopic stimulus conditions not examined here. Green, Dickinson, and Badcock (2017, 2018) demonstrated—at photopic levels—conditions where local processing dominates (fixed stimulus orientation) and where global processing is critical (random stimulus orientation). We randomly oriented our stimuli in each trial but found no evidence of global processing. However, our tests are scotopic, not photopic, and our stimuli are on a very different spatial scale than those used in photopic tests. Relative to the 0.5° radius stimuli typically presented photopically, our scotopic stimuli are huge, covering an area on the retina up to 256 times larger than the photopic stimuli.

Across the neural population of area V4, there is a stronger representation of acute curvature than obtuse curvature (Carlson, Rasquinha, Zhang, & Connor, 2011). We also know that parts of V4 respond specifically to closed shapes (Dumoulin & Hess, 2007). These two pathways both appear to affect RF radial deformation thresholds under photopic conditions. When curvature information is low, usually because of low RF (and thus low CCF), closed circle detectors may be contributing most strongly to the discrimination. However, when curvature information is high, curvature detectors in V4 may allow observers to discriminate between the smooth and deformed arcs of occluded RF patterns based on local information alone. In our scotopic testing, we were unable to demonstrate the contribution of closed circle detectors and found that for the conditions tested, local processing accounts for observer responses. Whether global processing can be found to exist under scotopic conditions remains to be determined.

Photopic RF patterns have been used in a clinical setting to investigate the effects of various eye diseases, including wet age-related macular degeneration (AMD), geographic atrophy, diabetic retinopathy, and deprivation amblyopia (Jeffrey et al., 2004; Wang et al., 2013; Wang et al., 2002). Elevated thresholds predict disease severity and may be more sensitive measures of disease progression than responses to the Amsler grid or similar tools (Keane et al., 2015; Vazquez & Knox, 2015). Histologic findings from donor AMD eyes show early and preferential loss of rods over cones from early in the disease (Curcio, Medeiros, & Millican, 1996). Scotopic thresholds and dark adaptation recorded across the central retina are correlated with AMD severity but relatively insensitive to early AMD (Flynn, Cukras, & Jeffrey, 2018). Our scotopic stimulus and testing procedure lend themselves to clinical investigations of rods and may provide the means to examine early rod dysfunction in retinal diseases such as AMD.

**Keywords:** scotopic, rods, contour integration, shape discrimination, radial frequency, receptive fields, psychophysics

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