Cortical and behavioral sensitivity to eccentric polar form

Damien J. Mannion

School of Psychology, University of Sydney, NSW, Australia, & Australian Research Council Centre of Excellence in Vision Science, Australia

Colin W. G. Clifford

Smith-Kettlewell Eye Research Institute, San Francisco, CA, USA

Patterns composed of local features aligned relative to polar angle, yielding starbursts, concentric circles, and spirals, can inform the understanding of spatial form perception. Previous studies have shown that starburst and concentric form instantiated in Glass patterns are, relative to spirals, both more readily detected in noise and evoke higher levels of blood-oxygen level-dependent (BOLD) signal, as measured with functional magnetic resonance imaging (fMRI), in the retinotopic cortex. However, such studies have typically presented the polar form at the center of gaze, which confounds the distribution of local orientations relative to fixation with variations in polar form. Here, we measure psychophysical detection thresholds and evoked BOLD signal to Glass patterns of varying polar orientation centered at eccentricity. We find an enhanced behavioral sensitivity to starburst and concentric form, consistent with previous studies. While visual areas V1, V2, V3, V3A/B, and hV4 showed elevated levels of BOLD activity to concentric patterns, V1 and V2 showed little to none of the increased activity to starburst patterns evident in areas V3, V3A/B, and hV4. Such findings demonstrate the anisotropic response of the human visual system to variations in polar form independent of variations in local orientation distributions.

Keywords: spatial vision, visual cortex, space and scene perception, shape and contour, middle vision, functional imaging


Introduction

Stimulation from circumscribed regions of visual space modulates the activity of individual neurons within primary visual cortex (V1). For most V1 neurons, this modulation depends upon the orientation of the stimulation within this local portion of the visual field (Hubel & Wiesel, 1959). With selectivities tiling the combination of visual field and orientation, the population of V1 neurons provides a rich decomposition of the orientation structure of the visual environment. However, our perception of world full of objects and global spatial structure requires subsequent processing and integration of this distributed representation.

Patterns with local orientations defined relative to polar angle can illuminate the processes of global feature integration. Manipulating the angular offset from polar constructs stimuli with particular global form (Glass & Perez, 1973; Mannion, McDonald, & Clifford, 2009, 2010b; Seu & Ferrera, 2001; Wilson & Wilkinson, 1998); coincident polar and local orientation produces starbursts, a 90° difference produces concentric circles, and intermediate differences produces spirals of varying pitch and sense (see Figure 1C). Critically, this manipulation modulates global form while retaining a common overall local orientation distribution (Mannion et al., 2009, 2010b; Seu & Ferrera, 2001; Wilson, Wilkinson, & Asaad, 1997). Hence, investigating the cortical processing of such stimuli can reveal mechanisms sensitive to global spatial structure.

Modulating polar orientation evokes anisotropic levels of blood-oxygen level-dependent (BOLD) signals, as measured with functional magnetic resonance imaging (fMRI), in human visual cortex (Mannion et al., 2010b). Observation of starburst and concentric global form instantiated in Glass patterns (Glass, 1969; Glass & Perez, 1973) produces elevated responses in comparison to spiral global form (Mannion et al., 2010b). Furthermore, concentric form evokes higher levels of activity than starburst (Mannion et al., 2010b). Such a profile of anisotropy accords with psychophysical estimates of observer sensitivity (Badcock & Clifford, 2006; Seu & Ferrera, 2001) and suggests that cortical processing confers a preferential response to starburst and concentric polar form that manifests in an elevated level of neural activity in early visual cortex.

However, previous studies have typically used stimuli in which the center of polar form coincides with the center...
of gaze. This configuration confounds global form with the distribution of local orientations indexed relative to fixation. For example, a starburst pattern is derived from local orientations radial to fixation and concentric circles from local orientations tangential to fixation. The higher levels of BOLD response evoked by local orientations radial to fixation (Clifford, Mannion, & McDonald, 2009; Mannion et al., 2010b; Mannion, McDonald, & Clifford, 2010c; Sasaki et al., 2006; though see Aspell, Wattam-Bell, Atkinson, & Braddick, 2010) make the precise source of the enhanced response to starburst patterns unclear—it may reflect a higher response to the global starburst form, a higher response to the constituent local radial elements, or an aggregate of both.

Here, we balance the distribution of local orientations by presenting polar form centered away from fixation. We characterize the processing of eccentric Glass patterns by measuring both psychophysical detection sensitivity and fMRI BOLD responses from retinotopic human visual cortex to variations in perceived polar form. We decompose the response to modulated polar Glass pattern orientation into two potential anisotropies: an asymmetry between starburst and concentric (Mannion et al., 2010b; Seu & Ferrera, 2001; Wilson & Wilkinson, 1998) and between starburst and concentric relative to spirals (Badcock & Clifford, 2006; Mannion et al., 2010b; Seu & Ferrera, 2001). Overall, the study aims to gauge the cortical and behavioral sensitivity to global form—evident in the

Figure 1. Display arrangement and stimulus demonstration. In both (A) psychophysics and (B) fMRI experiments, Glass patterns were presented at a constant eccentricity at eight locations equidistant in the angular visual field. The fMRI experiment sampled the range of polar Glass pattern orientations shown in (C), while the psychophysics experiment sampled every second column. The perceived spatial form evoked by the Glass patterns are starburst (0°), concentric (90°), and spirals of varying pitch and sense (anti-clockwise/clockwise) at intermediate polar angles. In the psychophysics experiment (A), the target was a Glass pattern of a known polar form at a certain coherence (shown in this example as a starburst pattern of 50% coherence on the right horizontal meridian), while the remaining patterns consisted entirely of noise dipoles. In the fMRI experiment (B), all patterns were of a common polar orientation and presented at full coherence. For clarity of presentation, the mean luminance background and positive and negative polarity dipoles in the experimental stimuli have been replaced by a white background and only negative polarity dipoles.
profile of anisotropy across polar orientation—in the absence of differential distributions of local orientation relative to fixation.

Methods

Subjects

Four subjects (two females) participated in the current study. Each subject completed both psychophysics and fMRI experiments, had normal or corrected-to-normal vision, and gave their informed consent prior to participation. A local ethics committee approved the experiment protocols.

Stimuli

Both psychophysics and fMRI experiments used a common stimulus arrangement, shown in Figures 1A and 1B. Glass patterns were centered at 5.18° eccentricity from fixation at eight locations evenly spaced in angle around the visual field. Each pattern was presented within a circular aperture 3.87° in diameter with 0.11° raised cosine ramped outer edges. Glass patterns were constructed by assigning a random position in the image as the base for each dipole, based on a uniform allocation over area. Dot pairs were then placed equidistant from each base with an inter-dot distance of 0.11° at an angle specified by the desired global shape (see Figure 1C). Each dot had a Gaussian profile (σ = 0.04°) and each dot pair was randomly assigned to be either a full contrast (>95%) increment or decrement from the mean luminance background, with the paired dots always having the same polarity. Stimuli were presented using PsychToolbox 3.0.8 (Brainard, 1997; Pelli, 1997).

Apparatus

Psychophysics

Stimuli were displayed on a 19" monitor (Diamond Digital) with a spatial resolution of 1024 × 768 pixels, temporal resolution of 85 Hz, and mean luminance of 38 cd/m². The monitor output was linearized via a single interpolation of luminance values measured with a SpectraScan PR-655 spectrophotometer (Photo Research, Chatsworth, CA). Subjects viewed the screen from a distance of 167 cm via a mirror mounted on the head coil, giving a viewing angle of 19.0° × 14.3° (1.12' per pixel). A Philips 3T scanner with a whole-head coil was used to conduct the MRI. Functional images were collected using a T₂* sensitive, boustrophedon, whole-brain field-echo echo-planar imaging pulse sequence (TR = 2.5 s, TE = 30 ms, flip angle = 90°, FOV = 240 × 138 × 240 mm, matrix = 80 × 80, voxel size = 3 mm isotropic). Images were acquired in 46 ascending interleaved slices in a tilted axial plane.

Analyses were performed on Matlab 7.8 (The Mathworks, Natick, MA): SPM5 (http://www.fil.ion.ucl.ac.uk/spm) was used for pre-processing and image handling, mrVista (http://white.stanford.edu/software) was used for retinotopic mapping, and custom routines were used for all other analyses.

Design

Psychophysics

A spatial eight-alternative forced-choice task was used to measure the coherence threshold for the detection of a Glass pattern of a given polar orientation (Figure 1A). The stimulus was presented for 658 ms (56 frames) in each trial, with the contrast ramped with a raised cosine profile during the first and last 82 ms (7 frames). The task of the observer was to identify the spatial position of a Glass pattern containing a known polar form. This target location was assigned randomly on each trial, and the remaining patterns were constructed with only random dipole orientations. Each run consisted of 30 trials in which the coherence (proportion of dipoles oriented according to the polar form) of the target Glass pattern was modulated under the Psi adaptive staircase procedure (Kontsevich & Tyler, 1999). A single polar orientation was considered in each run, and four repetitions were completed at each of eight polar orientations (Figure 1C).

fMRI

We used a continuous presentation paradigm (Mannion et al., 2010b, 2010c; Yacoub, Harel, & Ugurbil, 2008) to measure the BOLD response to modulations in Glass pattern polar orientation. Each subject completed eight runs during which the Glass pattern orientation changed with each volume acquisition (2.5 s) in stepwise 11.25° shifts (see Figure 1C). The direction of change alternated between clockwise and anti-clockwise over runs. The pattern was absent (replaced by the mean luminance...
background) in the first and last 250 ms of each volume to prevent transients induced by abrupt changes in orientation, and the pattern was updated with a new instantiation after 1 s. A full orientation cycle was presented in 40 s (16 volumes), and nine complete cycles were completed in each run. To control fixation and attention, subjects performed a behavioral task throughout all runs in which they responded to increments in the luminance of the central fixation dot. Behavioral performance was quantified by the normalized mutual information between task and response and was not significantly different ($p > 0.05$) in temporal windows around the principal polar orientations ($0^\circ$, $45^\circ$, $90^\circ$, and $135^\circ$) across subjects (Supplementary Figure 1).

**Analysis**

**Anisotropy**

Variations in response across Glass pattern polar orientation for both psychophysics (sensitivity) and fMRI (percent signal change) were summarized via the function:

$$R(\theta) = A_1 \cos(2\theta) + A_2 \cos(4\theta) + C,$$

where $\theta$ is the Glass pattern orientation ($0^\circ = \text{starburst}$, $45^\circ = \text{anti-clockwise spiral}$, $90^\circ = \text{concentric}$, and $135^\circ = \text{clockwise spiral}$; see Figure 1C), $R$ is the predicted sensitivity (psychophysics) or percent signal change (fMRI), $A_1$ and $A_2$ are the amplitudes of single and double peak components, and $C$ is a constant representing the mean response across all orientations. This function expresses the response across orientation as the sum of two anisotropies. The first ($A_1$) reflects an asymmetry of starburst relative to concentric polar Glass patterns: a higher response to starburst ($A_1 > 0$) or a higher response to concentric ($A_1 < 0$). The second ($A_2$) reflects an asymmetry of starburst and concentric relative to clockwise and anti-clockwise spirals: a higher response to starburst and concentric ($A_2 > 0$) or a higher response to clockwise and anti-clockwise spirals ($A_2 < 0$).

Fitted parameter values ($A_1$ and $A_2$) were obtained using fminsearch (Matlab) to minimize the sum of the squared errors between function output and measured responses. Confidence intervals for the fitted parameters were estimated from a bootstrapped distribution obtained by sampling subjects with replacement (10,000 iterations). A parameter was deemed statistically significant if its 95% bootstrapped confidence interval did not include zero.

**Psychophysics**

Coherence thresholds were specified as the $\alpha$ parameter in the adaptive staircase, corresponding to $65.6\%$ correct, at the end of each run. Thresholds were averaged across repetitions of each polar orientation and converted to sensitivity values as $1/\bar{\alpha}$.

**fMRI**

Between- and within-run subject movement was corrected and images were resliced using 4th degree B-spline interpolation. After discarding the first half-cycle of each run, a correction of $+2$ volumes (5 s) was applied to compensate for the lag in the hemodynamic response. Time courses from runs in which the polar orientation of the stimulus advanced clockwise were temporally reversed and were then combined with anti-clockwise runs to produce a mean time course for each voxel. The pattern orientation time course was normalized by subtracting and then dividing by the mean voxel response, high-pass filtered (128 s cutoff), and averaged over the nine cycles. For each voxel, this produced a 16-item vector of the evoked response to polar orientation in $11.25^\circ$ increments along the $[0^\circ, 180^\circ]$ interval.

We considered voxels within retinotopically defined visual areas V1, V2, V3, V3A/B, and hV4 (see Mannion et al., 2010c for details of retinotopic mapping and visual area definition procedures). Voxels with a maximum signal change greater than 2 standard deviations above the mean maximum signal change for a given visual area were discarded. The responses from the remaining voxels within a given visual area were then averaged.

**Results**

We measured psychophysical detection thresholds for global form in polar Glass patterns centered away from fixation. As shown in Figure 2, mean sensitivity across subjects (see Supplementary Figure 2 for individual

![Figure 2. Behavioral sensitivity for the detection of spatial form in noise for polar Glass patterns centered away from fixation; mean sensitivity over subjects (points, ±SEM) and fitted sinusoid (line, fill indicates bootstrapped 95% CI of the fitted function). An extra quarter cycle is wrapped at each end (dashed lines).](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932793/ on 11/14/2018)
subject data) was highest for concentric form (2.90, $SE = 0.07$), slightly reduced for starbursts (2.82, $SE = 0.10$), and lowest for anti-clockwise (2.09, $SE = 0.06$) and clockwise (2.16, $SE = 0.10$) spirals. A qualitative appreciation of the visual system’s higher sensitivity to concentric form and starbursts can be obtained by viewing Supplementary Movie 1.

The variation in sensitivity across orientation was well fit by a sum of sinusoids (Equation 1; $F_{2,5} = 71.4, p < 0.001, R^2 = 0.966$) with a significant positive double-peak component ($A_2 = 0.368, CI = [0.283, 0.452]$), reflecting an enhanced sensitivity to starburst and concentric form relative to spirals. While the measured sensitivity to concentric form was slightly higher than to starburst, a negative single-peak component capturing this asymmetry was not significant ($A_1 = -0.010, CI = [-0.121, 0.148]$).

Using a comparable stimulus arrangement, we measured the fMRI BOLD signal to variations in the polar orientation of Glass patterns centered away from fixation. As shown in Figures 3A–3E (see Supplementary Figure 3 for individual subject data), the mean response across subjects was greatest in all the visual areas (V1, V2, V3, V3A/B, and hV4) during observation of concentric Glass patterns. Starbursts tended to evoke similar levels of

Figure 3. Response of the retinotopic visual areas to the polar orientation of Glass patterns centered away from fixation. (A–E) Mean percent signal change (points, ±SEM) and fitted sinusoid (line, fill indicates bootstrapped 95% CI of the fitted function) from V1, V2, V3, V3A/B, and hV4. An extra quarter cycle is wrapped at each end (dashed lines). (F) Amplitudes of fitted two-component sinusoid for each visual area, with $A_1$ (anisotropy between starburst and concentric orientation) on the horizontal axis and $A_2$ (anisotropy of starburst and concentric relative to spirals) on the vertical axis. Ellipses show bootstrapped 95% CI of the fitted function parameters.
activity to spirals in V1 and V2 and increased in magnitude relative to spirals in V3, V3A/B, and hV4 while remaining below that evoked by concentric form. Such anisotropies were not evident in the foveal region of visual cortex, unstimulated by the Glass patterns, which showed little modulation in activity to the polar Glass pattern orientation (Supplementary Figure 4).

The variation in BOLD response across polar Glass pattern orientation was well fit by a sum of sinusoids (Equation 1) in each visual area (all \( p < 0.05 \); Table 1). Each area showed a significant negative single-peak component \( (A_1) \), indicative of the greater magnitude of BOLD signal evoked by concentric relative to starburst patterns. The double-peaked component \( (A_2) \) was weakly positive in V1 and non-significant in V2, suggesting that an anisotropy of starburst and concentric patterns relative to spirals is minimal in the earliest levels of the retinotopic cortex. This double-peaked component was significant and positive in V3, V3A/B, and hV4, signaling a higher response to starburst and concentric form relative to spirals. While the amplitude of the double-peaked component was smaller than the single-peaked component in V3 and V3A/B, they were of comparable magnitude in hV4. In summary (Figure 3F), each visual area showed elevated levels of BOLD activity to concentric relative to starburst Glass patterns \( (A_1 < 0) \), while areas V3, V3A/B, and hV4 (and weakly in V1) also showed increases for concentric and starburst patterns relative to spirals \( (A_2 > 0) \).

<table>
<thead>
<tr>
<th>Area</th>
<th>( F_{2,13} )</th>
<th>( p )</th>
<th>( R^2 )</th>
<th>( A_1 ) (95% CI)</th>
<th>( A_2 ) (95% CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>V1</td>
<td>9.15</td>
<td>0.003</td>
<td>0.585</td>
<td>(-0.031 (-0.044, -0.018))</td>
<td>(+0.014 (+0.001, +0.024))</td>
</tr>
<tr>
<td>V2</td>
<td>5.95</td>
<td>0.015</td>
<td>0.478</td>
<td>(-0.029 (-0.045, -0.012))</td>
<td>(+0.003 (-0.014, +0.019))</td>
</tr>
<tr>
<td>V3</td>
<td>31.1</td>
<td>&lt;0.001</td>
<td>0.827</td>
<td>(-0.052 (-0.078, -0.038))</td>
<td>(+0.028 (+0.021, +0.035))</td>
</tr>
<tr>
<td>V3A/B</td>
<td>21.8</td>
<td>&lt;0.001</td>
<td>0.770</td>
<td>(-0.051 (-0.083, -0.025))</td>
<td>(+0.028 (+0.014, +0.051))</td>
</tr>
<tr>
<td>hV4</td>
<td>22.5</td>
<td>&lt;0.001</td>
<td>0.776</td>
<td>(-0.038 (-0.061, -0.016))</td>
<td>(+0.037 (+0.023, +0.049))</td>
</tr>
</tbody>
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Table 1. Two-component sinusoid fit quality and estimated amplitude parameters, with bootstrapped confidence intervals, for each visual area.

Observers more readily detected global structure from noise for starburst and concentric polar form relative to spirals. This anisotropy to eccentric form accords with previous reports obtained with patterns centered at fixation (Achtman, Hess, & Wang, 2003; Badcock & Clifford, 2006; Dickinson & Badcock, 2007; Seu & Ferrera, 2001; though see Webb, Roach, & Peirce, 2008, for equivocal findings). This similarity suggests that anisotropies in the local orientation distribution relative to fixation have a minimal contribution to determining behavioral sensitivity to global form. Previous studies have also often reported a further anisotropy for concentric relative to starburst patterns in noise detection thresholds (Achtman et al., 2003; Seu & Ferrera, 2001; Wilson & Wilkinson, 1998). Here, the small difference in sensitivity between concentric and starburst patterns followed this direction but did not reach statistical significance.

Visual areas V1 and V2 both responded unequally to the modulations in the polar form of Glass patterns centered eccentrically, showing an enhanced response to patterns containing concentric global structure. This anisotropy agrees with the previously reported peaked response to modulations of polar form at concentric orientations (Mannion et al., 2010b). However, the response of V1 and V2 showed little to no sign of the additional peak to starburst form reported by Mannion et al. (2010b). This difference suggests that anisotropies in the local orientation structure relative to fixation—the radial bias (Clifford et al., 2009; Mannion et al., 2010b, 2010c; Sasaki et al., 2006)—may have contributed to previous reports of an enhanced response to starburst patterns in V1 and V2 when centered at fixation (Mannion et al., 2010b).

A view of the earliest levels of the cortical visual system as comprising neurons selective for the straight-line Cartesian orientation of local stimulation conflicts with the observed anisotropy to polar form in V1 and V2 in which concentric form evokes elevated responses. Feedback from higher visual areas possessing more complex orientation selectivity could potentially explain the anisotropic response to polar form in V1 and V2 (Ban et al., 2006). Alternatively, neurons in early visual cortex may themselves encode more complex stimulus features. Indeed, neurophysiological recordings have reported preferences for polar orientation in V1 and V2 neurons and an overrepresentation of neurons preferring concentric...
orientations (Hegdé & Van Essen, 2007; Mahon & De Valois, 2001). However, Smith, Kohn, and Movshon (2007) found no modulation in activity by polar Glass pattern orientation in V2 neurons, and previous neuroimaging studies have not found differences in polar form response in V1 and V2 (Wilkinson et al., 2000), including to stimuli presented at eccentricity (Swettenham, Anderson, & Thai, 2010). Hence, the role of V1 and V2 in polar form processing remains uncertain.

Beyond V2, elevations in response to patterns containing starburst form emerge to join the response peaks at concentric orientations. This anisotropy concurs with the findings of Mannion et al. (2010b) to stimuli centered at fixation and with previous reports of global form selectivity with ascension of the visual hierarchy (Dumoulin & Hess, 2007; Ohla, Busch, Dahlem, & Herrmann, 2005; Ostwald, Lam, Li, & Kourtzi, 2008; Pei, Pettet, Vildavski, & Norcia, 2005; Wilkinson et al., 2000). However, the enhanced activity to concentric patterns in V3A/B conflicts with the findings of Mannion et al. (2010b), who reported an anisotropy only for starburst patterns. Changes in anisotropic response in V3A/B to polar form centered at eccentricity could underlie this difference, although Swettenham et al. (2010) reported qualitatively similar magnitudes of response in V3A/B during observation of starburst and concentric Glass patterns centered at fixation and at eccentricity.

Although the anisotropy in higher visual areas resembles the enhanced behavioral sensitivity to starburst and concentric patterns observed psychophysically, the asymmetry between the BOLD response to starburst and concentric patterns appears much greater than is evident in behavior. Stimulus coherence could potentially explain this conflict; the small asymmetry evident in behavioral sensitivity at low coherences may expand to the larger differences observed here in the fMRI BOLD response to high stimulus coherence. Future studies measuring behavioral detection sensitivity for a range of pedestal stimulus coherences may be instructive in clarifying this discrepancy. Alternatively, higher cortical areas may further shape the anisotropy observed in hV4 and V3A/B to yield an anisotropy commensurate with that in behavioral sensitivity.

Viewing concentric Glass patterns evoked the highest levels of BOLD response, across variations in polar orientation, in each of the retinotopic visual areas V1, V2, V3, V3A/B, and hV4. Efficient coding theories posit that cortical processing is tailored to the properties of the natural environment (Barlow, 1961; Simoncelli & Olshausen, 2001), which contains an overrepresentation of smooth, closed contours such as circles (Chow, Jin, & Treves, 2002; Geisler, Perry, Super, & Gallogly, 2001; Sigman, Cecchi, Gilbert, & Magnasco, 2001). This relationship between BOLD activity and visual ecology suggests that visual cortex enhances the response to the most prevalent polar orientation structure of natural visual environments. However, we have previously argued that an efficient coding strategy would manifest as a reduction of the BOLD response to the most prevalent input configuration (Mannion, McDonald, & Clifford, 2010a; Mannion et al., 2010c), as the BOLD signal reflects energy expenditure (Logothetis & Wandell, 2004) that is likely to be minimized in the response of an efficient code to the most frequently encountered input (Baddeley, 1996). The apparent departure from such a scheme reported here may indicate that the visual system responds to the considerable orientation noise of Glass patterns by adopting an alternative strategy, such as sharpening the response to the most likely stimulus configuration (Murray, Schrater, & Kersten, 2004), which may be clarified in future studies by using simpler stimuli such as polar gratings. Alternatively, the utility of concentric orientations in the processing of ecologically relevant stimuli such as faces (Wilson, 1999) may merit an enhanced neural response. While the precise role of the natural environment remains uncertain, continued research relating anisotropies in the structure of natural visual environments to neural population coding (Ganguli & Simoncelli, 2010), cortical response, and behavioral sensitivity can illuminate the coding strategies of the visual system.

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Corresponding author: Damien J. Mannion.
Email: damien@ski.org.
Address: 2318 Fillmore St., San Francisco, CA 94115, USA.

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