Radial Biases in the Processing of Motion and Motion-Defined Contours by Human Visual Cortex

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Clifford CWG, Mannion DJ, McDonald JS. Radial biases in the processing of motion and motion-defined contours by human visual cortex. J Neurophysiol 102: 2974–2981, 2009. First published September 16, 2009; doi:10.1152/jn.00411.2009. Luminance gratings reportedly produce a stronger functional magnetic resonance imaging (fMRI) blood oxygen level–dependent (BOLD) signal in those parts of the retinotopic cortical maps where they are oriented radially to the point of fixation. We sought to extend this finding by examining anisotropies in the response of cortical areas V1–V3 to motion-defined contour stimuli. fMRI at 3 Tesla was used to measure the BOLD signal in the visual cortex of six human subjects. Stimuli were composed of strips of spatial white noise texture presented in an annular window. The texture in alternate strips moved in opposite directions (left–right or up–down). The strips themselves were static and tilted 45° left or right from vertical. Comparison with maps of the visual field obtained from phase-encoded retinotopic analysis revealed systematic patterns of radial bias. For motion, a stronger response to horizontal was evident within V1 and along the borders between V2 and V3. For orientation, the response to leftward tilted contours was greater in left dorsal and right ventral V1–V3. Radial bias for the orientation of motion-defined contours analogous to that reported previously for luminance gratings could reflect cue-invariant processing or the operation of distinct mechanisms subject to similar anisotropies in orientation tuning. Radial bias for motion might be related to the phenomenon of “motion streaks,” whereby temporal integration by the visual system introduces oriented blur along the axis of motion. We speculate that the observed forms of radial bias reflect a common underlying anisotropy in the representation of spatiotemporal image structure across the visual field.

INTRODUCTION

The receptive fields of neurons in early areas of visual cortex are organized into retinotopic maps of the visual field such that nearby neurons tend to respond to nearby regions of the retinal image (van Essen and Zeki 1978). A fundamental feature of these neurons is selectivity for attributes such as local orientation structure and direction-of-motion (Hubel and Wiesel 1962). Recently, it has been demonstrated that the representation of orientation in the early visual areas of human and nonhuman primates displays a systematic bias across the visual field such that grating stimuli generate greater functional magnetic resonance imaging (fMRI) blood oxygen level–dependent (BOLD) response in representations of the visual field where they are oriented radial to the point of fixation (Sasaki et al. 2006). This correlation between retinotopic preference and orientation preference is evident across retinotopic visual cortex as a greater response to vertical gratings along the representation of the vertical meridian, a greater response to horizontal gratings along the representation of the horizontal meridian, and a greater response to oblique gratings along the representation of the corresponding oblique meridian. This neurophysiological radial bias for orientation has a psychophysical correlate in that human observers show greatest contrast sensitivity to radial orientations (Rovamo et al. 1982; Sasaki et al. 2006).

Radial orientation bias in the BOLD response likely results from a disproportionate number of neurons being tuned to radial orientations (Bauer and Dow 1989; Durand et al. 2007). The bias in cortex might have its origin in retina (Levick and Thibos 1982) where ganglion cell receptive fields tend to be slightly elongated radially, possibly due to the fact that such cells are added radially during eye growth (Leventhal and Schall 1983). From a functional perspective, it has been argued that peripheral neurons with radially oriented receptive fields are particularly well suited to encode horizontal and vertical disparity for control of binocular fixation (Durand et al. 2007).

Analogous to radial orientation bias, single-cell studies in macaque have reported radial bias for the direction of visual motion in the middle temporal (MT) area (Albright 1989), the frontal eye fields (Xiao et al. 2006), and posterior parietal cortex (Steinmetz et al. 1987). However, direct evidence of radial motion bias in early visual areas remains equivocal. Kamitani and Tong (2006) found no clear pattern of global direction selectivity in human retinotopic cortex using fMRI. In contrast, Raemaekers et al. (2009) reported significant directional anisotropy in the BOLD response from areas V1–V3.

Here, we investigate the existence of radial biases in retinotopic visual cortex for: 1) the motion of unoriented textures and 2) the orientation of contours defined solely by the borders between strips of texture moving in opposite directions. The extraction of such motion-defined contours (sometimes termed “static kinetic boundaries”) from the image signal necessarily involves some form of nonlinear processing distinct from the linear operations sufficient to recover orientation defined by variations in luminance. Thus it is an open question whether the early visual areas will show a radial bias for the orientation of this class of stimulus.

METHODS

Subjects

Six experienced psychophysical observers, with normal or corrected-to-normal vision, participated in the current study: four males and two females, ranging in age from 24 to 41 yr. Subjects gave their informed consent and the protocol was approved by a local ethics committee.
Apparatus

A Philips 3-T scanner with a whole-head coil was used to conduct the MRI. Anatomical images, collected using a turbo field-echo protocol for enhanced gray–white contrast, consisted of whole-head scans in the axial and sagittal planes (voxel size = 1 mm isotropic) and a high-resolution partial head coronal scan (voxel size = 0.75 mm isotropic) to recover maximum detail in the occipital lobes. Functional images were collected using a T2*-sensitive, boustrophedon, field-echo echo planar imaging pulse sequence (repetition time = 3 s, time to echo = 30 ms, flip angle = 90°, field of view = 70.5 × 192 × 192 mm, matrix = 128 × 128, voxel size = 1.5 mm isotropic). Images were acquired in 47 ascending interleaved slices in the coronal plane covering the occipital lobes.

Stimuli were projected onto a screen positioned behind the bore using a Dell 5100MP projector with a display resolution of 1,024 × 768 pixels. Subjects viewed the screen from a distance of 167 cm via a mirror mounted on the headcoil, resulting in a viewing angle of 19.5 × 13.9°. Stimuli were presented using PsychToolbox 3.0.8 (Brainard 1997; Pelli 1997). Behavioral responses were indicated via a LU400-PAIR Lumina response pad (Cedrus, San Pedro, CA).

Except where otherwise specified, analyses were performed using SPM5 (http://www.fil.ion.ucl.ac.uk/spm) on Matlab 7.5 (The Math-Works, Natick, MA).

Stimuli

Stimuli were composed of 0.6° strips of spatial white noise texture with a check size of one pixel (1.1 min of arc) presented in an annulus 1–6° in radius surrounding a central fixation dot. The texture in alternate strips moved in opposite directions (left–right or up–down) at a speed of 3°/s. The strips themselves were static and tilted 45° either left or right from vertical. Pairing of the two strip orientations with the two texture motions was balanced across the four types of stimulus block (Fig. 1).

Design

Subjects observed 12 runs each of 315-s duration (105 volumes) of the experimental protocol. There were 21 blocks of 15 s in each run, four blocks of each of the four stimulus configurations, and five blank fixation periods. The blocks were ordered in a balanced design (each block type occurred an equal number of times before every other block type) and the first, last, and every fifth block were blank fixation periods. The spatial phase of the strips in each stimulus configuration was counterbalanced across blocks between four equally spaced values. To control fixation and attention, subjects performed a dimming task throughout each run, in which they responded to increments and decrements in the luminance of the central fixation dot.

fMRI acquisition and preprocessing

A mean anatomical image was formed for each subject by combining the axial and sagittal whole-head scans and the coronal partial-head scan. Before averaging, each anatomical image was inhomogeneity corrected (Manjón et al. 2007), coregistered, and resampled to a voxel resolution of 0.75 mm (isotropic) where necessary. Each subject’s mean anatomical was then segmented using the automatic routines of mrGray (Teo et al. 1997) and ITKGray (Yushkevich et al. 2006; http://white.stanford.edu/software) followed by careful hand editing.

Functional images were corrected for differences in slice timing with reference to the middle slice. Between- and within-run subject movements were estimated and corrected by applying the movement parameters and reslicing using fourth-degree B-spline interpolation.
The images were also placed into register with the world space of the subject’s mean anatomical by applying coregistration parameters to each image’s affine transformation matrix.

Region of interest (ROI) definition

In a separate scanning session, subjects completed standard protocols suitable for defining the early retinotopic regions of visual cortex during which they were presented with rotating wedge and expanding ring stimuli (Engel et al. 1997; Wandell et al. 2007). The functional data from this session were transformed onto a flattened representation of the cortical surface using mrVista (http://white.stanford.edu/software) to aid in the delineation of the borders between visual areas. Areas V1, V2, and V3 were defined manually based on the phase of the responses of each voxel with reference to canonical data from fMRI of human visual cortex (Larsson and Heeger 2006). It should be noted that our area V3 includes both dorsal V3 and its ventral counterpart, sometimes termed VP (e.g., Pitzalis et al. 2006). The mask defining each retinotopic area was transformed from the flat-map into the space of the subject’s anatomical, smoothed (full width at half-maximum = 1.5 mm), and resliced to the resolution of the functional images using fourth-degree B-spline interpolation. The voxels within each ROI contained a mask value that reflected the cumulative influence of such transformations. To prevent overlapping voxels between adjacent ROIs, each voxel was assigned to the ROI for which it possessed the greatest mask value.

Analysis

Functional data from the experimental runs were analyzed voxel by voxel in SPM5 using a general linear model. Responses to the different types of stimulus block were compared in two different contrasts. Collapsing responses over the orientation of the motion-defined contours, we performed a contrast between the response to horizontal and vertical motion to examine the representation of motion across the cortical surface. Collapsing over texture motion, we performed a contrast between leftward and rightward tilt to reveal the representation of contour orientation. The qualitative patterns of data that would be produced by radial biases for direction-of-motion and the orientation of motion-defined contours are illustrated in Figs. 2 and 3, respectively.

To enable a quantitative comparison of radial bias across visual areas and to establish a significant trend across subjects we computed a Radial Bias Index. Analysis was restricted to those voxels significant (P < 0.05, uncorrected) in a contrast of their response to all stimulus blocks versus fixation. We computed a Radial Bias Index for motion from the voxel-by-voxel bias toward horizontal or vertical motion (i.e., the signed magnitude of the contrast t-statistic). For each visual area, voxels were then binned according to their preferred meridian angle obtained from the phase of their response to the rotating wedge stimulus (Engel et al. 1997). For each bin, a bias was computed as the sum of the signed magnitudes of the t-statistics of all the voxels in that bin divided by the sum of their absolute values. If all voxels in a given bin showed a bias toward horizontal (vertical) then the bias of that bin would be +1 (−1). Finally, to compute a single value of Radial Bias Index for each visual area, a sinusoid was fitted to the binned bias values as a function of the meridian angle of the bin to quantify the degree to which the observed pattern of data corresponded to the predictions illustrated in Figs. 2 and 3. For each area, for each subject, a sinusoid was fitted with two free parameters (amplitude and mean level). The phase of the sinusoid was fixed such that its maximum amplitude coincided with the meridian angle at which the motion of the textures was radial, allowing for a lag of 4 s in the hemodynamic response. The value of the Radial Bias Index was taken to be the amplitude of the fitted sinusoid. It should be noted that fixing the phase of the sinusoid did not introduce an artificial bias into the estimate of the index because the amplitude could be either positive or negative in sign, so fitting to random data would give an expected Radial Bias Index of zero.

An analogous procedure was followed to compute a Radial Bias Index for the orientation of motion-defined contours.

Results

Mapping radial bias

A systematic pattern of bias across the cortical surface was evident in response to the axis of motion of the textures when data

![Image](https://www.jn.org)
were pooled across the orientation of the motion-defined contours (Fig. 4C). Coregistration of maps of differential activation with retinotopic maps obtained from phase-encoded analysis (Fig. 4A) revealed that representations of the vertical (horizontal) meridian tended to respond more strongly to vertical (horizontal) motion. Specifically, a bias for horizontal motion was evident within V1 and along the borders between V2 and V3; a bias for vertical motion was apparent along the borders between V1 and V2 and at the extremes of V3, consistent with the predicted radial bias for motion (Fig. 2).

Pooling data across the axis of motion of the textures revealed a different pattern of bias: the response to a given orientation was stronger in the quadrants of the visual field for which contour orientation was predominantly radial. Specifically, the response to leftward (rightward) tilted gratings...
tended to be stronger in the dorsal part of the left (right) visual cortex and the ventral part of the right (left) visual cortex (Fig. 4D), as predicted in Fig. 3.

A further experiment was run on subject CC with oblique directions of motion and horizontal and vertical contour orientations. The pattern of data once again indicated radial biases both for direction-of-motion and for the orientation of motion-defined contours (Supplemental Fig. S1).1

Quantifying radial bias

The results of a quantitative analysis of the variation in the proportion of voxels preferring a particular axis of motion as a function of the meridian angle of the visual field representation (in 10° bins) across both hemispheres are shown for one subject in Fig. 5A. Results of the analysis of motion-defined contour orientation for the same subject are shown in Fig. 5B.

To compare radial bias across visual areas and to establish a significant trend across subjects we computed a set of Radial Bias Indices as described earlier in METHODS, Analysis. Across subjects, this analysis revealed radial biases for motion and for the orientation of motion-defined contours each significant at \( P < 0.01 \) (one-sample \( t \)(5), two-tailed) in areas V1–V3 (Fig. 6).

Individual subject data are given in Table 1.

The data in Fig. 6B indicate a larger radial bias for motion-defined contour orientation in areas V2 and V3 than that in primary visual cortex. Post hoc comparison of the average of each subject’s radial bias index from areas V2 and V3 with the magnitude of their index from V1 revealed a significant increase in radial bias beyond V1 (paired \( t \)(5) = 3.99, \( P = 0.010 \), two-tailed).

1 The online version of this article contains supplemental data.

DISCUSSION

We have shown radial bias in areas V1–V3 of human visual cortex, both for motion and for the orientation of motion-defined contours. In the following text, we discuss the implications for understanding the processing of motion and motion-defined contours, the possible role of higher-level influences on the observed pattern of data, and the study of orientation and motion coding using multivariate pattern classification.

Recovering the orientation of motion-defined contours

Our finding of a bias in the response of areas V1–V3 to motion-defined contours extends the generality of a previous report of radial bias for the orientation of luminance gratings in the retinotopic areas of human and macaque visual cortex (Sasaki et al. 2006). The existence of analogous biases for luminance- and motion-defined stimuli is consistent with the operation of cue-invariant mechanisms. However, it is equally consistent with processing by distinct but spatially overlapping neuronal populations subject to similar anisotropies in orientation tuning. If it is indeed the case that different mechanisms are involved then it appears that they are subject to similar constraints on function and/or development.

Although the processing of motion-defined contours has been taken as a signature of the kinetic occipital region of human visual cortex (Dupont et al. 1997; Van Oostende et al. 1997; although see also Tyler et al. 2006; Zeki et al. 2003), responses to motion-defined contours have been observed as early as V1 (Lamme et al. 1993, 1994; Marcar et al. 2000; Reppas et al. 1997). However, response to motion-defined
contours does not necessarily indicate coding of their orientation. Indeed, evidence from single-cell recordings indicates that neurons in V1 and V2 differ greatly in their orientation selectivity for such stimuli (Marcar et al. 2000). The current data show that patterns of BOLD activation to motion-defined contours do in fact depend systematically on their orientation as early as V1. However, the radial bias reported here for the orientation of motion-defined contours is significantly greater in areas V2 and V3 than that in V1, consistent with the single-cell data of Marcar et al. (2000). This pattern of results suggests important roles for both V1 and V2 in extracting the orientation of motion-defined contours.

Radial bias for motion

The results in Fig. 6A show a radial bias for the motion of unoriented textures that is significant across subjects in each of areas V1–V3. It would be tempting to suggest that this radial bias for motion is a “new” form of radial bias, distinct from radial bias for orientation. However, it is possible that much of the observed radial bias for motion is actually due to oriented rather than properly directional energy within the stimulus. Low-pass temporal filtering of the stimulus image sequence introduces oriented blur, or “motion streaks” (Geisler 1999). Thus radial bias in the response of temporally low-pass spatially oriented filters could in principle be sufficient to account for the pattern of bias between horizontal and vertical motion that we observe across retinotopic visual cortex.

The data of Raemaekers et al. (2009) show systematic differences in the responses to centripetal and centrifugal motion (both of which are stronger than that for tangential motion). Such biases between opposite directions of motion cannot be explained by the response of temporally low-pass filters since opposite directions of motion produce streaks with the same orientation. Instead, they suggest a bias in the responses of temporally band-pass filters processing directional motion proper rather than oriented motion blur.

Another aspect of the data from Raemaekers et al. (2009) deserves comment in light of the current study. They found that interrupting their motion stimulus with uniform gray bars orthogonal to the direction of motion appeared to nullify radial bias in areas V1–V3. They interpreted this result as evidence that extraclassical receptive field effects were mediating radial motion bias. However, the current data suggest an alternative and arguably more parsimonious interpretation of those findings. By dividing their stimulus into strips, Raemaekers et al. (2009) introduced oriented contours into their display. Although there was no difference in mean luminance between the moving texture on one side of each contour and the gray bar on the other, the present study has shown that contours defined by cues other than luminance differences can still produce a radial bias. Thus we suggest that the response measured by Raemaekers et al. (2009) in fact represented the superposition of a motion response and an orientation response, both of which were subject to radial bias. In the case where the orientation of the strips was orthogonal to the direction of motion these effects would tend to nullify one another, resulting in little or no net anisotropy in the response across the visual field.

Possible higher-level influences

Recurrent processing appears to be a fundamental characteristic of the way brains operate (Salin and Bullier 1995).

TABLE 1. Radial bias indices by subject and visual area

<table>
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<th>CC</th>
<th>EG</th>
<th>SM</th>
<th>DM</th>
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<th>TF</th>
<th>Mean</th>
<th>SE</th>
<th>t(5)</th>
<th>P</th>
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<td>Motion</td>
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<tr>
<td>V1</td>
<td>0.481</td>
<td>0.327</td>
<td>0.104</td>
<td>0.573</td>
<td>0.387</td>
<td>0.262</td>
<td>0.356</td>
<td>0.067</td>
<td>5.27</td>
<td>0.0033</td>
</tr>
<tr>
<td>V2</td>
<td>0.635</td>
<td>0.355</td>
<td>0.129</td>
<td>0.671</td>
<td>0.385</td>
<td>0.307</td>
<td>0.414</td>
<td>0.084</td>
<td>4.92</td>
<td>0.0044</td>
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<tr>
<td>V3</td>
<td>0.497</td>
<td>0.260</td>
<td>0.065</td>
<td>0.369</td>
<td>0.274</td>
<td>0.270</td>
<td>0.289</td>
<td>0.058</td>
<td>4.98</td>
<td>0.0042</td>
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<td>Orientation</td>
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<td></td>
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<tr>
<td>V1</td>
<td>0.602</td>
<td>0.183</td>
<td>0.478</td>
<td>0.237</td>
<td>0.249</td>
<td>0.333</td>
<td>0.347</td>
<td>0.066</td>
<td>5.25</td>
<td>0.0033</td>
</tr>
<tr>
<td>V2</td>
<td>0.854</td>
<td>0.385</td>
<td>0.605</td>
<td>0.325</td>
<td>0.257</td>
<td>0.427</td>
<td>0.476</td>
<td>0.090</td>
<td>5.31</td>
<td>0.0032</td>
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<tr>
<td>V3</td>
<td>0.830</td>
<td>0.338</td>
<td>0.642</td>
<td>0.619</td>
<td>0.371</td>
<td>0.275</td>
<td>0.513</td>
<td>0.089</td>
<td>5.78</td>
<td>0.0022</td>
</tr>
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</table>
However, the temporal resolution of the fMRI BOLD signal is insufficient to discriminate feedforward and feedback activation. Furthermore, the BOLD signal probably reflects not only neuronal spiking within a region but also the synaptic input to that region (Logothetis et al. 2001). Thus we must consider the possibility that the radial bias we observe has its origin in top-down rather than bottom-up neural signals.

For feedback to produce systematic patterns of radial bias across the cortical surface it must be targeted in some way. For example, feedback from orientation-selective neurons might target similarly tuned cells. In this case, the pattern of bias in the target region would reflect spatial anisotropies in orientation tuning at this earlier level of processing. Another possibility is that feedback selects its targets on the basis of location within the retinotopic map rather than feature selectivity (Bullier et al. 1988). In this case, the pattern of spatial bias in the target region would mirror that at the higher level of processing. Of course, these two forms of targeting are not mutually exclusive. In combination they might serve to amplify one another to produce the large radial biases observed here and by Sasaki et al. (2006).

Top-down modulation is known to affect cerebral blood flow through feature- and space-based attention (Corbetta et al. 1990; Gandhi et al. 1999; Martínez et al. 1999; Somers et al. 1999). It is possible, for example, that the greater BOLD response observed in V1 to stimuli containing motion-defined contours than that to uniform translational motion (Reppas et al. 1997) might simply reflect the allocation of attention to the contours. However, attentional modulation is unlikely to explain the pattern of data observed in the current study for the following reasons. First, subjects were performing a dimming task at fixation throughout the scans, diverting attentional resources away from the stimulus. Second, the patterns of radial bias for orientation and motion were extracted from the same set of data. For feature-based attentional modulation to produce both patterns of bias subjects would have to divide or alternate their attention between the motion of the textures and the orientation of the contours. Third, the spatial patterns of bias across the cortical surface did not reflect the location of features within the visual field (e.g., on the rightward oblique meridian) or the feature itself (e.g., rightward tilt) but a conjunction of the feature and its position (e.g., radial orientation).

For attentional modulation to produce such a specific pattern of results there would need to be a spatially structured pattern of interaction between feature- and space-based attention. However, we note that neural integration of spatial and feature-based information has recently been demonstrated in the context of visual search in areas including the intraparietal sulcus (Egner et al. 2008). Thus it is possible that the attention could, at least in principle, produce complex patterns of modulation in early visual areas.

**Implications for studies using multivariate pattern classification**

Several recent studies of orientation and motion coding have used techniques based on multivariate pattern classification in their analyses (Haynes and Rees 2005; Kamitani and Tong 2005, 2006; Serences and Boynton 2007a,b; Sumner et al. 2008). The rationale for using such techniques is their sensitivity to subtle patterns of variation in the data that cannot be recovered by univariate statistical analysis performed at the level either of single voxels or of functionally defined regions of interest. One way in which classifiers might extract information is by exploiting subtle biases in the way that spatial maps of neuronal orientation and direction preference are sampled at the level of individual voxels (e.g., Boynton 2005), although this issue remains contentious (Kamitani and Sawahata 2009; Op de Beeck 2009).

Optical imaging in macaque indicates that areas V1–V3 are organized into domains of neurons with similar orientation preference. The spatial scale over which these cortical feature maps are organized is of the order of a few hundred microns (Vanduffel et al. 2002). High-resolution fMRI indicates that the spacing between orientation columns in human primary visual cortex is of the order of 1.6 mm (Yacoub et al. 2008), comparable with the size of a voxel in a typical fMRI study (here cubic, side 1.5 mm). Thus it is likely that any given voxel will sample a biased distribution of orientation-tuned neurons. Multivariate pattern classification across a region will then exploit these voxelwise biases to recover information on the orientation of the stimulus.

The radial bias we have observed is evident at a spatial scale intermediate between single voxels and whole visual areas. In the presence of such systematic patterns of bias across the visual field, the value of using multivariate pattern classification is questionable. However, radial bias can be avoided by the use of stimuli matched everywhere for their radial components. Examples of such stimulus pairs are opposite rotational motions or spiral forms of opposite sense. Studies using these types of stimuli have confirmed that the effects of radial bias are not necessary for successful classification of motion (Kamitani and Tong 2006; Seymour et al. 2009) and orientation (Mannion et al. 2009) in early visual areas.

**Conclusion**

We have demonstrated that the phenomenon of radial bias (Sasaki et al. 2006) is not peculiar to orientation defined by variations in luminance. Specifically, we observed radial bias in the fMRI BOLD response of areas V1–V3 of human visual cortex to the direction-of-motion of unoriented textures and to the orientation of motion-defined contours. Thus not only is there an anisotropy in the way that all of these attributes are represented across the visual field but the qualitative form of that anisotropy is same. This is consistent with two mechanistic interpretations that need not be mutually exclusive. One possibility is that radial bias reflects processing by a common mechanism sensitive to orientation defined by luminance, to the orientation of motion trajectories, and to the orientation of motion-defined contours. A second possibility is processing by distinct mechanisms each exhibiting a common anisotropy in the representation of image structure across the visual field. Future work could profitably be directed to distinguishing between these accounts of radial bias.

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