Orientation Anisotropies in Human Visual Cortex

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INTRODUCTION

The spatial arrangement of the visual image contains important information about the external environment. Previous functional MRI (fMRI) research has yielded differing accounts of how the activity in human visual cortex is modulated by the orientation of such spatial structure. The distribution of response magnitude for varied stimulus orientation has been reported to be anisotropic in V1 (Furmanski and Engel 2000; Furmanski et al. 2004; Swisher et al. 2010), anisotropic also in ventral retinotopic regions (Serences et al. 2009), or isotropic (Kamitani and Tong 2005; Yacoub et al. 2008). When present, the anisotropy has taken the form of either an increased response to horizontal and vertical orientations (Furmanski and Engel 2000; Furmanski et al. 2004), oblique orientations (Swisher et al. 2010), or an orientation intermediate to the cardinal and primary oblique orientations (Serences et al. 2009). Hence, the nature of the distribution of fMRI responses to varying stimulus orientation remains equivocal.

Although such studies considered pattern orientation independent of position in the visual field, anisotropic response distributions have been reported across the early human visual system when pattern orientation is specified relative to the local visual field meridian (Fig. 1). Specifically, responses are enhanced when the local pattern orientation is coincident with the angular meridian (radial) compared with when it is tangential (Clifford et al. 2009; Sasaki et al. 2006). An important consequence of this meridian-relative anisotropy is that it confers difficulties in the interpretation of putative anisotropies in field-independent pattern orientation, particularly when the stimulus (Furmanski and Engel 2000; Furmanski et al. 2004) or analysis (Serences et al. 2009; Yacoub et al. 2008) is restricted to a subregion of the visual field. In this circumstance, inferences about anisotropies in field-independent orientation can be confounded with those in meridian-relative orientation; for example, a stimulus restricted to the vertical visual field meridian will produce responses in which only the vertical field-independent orientation is also a radial meridian-relative orientation.

The aim of this study was to measure the distribution of visual system responses to varied pattern orientation by considering both field-independent and meridian-relative indices. We used fMRI to measure the blood-oxygen level-dependent (BOLD) response to a sinusoidal grating that varied in orientation and to map the preferred visual field meridia from within the early retinotopic regions of human visual cortex. We report the presence of significant anisotropies to both field-independent and meridian-relative orientation from within visual areas V1, V2, V3, and V3A/B. Although the form of meridian-relative anisotropy is consistent with previous reports of a preference for radial orientations, the anisotropy in field-independent orientation is characterized by a reduced response to horizontal orientations.

METHODS

Subjects

Four experienced psychophysical observers participated in this study. Each subject received a recent optometric examination, and all subjects, including those with clinically normal vision, wore customized corrective goggles during the experiment. Subjects gave their informed consent, and the protocol was approved by a local ethics committee.

Apparatus

A Philips 3T scanner with a whole head coil was used to conduct the MRI. Functional images were collected using a T2* sensitive, boustrophedon, field-echo-planar imaging pulse sequence (TR = 3 s, TE = 32 ms, flip angle = 90°, FOV = 69 × 192 × 192 mm, matrix = 128 × 128, voxel size = 1.5 mm isotropic). Images were acquired in 46 ascending interleaved slices in a tilted coronal plane covering the occipital lobes. Anatomical images were collected using a turbo field-echo protocol and 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. Stimuli were displayed on a screen positioned behind the bore using a 5100MP projector (Dell, Round Rock, TX) with a spatial resolution of 1,024 × 768 pixels (1.12° per pixel) and temporal resolution of 60 Hz. The projector output was linearized via spline interpolation of luminance values measured with a SpectraScan PR-655 spectropho...
Stimuli

Separate stimulus sets were constructed to allow for modulation of pattern orientation and to perform retinotopic mapping. Pattern orientations were defined using a sinusoidal grating with a spatial frequency of 3.35 cycles/° (Fig. 2A), which is within a spatial frequency range shown to evoke high BOLD signal magnitudes in the early visual areas (Kay et al. 2008; Singh et al. 2000). The grating was presented at full contrast within an annulus (0.75° inner radius, 7.2° outer radius, 0.35° raised cosine window at inner and outer edges) on a background equal to the mean grating luminance.

Retinotopic mapping was performed using a wedge that opened 15° shifts (Fig. 2). The direction of change alternated between clockwise and anticlockwise over runs. The direction of motion in the wedge strips were assigned randomly at the beginning of each volume to prevent transients induced by abrupt changes in orientation, and the phase of the grating was updated with a new random value at 1 Hz. Stimulus onset, offset, and phase changes were presented in a square-wave temporal cycle. A full orientation cycle was presented in 48 s (16 volumes), and eight complete cycles were completed in each run.

Each subject completed four retinotopic mapping runs, during which the polar angle of the wedge changed every 1.5 s in stepwise 11.25° shifts (Fig. 2B). The direction of change alternated between clockwise and anticlockwise over runs. The grating was absent in the first and last 250 ms of each volume to prevent transients induced by abrupt changes in orientation, and the phase of the grating was updated with a new random value at 1 Hz. Stimulus onset, offset, and phase changes were presented in a square-wave temporal cycle. A full orientation cycle was presented in 48 s (16 volumes), and eight 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. Performance on the fixation task was quantified by the mutual information between increment onset and response and was not significantly different (1-way ANOVA, P > 0.05) in windows around the principal grating orientations (0, 45, 90, and 135°) across subjects.

Data preprocessing

Functional images were corrected for differences in slice acquisition time with the middle slice as reference. Between- and within-run subject movement was corrected, and images were resliced using fourth-degree B-spline interpolation. After discarding the first half-cycle of each run, a correction of +2 volumes (6 s) was applied to compensate for the lag in the hemodynamic response. Time courses...
from runs in which the stimulus advanced clockwise were temporarily reversed and were then combined with anti-clockwise runs to produce mean time courses for pattern orientation and spatial polar angle.

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 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.

**Analysis**

The responses to the retinotopic mapping (polar wedge) stimulus were used to define the visual areas in early retinotopic cortex. Using mrVista, the preferred visual field polar angle of each voxel was estimated as the phase of the best-fitting sinusoid at the cycle frequency. The inplane voxels were transformed onto a flattened representation of the cortical surface, and the map of angular preferences was used to manually define areas V1, V2, V3, V3A/B, and hV4 based on the nomenclature and criteria of Larsson and Heeger (2006) and Wandell et al. (2007). To support appropriate area definition, eccentricity maps from previous studies with common subjects (Manjon et al. 2009) were also consulted. To restrict visual area definitions to stimulated portions of the visual field, voxels of low coherence (<0.1) to the polar wedge stimulus and those within the fovea were excluded from further analysis. The visual area definitions are shown for each subject in Supplementary Fig. S1.

The response to the pattern orientation stimulus cycle was calculated for each voxel within the identified visual areas. The pattern orientation time course was normalized by subtracting and dividing by the mean voxel response, high-pass filtered (128 s cut-off), and averaged over the eight cycles. For each voxel, this produced a 16-item vector of the evoked response to pattern orientation in 11.25° increments along the [0, 180°] interval. Voxels with a maximum signal change >2 SD above the mean maximum signal change for a given visual area were discarded from further analysis.

The voxels within each visual area were binned according to their preferred spatial meridian (calculated by wrapping the preferred visual field polar angle at 180°), with bin centers corresponding to the 16 pattern orientations. The pattern orientation response vectors were averaged across those voxels within a given visual area with a common spatial polar meridian bin. The data for each subject and visual area thus formed a 16 × 16 matrix (pattern orientation × spatial polar meridian). A schematic of this processing procedure is presented in Fig. 3. Finally, this data matrix was sheared to transform the dimension indexing spatial polar meridian to index the circular distance between pattern orientation and spatial polar meridian (meridian-relative orientation).

A two-way repeated measures ANOVA was conducted for each visual area with subjects as a random factor and field-independent orientation and meridian-relative orientation as fixed factors with 16 levels. Because no statistical comparisons were applied across visual areas and each visual area was considered to comprise a separate statistical “family” (Ludbrook 1998), no correction for performing multiple ANOVAs (one for each of 5 visual areas) was applied. Violations of the assumption of sphericity were corrected by using Huynh-Feldt coefficients to reduce the effective degrees of freedom when assessing statistical significance.

**FIG. 2.** Illustration of orientation stimulus (A) and paradigm (B) and retinotopic mapping wedge stimulus (C) and paradigm (D). A: pattern orientations were defined using a sinusoidal grating (horizontal/0° in this example). B: single cycle (48 s) of the grating presentation sequence. The grating orientation changed in 11.25° stepwise shifts every 3 s, with a 250 ms period at the onset and offset of orientation change in which the grating is absent. The grating orientation advanced anticlockwise, as shown in this example, on one half the runs, whereas it advanced clockwise during the remaining runs. C: retinotopic mapping was performed using a polar wedge stimulus (located along the right horizontal/0° visual field meridian in this example). D: single cycle (36 s) of the retinotopic mapping sequence. The location of the wedge in the visual field changed in 15° stepwise shifts every 1.5 s (every second step shown in figure). The wedge location advanced anticlockwise around the visual field, as shown in this example, on one half the runs, whereas it advanced clockwise during the remaining runs.
The magnitude of BOLD activity was significantly anisotropic across meridian-relative orientation in all areas (V1: $F_{5,170} = 12.13, P < 0.001$; V2: $F_{1,64.7} = 16.43, P = 0.009$; V3: $F_{2,47.3} = 13.73, P = 0.003$; V3A/B: $F_{7,42.2} = 7.61, P < 0.001$; hV4: $F_{4.8,14.4} = 4.22, P = 0.015$). As shown in Fig. 4B, the greatest BOLD responses were obtained when the pattern orientation and visual field meridian were near coincident (meridian-relative orientation $\sim 0^\circ$), and the magnitude of response gradually reduced with increasing circular distance between the pattern orientation and the visual field meridian. This profile of meridian-relative anisotropy was consistent across all the visual areas.

The magnitude of anisotropy, as defined by the range of the fMRI signal change across orientation, was lower for meridian-relative orientation relative to field-independent orientation. Although this may be indicative of an increased strength of the field-independent orientation anisotropy in comparison with the anisotropy in meridian-relative orientation, it may also reflect the inevitable loss in precision when estimating meridian-relative orientation caused by the reliance on retinotopic mapping in this experiment.

There were no significant interactions in visual areas V1, V2, V3, and V3A/B (all $P > 0.05$), which may be suggestive of an independence between the observed field-independent and meridian-relative effects or may reflect insufficient statistical power to detect such interactions in this experiment. Although the interaction was significant in hV4 ($F_{225,0.675} = 1.27, P = 0.012$), further analysis showed no clear pattern of factor level dependence on the responses to either field-independent or meridian-relative orientation. We speculate that the less precise visual field polar angle mapping of hV4 (see Supplementary Fig. S1) may have restricted the ability to observe consistent meridian-relative anisotropies across the range of visual field meridia.

**DISCUSSION**

We studied modulations in the response of human visual cortex induced by both the orientation of an observed pattern and by the conjunction of pattern orientation and angular position in the visual field. Using fMRI, we identified the preferred visual field meridian of voxels within retinotopic regions of human visual cortex and measured their responses to a sinusoidal grating that varied in orientation. We report an anisotropic distribution of responses to field-independent pattern orientation within areas V1, V2, V3, and V3A/B, with a form characterized by the lowest response to horizontal, intermediate at vertical, and highest at oblique orientations. We also report that, when orientation is considered relative to angular position in the visual field, an anisotropic distribution of responses is observed in V1, V2, V3, V3A/B, and hV4, in which the greatest response is obtained when the pattern orientation and visual field meridian are parallel.
The functional role of anisotropies in the visual system can be informed by considering the structure of typical system input. The distribution of field-independent orientation content in typical natural scenes is anisotropic, with horizontal and vertical more prevalent than obliques (Coppola et al. 1998; Dragoi et al. 2001; Hansen and Essock 2004) and horizontal more prevalent than vertical (Hansen and Essock 2004). The apparent inversion of this distribution in the magnitude of response to field-independent orientation in this study, most clearly evident in V1, suggests a representational strategy that accommodates anisotropies present in a typically observed scene (Essock et al. 2003). Such a strategy would allow for a redistribution of the anisotropic input structure, potentially leading to an isotropic representation of field-independent orientation (Essock et al. 2003). The presence of such a whitening mechanism would be consistent with those commonly thought to operate across spatiotemporal frequency (Dan et al. 1996; Field 1987; Webster and Miyahara 1997) and with the principle of efficient neural coding (Barlow 1961; Field 1987; Simoncelli 2003).

The measured fMRI activity has its substrate in changes in the excitatory and inhibitory balance within the collection of neurons sampled within each voxel (Logothetis 2008). Nonhuman neurophysiology indicates that the greatest number of cortical neurons respond to horizontal field-independent orientation, reduced at vertical, and the least at the obliques (Li et al. 2003). This numerical anisotropy suggests that an integrated population response would show strong levels of matching anisotropy in response to field-independent orientation, which would enhance the anisotropy of typical natural scenes (Essock et al. 2003; Hansen and Essock 2004). The clear departure from such a prediction in the field-independent orientation anisotropy in fMRI activity reported here suggests the presence of a mechanism that adjusts the contribution of neurons according to their preferred field-independent orientation (Essock et al. 2003, 2009; Hansen et al. 2003). Such a normalization mechanism could be implemented by having orientation selectivity bandwidths that are inversely proportional to the numerical field-independent orientation anisotropy, as reported by Li et al. (2003), or by a gain-control process similar to those commonly considered to operate within the early cortical visual system (Hansen et al. 2003; Heeger 1992).

However, the meridian-relative anisotropy observed in this study suggests that such a normalization mechanism does not have universal application in the early visual system. Analyses of the meridian-relative orientation structure of natural scenes have shown a preponderance of orientations radial to the image center (Bruce and Tsotsos 2006) and to the center of simulated gaze (Rothkopf et al. 2009). Nonhuman neurophysiology has shown an overrepresentation of cortical neurons preferring radial meridian-relative orientations (Leventhal 1983) that is also present in the retina (Levick and Thibos 1982). The measured fMRI activity across meridian-relative orientation reported here corresponds to this profile of anisotropy, with radial orientations producing greater activity than tangential. Thus the representation of meridian-relative orientation in the
early visual system seems to reproduce and enhance the meridian-relative anisotropy present in typical system input.

The apparent differences in the representational strategy for field-independent and meridian-relative orientation may potentially be related to divergent behavioral relevance of the two indices. Redistribution of the field-independent anisotropy in a typical natural image would be an appropriate strategy where the relevance of features in the environment does not correspond to their prevalence. If there is no consistent relationship between feature relevance and field-independent orientation, this redistribution would allow an efficient isotropic representation of field-independent orientation (Essock et al. 2003; Hansen et al. 2003). Conversely, radial meridian-relative orientations have been associated with computations such as the establishment of geometric perspective (Bruce and Tsotsos 2006; Rothkopf et al. 2009) and optic flow (Geisler 1999; Lee 1980; Raemaekers et al. 2009), and thus a cortical representation that preserves the meridian-relative anisotropy may be behaviorally beneficial. Such optimization of visual system anisotropies in accordance with ecological demands seems to be a common principle across species (O’Carroll et al. 1996).

The meridian-relative anisotropy reported here is consistent with the increased behavioral sensitivity for radial meridian-relative orientations (Rovamo et al. 1982; Sasaki et al. 2006; Westheimer 2003a). However, the form of field-independent anisotropy highlights a difficulty in establishing the link between behavioral performance and neural activity (Teller 1984). Sensitivity to field-independent orientation is superior, across a variety of behavioral indices, at horizontal and vertical compared with the obliques—the oblique effect (Appelle 1972). This psychophysical anisotropy is inconsistent with the anisotropy in field-independent orientation reported here, in which horizontal orientations produce the lowest levels of activity, suggesting that the magnitude of evoked activity in the early visual system does not necessarily determine behavioral sensitivity (Westheimer 2003b). Furthermore, an overrepresentation of horizontal and vertical detecting mechanisms is insufficient to explain the dependence of the oblique effect on the image spectrum (Essock et al. 2003, 2009; Hansen and Essock 2006) and complexity (Jenkins 1985; Wilson et al. 2001). Further research is thus needed to clarify the relationship between field-independent orientation anisotropies evident in behavioral performance and those evident in measures of neural activity.

The nature of the anisotropies reported in this study may be contingent on the particular choice of stimulus attributes and behavioral task. Both field-independent and meridian-relative anisotropies have been shown to vary with spatial frequency and eccentricity (Heeley and Timney 1988; Li et al. 2003; Raemaekers et al. 2009; Rovamo et al. 1982; Vandebussche et al. 1986). However, such interactions typically involve a modulation of the strength or existence, rather than the form, of the anisotropy. Furthermore, the reported profiles of anisotropy may be contingent on the task performed by the observer. In this experiment, having observers complete a task at fixation that was unrelated to the experimental stimulus allowed us to limit the influence of eye movements and shifts in attention on the measured BOLD responses. However, it is possible that requiring observers to complete a task involving the stimulus (such as discrimination or change detection) may engage different neural mechanisms and result in alterations to the form of evoked orientation anisotropy (Williams 1982).

In conclusion, we report the presence of significant anisotropies in the response of human visual cortex to pattern orientation. Consideration of field-independent orientation showed anisotropic responses within V1, V2, V3, and V3A/B, characterized by a decreased response to horizontal orientations, intermediate response to vertical orientations, and the highest response to oblique orientations. When orientation was considered relative to angular position in the visual field, meridian-relative anisotropies were observed in areas V1, V2, V3, V3A/B, and V4, in which radial orientations produced greater responses than those that were tangential. We speculate that such anisotropies are related to the behavioral relevance of feature orientation, with anisotropic field-independent orientation content in typical scenes being redistributed via a neural normalization process to produce an efficient isotropic representation, whereas anisotropic meridian-relative orientation content is maintained in the cortical representation. Future research is needed to elucidate the precise nature of the field-independent redistributive process and to directly study the cortical representation of the orientation structure of natural environments.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

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