

Orientation selectivity and stimulus vignetting in human visual cortex

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Abstract:

Neural selectivity to orientation is one of the simplest and most thoroughly-studied cortical sensory features. Here, we show that a large body of research that purported to measure orientation tuning may have in fact been inadvertently measuring sensitivity to second-order changes in luminance, a phenomenon we term ‘vignetting’. Using a computational model of neural responses in primary visual cortex (V1), we demonstrate the impact of vignetting on simulated V1 responses. We then used the model to generate a set of predictions, which we confirmed with functional MRI experiments in human observers. Our results demonstrate that stimulus vignetting can wholly determine the orientation selectivity of responses in visual cortex measured at a macroscopic scale, and suggest a reinterpretation of a well-established literature on orientation processing in visual cortex.

Keywords: orientation; multivariate classification; primary visual cortex; fMRI; vignetting

Background

Primary visual cortex (V1) is likely the best studied sensory cortical area, and is a model for understanding broad principles of cortical processing. Similarly, orientation in V1 is likely one of the simplest and best studied cortical sensory features. Yet the map of orientation preference in V1 is inadequately understood. At a fine scale, the map shows an orderly periodic structure with pinwheels in hypercolumns, which have a periodicity of about 1 mm in monkeys (Hubel and Wiesel, 1963), and which are thought to be slightly larger in humans.

We and others, using fMRI, discovered a coarse-scale orientation bias in human V1; each voxel exhibits an orientation preference that depends on the region of space that it represents (Freeman et al., 2011). We observed a radial bias in the peripheral representation

of V1: voxels that responded to peripheral locations near the vertical meridian tended to respond most strongly to vertical orientations; voxels along the peripheral horizontal meridian responded most strongly to horizontal orientations; likewise for oblique orientations.

While the neural architecture that gives rise to orientation selectivity is well understood, the neural basis for the coarse-scale orientation bias remains unknown. Carlson (2014) proposed that the coarse-scale bias is a byproduct of the edge of the stimulus, referring to it as an “edge effect”. By this account, the coarse-scale bias does not directly reflect enhanced neural responses for particular orientations, but rather reflects properties of the stimuli. This account, if correct, would require the reinterpretation of a vast number of previous studies, since in nearly all experiments on orientation, the stimuli are confined by the edges of a finite aperture, or, at very least, by the edge of the display screen.

Here, we develop a theoretical account of the edge effect (Carlson, 2014), and show that it applies not only to stimulus edges but to a much broader class of stimuli. We use the term “stimulus vignetting” to refer to this effect, emphasizing that it is not the edge per se, but rather an interaction between the orientation of the stimulus and a second feature of the display (the aperture or “vignette”) that bounds the stimulus. We used an image-computable model of V1 activity to generate predictions, which we then tested with empirical data from fMRI experiments. Our results provide a framework for reinterpreting a wide-range of findings in the visual system.

Methods

Theoretical Model

The image-computable model is based on the steerable pyramid (Simoncelli et al., 1992), a subband image transform that decomposes an image into orientation and spatial frequency channels (Figure 1). The pyramid simulates the responses of a large number of linear receptive fields (RFs), each of which computes a weighted sum of the stimulus image; the weights determine the orientation and spatial frequency tuning. RFs with the same orientation and spatial-frequency tuning, but shifted to different locations, are called a “channel”. The RFs cover all orientations and spatial frequencies evenly (i.e., the sum of the squares of the tuning curves is exactly equal to one for all orientations and spatial frequencies).

We used the theoretical model to predict fMRI responses to a wide range of stimuli. We then chose stimuli that were predicted to have opposite patterns of orientation bias when measured with fMRI. Predicted responses were calculated by finding the scale with maximal responses, summing the energy responses for the channels at that scale, and averaging across stimulus grating phases.

Functional MRI Experiments

Experiments at 3T were conducted at NYU Center for Brain Imaging. Experiments at 7T were conducted at Functional Magnetic Resonance Imaging Core Facility at NIH. Methods were similar between the two sites. Fourteen observers (8 females, aged 22-27 years) with normal or corrected-to-normal vision participated in the study.

Stimuli. The novel stimuli consisted of two gratings (a carrier and a modulator) multiplied by one another (Figure 2). The carrier grating consisted of a large, oriented sinusoidal Cartesian grating presented within an annulus. The orientation of the carrier grating cycled through 16 evenly-spaced angles between 0° and 180° (1.5 s per orientation), clockwise in half of the runs and counter-clockwise in the other half.

responses because it did not change during the course of a scanning run.

Behavioral task. Throughout each run, observers continuously performed a demanding two-interval, forced-choice task to maintain a consistent behavioral state and stable fixation, and to divert attention from the main experimental stimuli.

Results

We began by simulating the results of our previous fMRI experiment (Freeman et al., 2011) with an image-computable model of V1. The inputs to the model were identical to the stimuli used by Freeman et al. (2011). We measured the model’s responses to each image separately. To simulate an fMRI voxel’s, we summed the model responses across all orientation channels. Importantly, the model’s response should not exhibit any orientation tuning, since we summed across all of the orientation channels. But the simulated neural responses exhibited a clear coarse-scale bias for orientation (Carlson, 2014). The coarse-scale orientation bias matched Freeman et al. (2011) in that the largest responses were observed for radial orientations (Figure 1).

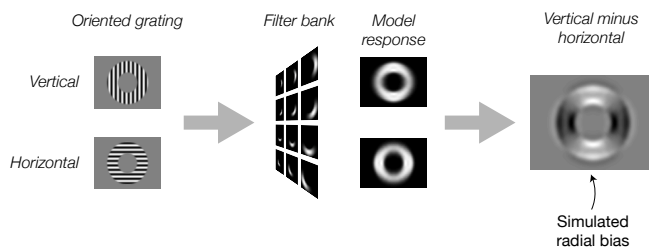


Figure 1: Simulated neural responses illustrating the impact of stimulus vignetting. Oriented gratings were used as input to the model. Model responses were computed separately for vertical (top) and horizontal (bottom) gratings. Finally, model output was computed as the responses to vertical minus response to horizontal gratings. Model exhibits a preference for horizontal gratings along the horizontal meridian and a preference for vertical gratings along the vertical meridian (i.e., a radial bias).

Having established that stimulus vignetting can produce a radial coarse-scale bias, we next asked whether the computational model predicts the influence of vignetting on responses to novel stimuli. To test this possibility, we generated a novel set of stimuli with vignettes that were orthogonal to one another. If the vignette affects orientation bias, changing the vignette should have a predictable effect on orientation bias.

The novel stimuli for this simulation were created by multiplying oriented gratings with a radial or angular polar grating. These compound stimuli were then passed through the model. Subtracting horizontal from vertical carrier grating outputs resulted in an image of orientation bias for the model.

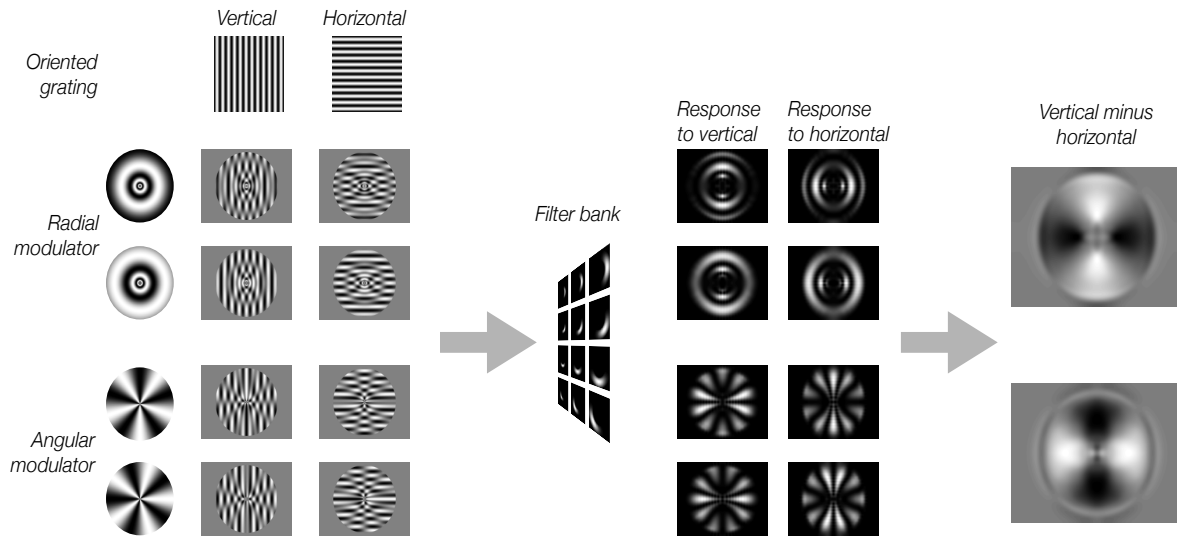


Figure 2. Model predictions for modulated gratings. Each of the eight stimuli were created by multiplying a vertical or horizontal grating by a radial or angular modulator. These stimuli were used as input to the model. Model responses were computed as in Figure 1. For radial modulated gratings (top two rows), the model exhibits a radial preference: larger responses to horizontal gratings along the horizontal meridian, larger responses to vertical gratings along the vertical meridian. However, for angular modulated gratings (bottom two rows), the orientation preference is tangential: larger responses for horizontal gratings along the vertical meridian and larger responses for vertical gratings along the horizontal meridian.

The model predicted that the coarse-scale orientation bias should depend on the modulator. The radial modulator evoked a coarse-scale bias that was radial (Figure 2). In other words, at regions around the vertical meridian there is a greater response for the vertical orientation than for the horizontal orientation (light regions in Figure 2), and vice versa around the horizontal meridian (dark regions in Figure 2). The model predicted that changing the orientation of the modulator should affect the orientation preference to the carrier grating. We found that the angular modulator evoked a coarse-scale bias that was tangential. Thus, at the vertical meridian the horizontal grating yielded higher responses, and at the horizontal meridian the vertical grating evokes higher responses.

We found evidence of stimulus vignetting at both 3T and 7T field strengths, at different spatial resolutions, and for both square wave and sinusoidal modulators, as predicted by the theoretical model. The radial modulator evoked a radial bias (i.e., orientation preferences pointing inward toward the fovea). The angular modulator evoked a tangential bias (i.e., orientation preferences that were rotated by 90 deg from radial) (Figure 3). Furthermore, on a voxel-by-voxel basis, preferred orientations were shifted by 90 deg across modulators.

Conclusions

Our results show that stimulus vignetting strongly affects voxel orientation bias. This suggests that results from many fMRI studies attempting to measure neural orientation tuning properties may actually reflect stimulus vignetting. Since stimulus vignetting masquerades as orientation selectivity amongst voxels that correspond to the stimulus edge, and because edges tend to be continuous over a large spatial extent, vignetting will generally result in a coarse-scale map of orientation bias.

Stimulus vignetting is a general issue of concern in visual neuroscience. According to the theoretical model that we have applied here, whenever a neuron's receptive field overlaps a stimulus edge or a change in contrast, stimulus vignetting will spread the Fourier power and affect the neuron's response. As a result, such a neuron may exhibit ostensible orientation tuning even when it is not orientation selective. Furthermore, even if a neuron is truly orientation selective, measurements of its orientation tuning may be affected by the aperture shape.

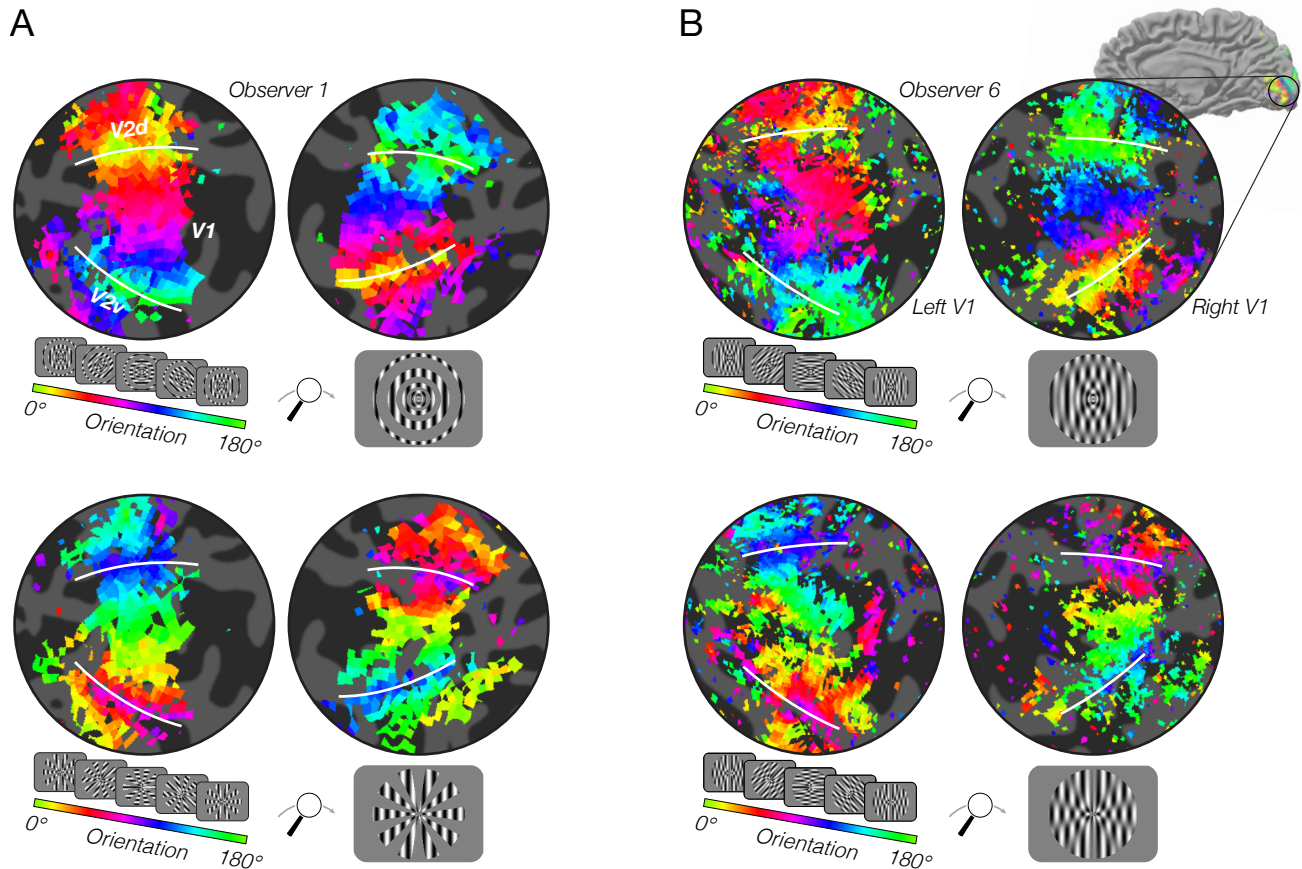


Figure 4. fMRI measurements of orientation bias depend on stimulus vignetting. (A) Top: Responses to oriented gratings multiplied by a static radial modulator (shown in inset). Hue indicates phase of the best fitting sinusoid. White lines indicate V1/V2 boundaries. Bottom: Responses to the same oriented grating as in A, but here the grating is multiplied by an angular modulator. As predicted by the model, the radial modulator gave rise to a radial orientation bias, while the angular modulator gave rise to a tangential orientation bias. (B) High-resolution, high field strength measurements of orientation preference for radial and angular modulators. Stimuli and conventions same as for A, except the modulators were radial and angular sinusoids.

Acknowledgments

Supported by NIH grants R01-EY025673, and by the Intramural Research Program of the National Institutes of Health (ZIA- MH-002909) - National Institute of Mental Health Clinical Study Protocol 93-M- 0170, NCT00001360. ZNR was supported by The ELSC Postdoctoral Fellowship Abroad, Hebrew University of Jerusalem. Special thanks to Eero Simoncelli and to Peter Bandettini for helpful comments.

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