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Radial bias is not necessary for orientation decoding

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ABSTRACT

Multivariate pattern analysis can be used to decode the orientation of a viewed grating from fMRI signals in early visual areas. Although some studies have reported identifying multiple sources of the orientation information that make decoding possible, a recent study argued that orientation decoding is only possible because of a single source: a coarse-scale retinotopically organized preference for radial orientations. Here we aim to resolve these discrepant findings. We show that there were subtle, but critical, experimental design choices that led to the erroneous conclusion that a radial bias is the only source of orientation information in fMRI signals. In particular, we show that the reliance on a fast temporal-encoding paradigm for spatial mapping can be problematic, as effects of space and time become conflated and lead to distorted estimates of a voxel's orientation or retinotopic preference. When we implement minor changes to the temporal paradigm or to the visual stimulus itself, by slowing the periodic rotation of the stimulus or by smoothing its contrast-energy profile, we find significant evidence of orientation information that does not originate from radial bias. In an additional block-paradigm experiment where space and time were not conflated, we apply a formal model comparison approach and find that many voxels exhibit more complex tuning properties than predicted by radial bias alone or in combination with other known coarse-scale biases. Our findings support the conclusion that radial bias is not necessary for orientation decoding. In addition, our study highlights potential limitations of using temporal phase-encoded fMRI designs for characterizing voxel tuning properties.

Introduction

Orientation-selective neurons in the primary visual cortex (V1) are clustered at submillimeter scales to form cortical columns and pinwheel-like structures (Bartfeld and Grinvald, 1992; Blasdel, 1992; Ohki et al., 2006). Although orientation selectivity is predominantly organized at a fine spatial scale, Kamitani and Tong (2005) discovered that the orientation of a viewed grating can be accurately decoded from fMRI activity patterns in the human visual cortex. They hypothesized that orientation decoding was possible at standard fMRI resolutions due to local anisotropies in the distribution of orientation-selective columns, as this would lead to subtle imbalances in orientation preference at spatial scales exceeding the width of individual columns. Subsequent high-resolution fMRI studies have demonstrated the presence of orientation-selective signals in V1 at millimeter and submillimeter scales (Moon et al., 2007; Swisher et al., 2010; Yacoub et al., 2008). However, differential responses to orientation can also be found at much coarser spatial scales. For example, some studies have reported stronger overall V1 responses for cardinal than for oblique orientations (Furmanski and Engel, 2000), while others suggest that disproportionately more voxels prefer cardinal over oblique orientations (Sun et al., 2013). A retinotopically organized bias in favor of radial orientations (relative to the fovea) has also been found in human V1 (Sasaki et al., 2006). This *radial bias* appears quite prominent, and may originate from a bias evident in the elongated dendritic fields of retinal ganglion cells (Schall et al., 1986). Recent studies have revealed stronger responses for radial than tangential orientations in the human lateral geniculate nucleus (Ling et al., 2015), consistent with the possibility of a retinal contribution to the radial bias effects observed in V1.

In several recent studies, researchers have attempted to determine the extent to which fMRI decoding of stimulus orientation depends on fine-scale or coarse-scale biases (Alink et al., 2013; Kriegeskorte et al., 2010; Mannion et al., 2010; Op de Beeck, 2010; Swisher et al., 2010). This is an important question as it pertains not only to the functional organization of feature selectivity in the visual cortex, but also has direct relevance to understanding the types of information that can be detected in multivariate fMRI activity patterns (Swisher et al., 2010; Gardner, 2010; Shmuel et al., 2010; Tong and Pratte, 2012) and at the scale of individual voxels (Brouwer and Heeger, 2009; Kay et al., 2008; Kriegeskorte et al., 2010; Naselaris et al., 2011; Serences et al., 2009).

A recent study by Freeman et al. (2011) addressed this issue by using a temporal phase-encoding approach to measure V1 responses to periodic rotations of an oriented grating, and comparing these orientation preference maps with those evoked by a retinotopic radial mapping stimulus (Fig. 1A, B). Orientation was accurately decoded from the

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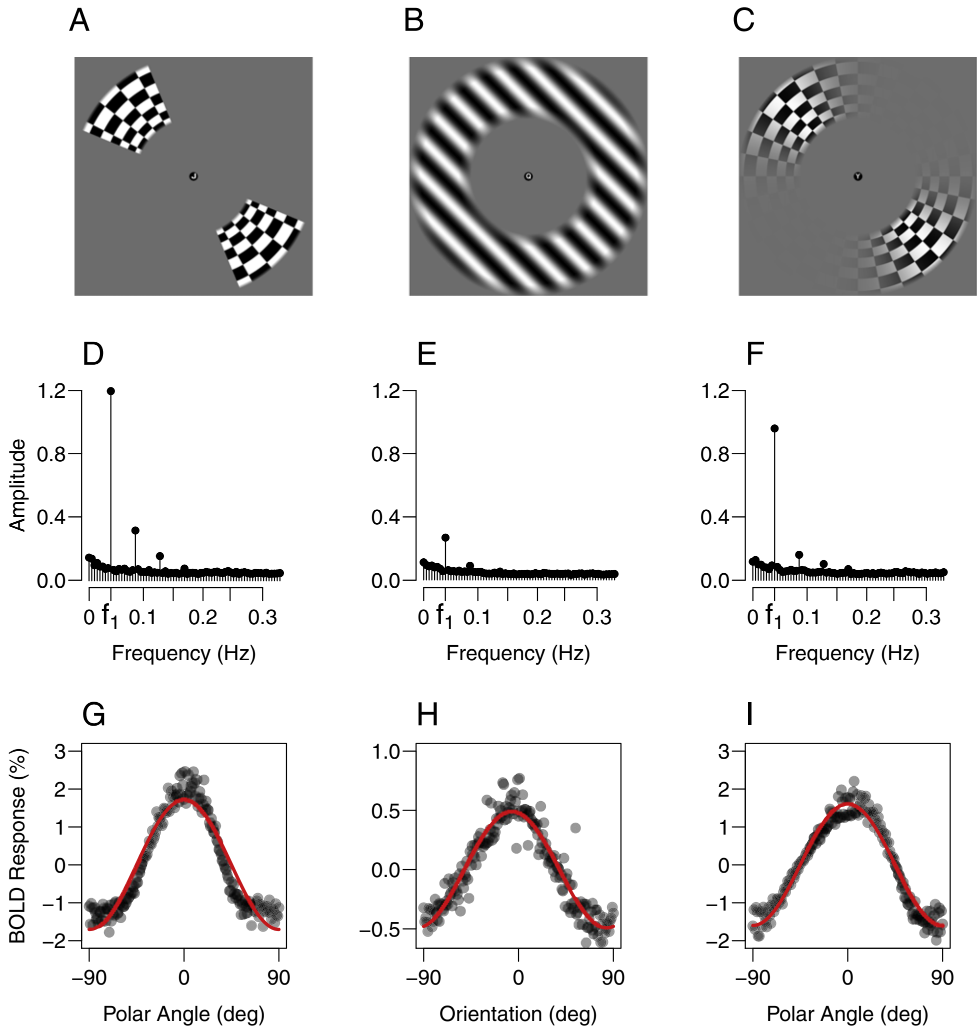

Fig. 1. Experimental stimuli and the resulting BOLD responses. Top row shows examples of the retinotopy wedge used in Experiment 1 and Experiment 3 (A), the oriented grating used in Experiment 1–Experiment 3 (B) and the smoothed retinotopy wedge used in Experiment 2 (C). The middle row shows power spectrums of the BOLD signal in response to the wedge stimulus (D), oriented grating (E) and smoothed wedge (F), averaged over participants. The bottom row shows the corresponding BOLD signals from a representative participant to the wedge (G), grating (H) and smoothed wedge stimuli (I). The responses of individual voxels in V1 were phase locked to their retinotopic phase preference and averaged. The line shows the best-fitting cosine function to the data in each panel.

original activity patterns obtained at standard fMRI resolutions, but after analytic removal of the radial bias component, orientation decoding fell to chance levels. From these results, Freeman et al. concluded that radial bias was the *only* source of orientation information in the fMRI signal, and thus *necessary* for orientation decoding. Curiously however, other fMRI studies have demonstrated the presence of other sources of orientation information in the visual cortex, distinct from radial bias (Alink et al., 2013; Freeman et al., 2013; Mannion et al., 2009; Swisher et al., 2010). Thus, conflicting results have emerged in the literature, and it has remained unclear as to why radial bias appears to be necessary for orientation decoding in some studies but not others.

In the present study, our goal was to reconcile these disparate findings regarding whether radial bias might be necessary for orientation decoding. Our first step was to replicate the stimulus conditions, experimental parameters, and analytical procedure of Freeman et al. (2011), as their study was the first to report that orientation decoding depends entirely on radial bias. Across a series of experiments, we find that subtle but critical choices in experimental design led to erroneous conclusions in the Freeman et al. study. They relied on a temporal-encoding approach to characterize the orientation and polar-angle retinotopic preferences of individual voxels. Such an approach provides a fast, efficient method for spatial mapping (Engel, 2012), but has the potential to conflate effects of space and time. Moreover, different types of visual stimuli can evoke different spatiotemporal profiles of activity in the cortex, such that information about a stimulus may be conveyed not only at the fundamental frequency of the paradigm but also in the form of higher order temporal harmonics. Such considerations proved important when comparing the accuracy of decoding performance across orientation and polar-angle conditions.

In Experiment 1, we replicate the experimental results of Freeman et al., but show that the polar-angle retinotopy stimulus evokes higher-order harmonic responses, such that residual information persists about the retinotopy stimulus following removal of the fundamental component. In comparison, decoding of orientation is driven largely by the fundamental component. As a consequence, Freeman et al.'s approach of comparing decoding performance for orientation and polar angle, following the removal of the fundamental component, leads to an invalid procedure for estimating chance-level orientation decoding. In Experiment 2 and Experiment 3, we implemented minor changes to the spatiotemporal paradigm, by slowing the rotation of the stimulus or by smoothing the contrast-energy profile of the retinotopy stimulus to avoid evoking harmonic responses. These modest manipulations were sufficient to produce failures to replicate the original study, and suggest that orientation information persists following the removal of