

Can visual information encoded in cortical columns be decoded from magnetoencephalography data in humans?



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ABSTRACT

It is a principal open question whether noninvasive imaging methods in humans can decode information encoded at a spatial scale as fine as the basic functional unit of cortex: cortical columns. We addressed this question in five magnetoencephalography (MEG) experiments by investigating a columnar-level encoded visual feature: contrast edge orientation. We found that MEG signals contained orientation-specific information as early as approximately 50 ms after stimulus onset even when controlling for confounds, such as overrepresentation of particular orientations, stimulus edge interactions, and global form-related signals. Theoretical modeling confirmed the plausibility of this empirical result. An essential consequence of our results is that information encoded in the human brain at the level of cortical columns should in general be accessible by multivariate analysis of electrophysiological signals.

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Introduction

The basic format in which the primary visual cortex (V1) represents the visual world is the orientation of contrast edges (Hubel and Wiesel, 1959, 1968). Invasive research in animals and ultrahigh-resolution fMRI in humans have shown that neurons tuned to a particular edge orientation cluster in sub-millimeter size columns (Bartfeld and Grinvald, 1992; Vanduffel et al., 2002; Yacoub et al., 2008). Thus, the size of orientation columns is smaller than the sampling resolution of standard fMRI (3 mm) and magnetoencephalography (MEG), seemingly raising a barrier to resolving orientations from brain data obtained with standard noninvasive techniques. However, ten years ago two studies claimed to have crossed this boundary using standard resolution fMRI (Haynes and Rees, 2005; Kamitani and Tong, 2005), showing that grating orientation can be decoded from fMRI activation patterns.

This claim has sparked a debate and has been challenged in at least two ways (Mannion et al., 2009, 2010; Kriegeskorte et al., 2010; Freeman et al., 2011, 2013; Alink et al., 2013; Carlson, 2014; Wardle et al., 2015; Pratte et al., 2014). First, interpretation of fMRI results is confounded by the complex relationship between neuronal activity, the BOLD response, and the voxel-wise sampling of BOLD activity (Logothetis and Wandell, 2004). For example, modeling voxels as compact kernels or complex spatiotemporal filters greatly influences the sampling of columnar level activity (Kriegeskorte et al., 2010), and

thus complicates the interpretation of the spatial scale of the underlying signal sources.

Second, it has been argued that orientation stimuli used to probe V1 activity might also elicit orientation-specific coarse-scale activation patterns far above the size of orientation columns. Such coarse-scale activation patterns might result from a relatively stronger representation for particular orientations (Pettigrew et al., 1968; Maffei and Campbell, 1970; Mansfield, 1974; Rose and Blakemore, 1974; Kennedy and Orban, 1979; Furmanski and Engel, 2000; Li et al., 2003; Sasaki et al., 2006; Mannion et al., 2009; Freeman et al., 2011, 2013; Alink et al., 2013), boundary interaction effects between background and stimulus (Carlson, 2014), and perceptual binding processes influenced by the global form of the stimulus (Alink et al., 2013).

Here, we circumvent the first challenge by taking an alternative approach: we used MEG instead of fMRI to resolve orientation from brain signals. MEG measures direct neuronal activation without the complex convolution of the BOLD response, and its fine temporal resolution enables us to dissociate the contribution of early first-pass visual responses from late processing along the ventral visual pathway and other feedback signals. To address the second challenge, we used multiple sets of controlled stimuli to investigate alternative hypotheses of coarse-scale confounds in orientation decoding. Finally, we conducted a modeling experiment to examine whether simulated activation patterns in V1 at the spatial scale of orientation columns are discriminable from modeled MEG signals.

We found that MEG signals contained orientation-specific information even when controlling for known stimulus-induced coarse-scale activation confounds. Modeling demonstrated the theoretical feasibility

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of discriminating cortical activation patterns that differ at the spatial scale of cortical columns. Together, assuming that all coarse scale confounds have been properly controlled, our results indicate that orientation encoding in humans at the level of cortical columns is directly accessible to experimental investigation using noninvasive electrophysiological methods. This suggests that other information encoded in the human brain in fine-grained distributed activation patterns is accessible by multivariate analysis of electrophysiological data.

Materials and methods

Participants

Experiments 1 to 5 included 12, 13, 16, 12, and 12 right-handed, healthy volunteers with normal or corrected-to-normal vision, respectively. Some subjects participated in more than one experiment, with the overall population being 20 males and 25 females, with mean age \pm s.d. = 23.68 ± 4.55 . The study was conducted according to the Declaration of Helsinki and approved by the local ethics committee at Massachusetts Institute of Technology.

Experimental design and stimulus material

The stimulus sets comprised diverse visual stimuli differing in local orientation and overlaid on a uniform gray background, such that stimuli and background were of equal mean luminance. All stimuli were created by in-house scripts using Matlab (2014a, The MathWorks, Natwick, MA, USA). For experiments 1–3 and 5 stimuli were presented in an annulus with an outer radius of 10° and an inner radius of 1° . The inner radius served to prevent interaction effects between the orientation contrast edges and a fixation cross presented at the center of the stimulus during the experiments. For experiment 4 the annulus was deformed into an ellipse.

The aim of experiment 1 was to establish whether edge orientation was discriminated by visual representations independent of cardinal bias, i.e., coarse-scale neuronal responses preferential to 0° vertical and 90° horizontal orientations. For this, we created sinusoidally modulated Cartesian gratings of $+45^\circ$ and -45° orientations, and thus equidistant from the two cardinal orientations (Fig. 1A). Such oblique stimuli remove potential overrepresentations caused by uneven proximity to the cardinal directions. Additionally, each of the two

oblique gratings was created in two exemplars with a half cycle phase shift to 1) allow investigation of phase representations, and 2) ensure any identified orientation representations are not confounded by local luminance differences due to a particular choice of phase (Ramkumar et al., 2013). Cartesian gratings had a frequency of 2 cycles per degree visual angle, following previous experiments that found decodable patterns in fMRI brain responses (Yacoub et al., 2008; Haynes and Rees, 2005).

The aim of experiment 2 was to investigate the representation of local edge orientation for finer orientation differences, and to estimate the strength of the cardinal bias. The stimulus set was designed as in experiment 1 except with a finer range of orientation differences in 30° steps from 0 – 150° (Fig. 2A). This allowed comparison of brain responses to gratings differing by as little as 30° , and comparison of brain responses to cardinal (0° , 90°) and oblique (30° , 60° , 120° , 150°) orientations directly.

The aim of experiment 3 was to address the role of radial bias in orientation representation, i.e., the coarse-scale overrepresentation of orientations parallel to a line through the center of fixation. For this, we used logarithmic spirals construed such that their edges were at an angle $+45^\circ$ (turning direction clockwise) or -45° (turning direction anti-clockwise) relative to a line through the center of the stimulus (the radial line) at any position in the stimulus, resulting in a local orientation disparity of 90° (Fig. 3A). While being maximally different in local orientation, both spirals had orientation equidistant from the radial line, thus controlling the radial bias. The logarithmic spirals had 20 contrast cycles and were constructed in two phase exemplars with a half cycle phase shift following the reasoning of experiment 1.

The aim of experiment 4 was to investigate the representation of edge orientation independent of boundary interaction effects between background and stimulus. A perfect ice-cube model of V1, thus without bias for any orientation, can still produce outputs differing in coarse scale for different orientations (Carlson, 2014): The representation of a perfectly circular grating is in fact an ellipse elongated in the direction of the grating and compressed in the orthogonal direction. Thus, differences in brain responses to different orientations might be explained by coarse-scale differences in the location of those edge effects. To counteract this edge-related effect, we created stimuli whose annulus was deformed into ellipsoidal shapes in the opposite direction to the one predicted by the ice-cube model. In detail, we compressed the annulus in the orientation of the grating and elongated it in the orthogonal direction. Deformations were 2, 5, 10 and 20% of the radius

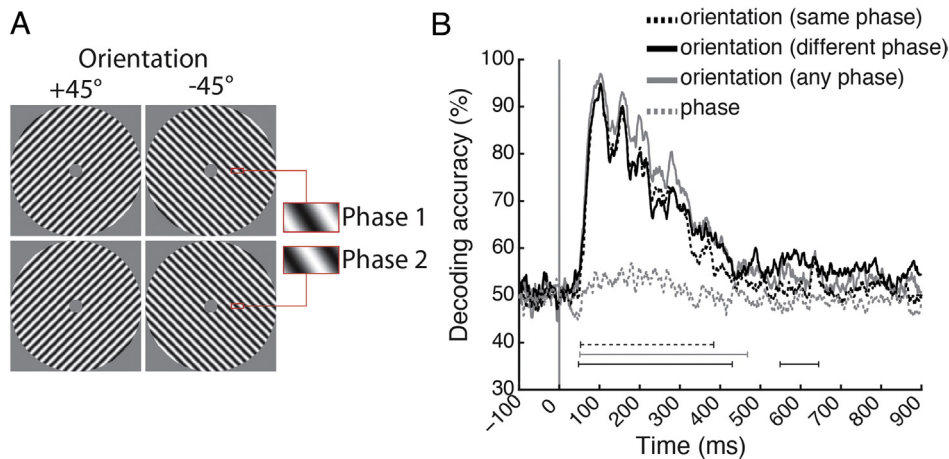


Fig. 1. Orientation decoding of oblique gratings. A) The stimulus set comprised oblique gratings tilted right or left (orientation $\pm 45^\circ$) with two phase exemplars having a half cycle phase shift. B) Time course of orientation decoding in 3 cases: the classifier training and testing sets comprised grating stimuli of the same phase, different phase, or any phase. Grating orientation was robustly decoded in all analyses (also see Table 1A). There was no evidence for the representation of phase (classifier training and testing sets had the same orientation). Gray vertical line indicates stimulus onset. Lines below plots indicate significant time points, color-coded as in decoding curves ($N = 12$; $p < 0.05$ cluster definition threshold, $p < 0.05$ cluster threshold).

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