NeuroImage 110 (2015) 219–222

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Comments and Controversies

Orientation decoding: Sense in spirals?

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ARTICLE INFO

Article history:
Accepted 19 December 2014
Available online 27 December 2014

Keywords:
fMRI
Visual cortex
Computational neuroimaging
Multivariate analysis
Spatial vision

ABSTRACT

The orientation of a visual stimulus can be successfully decoded from the multivariate pattern of fMRI activity in human visual cortex. Whether this capacity requires coarse-scale orientation biases is controversial. We and others have advocated the use of spiral stimuli to eliminate a potential coarse-scale bias—the radial bias toward local orientations that are collinear with the centre of gaze—and hence narrow down the potential coarse-scale biases that could contribute to orientation decoding. The usefulness of this strategy is challenged by the computational simulations of Carlson (2014), who reported the ability to successfully decode spirals of opposite sense (opening clockwise or counter-clockwise) from the pooled output of purportedly unbiased orientation filters. Here, we elaborate the mathematical relationship between spirals of opposite sense to confirm that they cannot be discriminated on the basis of the pooled output of unbiased or radially biased orientation filters. We then demonstrate that Carlson's (2014) reported decoding ability is consistent with the presence of inadvertent biases in the set of orientation filters; biases introduced by their digital implementation and unrelated to the brain's processing of orientation. These analyses demonstrate that spirals must be processed with an orientation bias other than the radial bias for successful decoding of spiral sense.

Functional magnetic resonance imaging (fMRI) of the blood oxygenation level-dependent (BOLD) signal allows us to observe patterns of activity in the brain (Logothetis, 2008). In human early visual cortex, these activity patterns convey information about characteristics of images presented to the subject such as their form, color, and motion (Kamitani and Tong, 2005, 2006; Haynes and Rees, 2005; Mannion et al., 2009; Freeman et al., 2011, 2013; Alink et al., 2013; Brouwer and Heeger, 2009; Parkes et al., 2009; Goddard et al., 2010), as well as to conjunctions of these attributes (Sumner et al., 2008; Seymour et al., 2009, 2010; Zhang et al., 2014). However, the source of the information in these activity patterns remains a subject of ongoing debate (Op de Beeck, 2010; Kamitani and Sawahata, 2010; Clifford et al., 2011; Freeman et al., 2011, 2013; Alink et al., 2013). Data acquired during fMRI are represented in spatial samples (voxels) whose volume is generally of the order of a few cubic millimeters. This spatial resolution is rather coarser than the scale at which features such as orientation and color have been observed to be mapped onto the surface of mammalian visual cortex (Vanduffel et al., 2002; Yacoub et al., 2008; Xiao et al., 2003, 2007). It has been suggested that information about features such as orientation is nonetheless available at the spatial scale of voxels by virtue of random variability in the spatial distribution of these fine-scale feature maps or their supporting vasculature (Boynton, 2005; Kamitani and Tong, 2005, 2006; Haynes and Rees, 2005; Swisher et al., 2010). However, it has also been claimed that only much coarser scale biases in the way orientation is mapped to the cortical surface allow information about oriented image structure to be recovered from patterns of activity in early visual areas (Freeman et al., 2011, 2013).

One such coarse-scale bias that has been observed in the response of early visual cortex to orientation is radial bias: a preference for orientations radial to the point of fixation. Radial bias has been observed in the topographic representations of the visual field that characterize the early areas of visual cortex (Sasaki et al., 2006; Clifford et al., 2009; Mannion et al., 2010; Freeman et al., 2011, 2013), although it is likely that a component of it is inherited from earlier in the visual pathway (Levick and Thibos, 1982; Schall et al., 1986; Shou and Leventhal, 1989; Smith et al., 1990). When subjects are presented with a wide-field, obliquely oriented grating, for example, the response in the two quadrants of the visual field where the orientation is close to radial is typically larger than the response to the opposite oblique orientation (Sasaki et al., 2006). Thus, simply observing the pattern of activity across the four quadrants of early visual areas would be sufficient to discriminate which of two oblique orientations is being viewed by the subject (Fig. 1).

To remove the confounding effect of radial bias on information about spatial image structure, several studies have used spirals as stimuli (Mannion et al., 2009; Seymour et al., 2010; Alink et al., 2013; Freeman et al., 2013). The logic of this manipulation is that, in a pair of

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http://dx.doi.org/10.1016/j.neuroimage.2014.12.055
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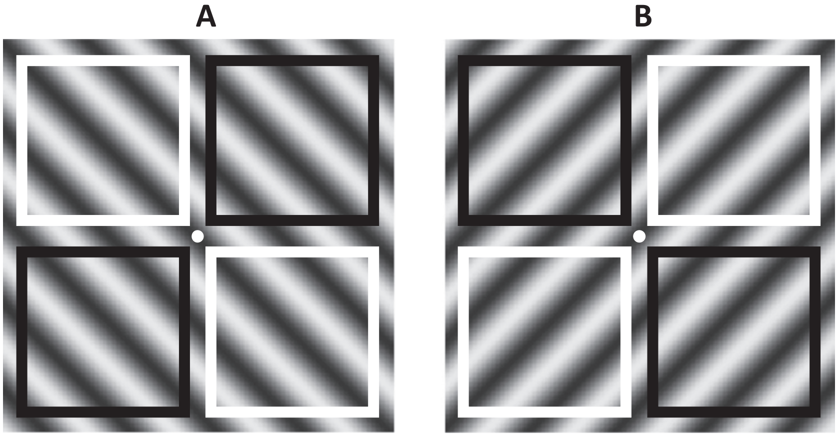

Fig. 1. Local orientation structure of oblique gratings relative to fixation. (A) For a centrally fixating observer viewing an oblique grating, two diagonally opposite quadrants of the visual field (outlined in white) contain predominantly radial orientations while the orientations in the other two quadrants (outlined in black) are predominantly tangential. (B) This configuration is reversed for an orthogonal grating.

spirals of opposite sense, the local orientation at corresponding points in the two images is always at equal but opposite angles from radial (Fig. 2A). Formally, let I_+ and I_- be two similar spirals of opposite sense:

$$I_+(r,\theta) = \exp(i*(k_r r + k_\theta \theta + \varphi_0))*W(r) \tag{1}$$

$$I_-(r,\theta) = \exp(i*(k_r r - k_\theta \theta + \varphi_0))*W(r) \tag{2}$$

where k_r and k_θ are the radial and angular frequency, respectively, of the spiral, $W(r)$ is any circularly symmetric stimulus window, and φ_0 determines the spatial phase.

Then, for any meridian orientation θ_0:

$$I_-(r,\theta-\theta_0) = \exp(i*(k_r r - k_\theta(\theta-\theta_0) + \varphi_0))*W(r) \tag{3}$$

$$I_-(r,\theta-\theta_0) = \exp(i*(k_r r + k_\theta(\theta_0-\theta) + \varphi_0))*W(r) \tag{4}$$

$$I_-(r,\theta-\theta_0) = I_+(r,\theta_0-\theta) \tag{5}$$

Thus, spirals of opposite sense are mirror images of one another over any meridian (Fig. 2B) and a bias to response more strongly to radial orientations will provide no information upon which to discriminate which of two opposite spirals is being viewed. It is also evident that a

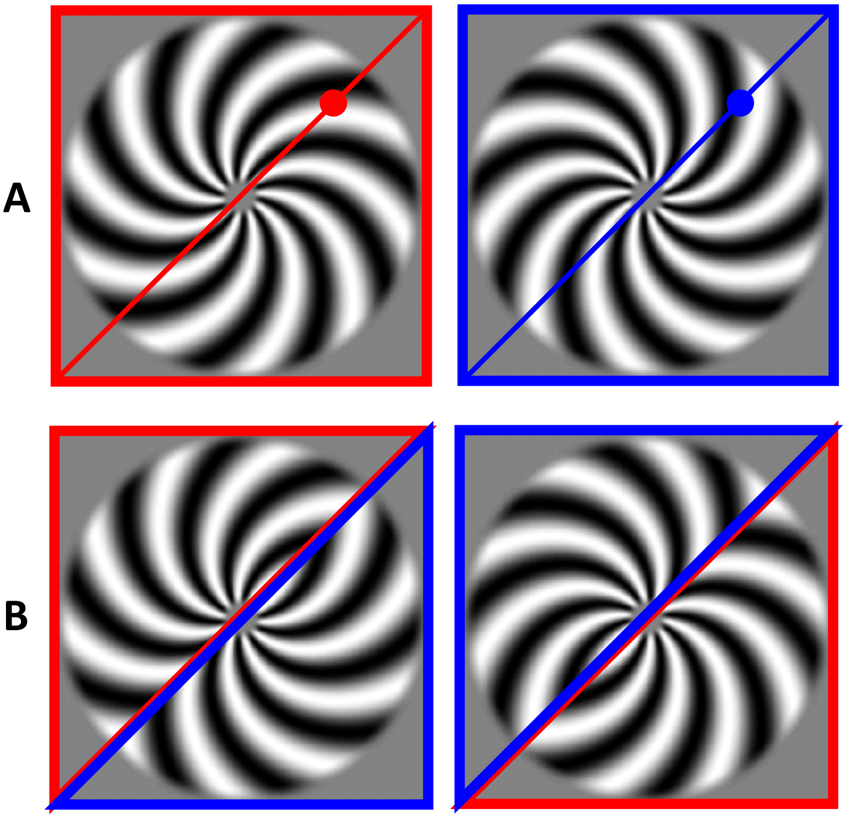

Fig. 2. Symmetry between spirals of opposite sense. (A) In a pair of spirals of opposite sense, local image orientation at corresponding points in the two images is always at equal but opposite angles from radial. (B) Spirals of opposite sense are mirror images of one another over any meridian.