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Cortical specialization for concentric shape processing

Serge O. Dumoulin *, Robert F. Hess

McGill Vision Research Unit, Department of Ophthalmology, McGill University, Montréal, Canada

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Abstract

It is current dogma that neurons in primary visual cortex extract local edges from the scene, from which later visual areas reconstruct more meaningful shapes. In intermediate areas, such as area V4, responses are driven by features more complex than local oriented edges but more basic than meaningful shapes. The present study was motivated by the proposal that concentric (circular) shape processing is an important aspect of intermediate shape processing and is proposed to occur in area V4. However, previous studies are not able to discriminate between the number of orientations within the image nor how these orientations vary across space (orientation gradient, contrast or curvature) as opposed to concentric shape processing *per se*. We address the question whether V4 responses are driven by curvature or circularity. We use fMRI and tightly controlled narrowband stimuli with identical local and global properties. These patterns either form random or circular patterns with tightly matched orientation gradients and therefore similar curvature. We find stronger responses to circular patterns in areas V3/VP and V4. Our results suggest that extracting circular shape is an important step in intermediate shape processing.

Keywords: Functional brain imaging; fMRI; Spatial vision; Form vision; Curvature

1. Introduction

A crucial role of our visual system is to detect and segregate objects. In primary visual cortex (V1) local, oriented edges from the visual scene are extracted (Hubel & Wiesel, 1959, 1962), and V1 has been considered as a bank of oriented filters (De Valois & De Valois, 1988). These filters are the basis of shape perception, from which later visual areas reconstruct more meaningful objects. In intermediate areas, such as area V4, responses are driven by features more complex than local oriented edges but more basic than meaningful objects (Desimone & Schein, 1987; Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Pasupathy & Connor, 1999, 2001, 2002; Pollen, Przybyszewski, Rubin, & Foote, 2002; Schiller & Lee, 1991).

The present study was motivated by the proposal that concentric (circular) shape processing is an important aspect of intermediate shape processing and is proposed to occur in area V4 (Gallant et al., 1993, 1996; Wilkinson et al., 2000; Wilson, Wilkinson, & Asaad, 1997; Wilson & Wilkinson, 1998). This hypothesis is supported by electrophysiological studies describing neurons that respond at least twice as strong to concentric, radial or hyperbolic stimuli than to 1D sinusoidal (parallel) gratings in macaque V4 (Gallant et al., 1993, 1996). Human event-related potentials (ERP) have also reported stronger responses to concentric and radial shapes than to parallel patterns (Pei, Pettet, Vildavski, & Norcia, 2005). The importance of concentric shape processing is further supported by human psychophysics, where sensitivity to shape discrimination has been reported to be the highest for circular shape (Achtman, Hess, & Wang, 2003; Hess, Wang, & Dakin, 1999; Kurki & Saarinen, 2004; Levi & Klein, 2000; Wilson et al., 1997; Wilkinson, Wilson, & Habak, 1998), and sensitivity to closed contours is much higher than nonclosed contours (Kovács & Julesz, 1993). This hypothesis is

* Corresponding author. Present address: Department of Psychology, Stanford University, Stanford, USA.
E-mail address: serge.dumoulin@stanford.edu (S.O. Dumoulin).

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further supported by a study of a patient with a lesion around area V4 that is deficient in concentric shape processing (Gallant, Shoup, & Mazer, 2000). Lastly, using functional magnetic resonance imaging (fMRI) Wilkinson et al. (2000) reported that human V4 responded stronger to concentric and radial shapes than to parallel patterns, confirming the importance of concentric shape processing in humans.

On the other hand, concentric and parallel patterns differ in a number of image properties, such as number of orientations and how these orientations vary across space, either semi-randomly (orientation contrast) or smoothly (curvature). Therefore, these previous studies cannot discriminate between number of orientations, orientation contrast or curvature as opposed to concentric shape processing *per se*. Early visual cortex is known to be modulated by orientation contrast (Allman, Miezin, & McGuinness, 1985; Dumoulin & Hess, 2006; Fitzpatrick, 2000; Kastner, Weerd, & Ungerleider, 2000; Williams, Singh, & Smith, 2003; Zenger-Landolt & Heeger, 2003), and curvature has been proposed to be a critical tuning dimension for early visual cortex (e.g. V2 Ito & Komatsu, 2004) and in particular V4 (Pasupathy & Connor, 1999, 2001, 2002; Pollen et al., 2002). In support of the importance of curvature rather than circularity, psychophysical studies have suggested that it is the curvature smoothness rather than contour closure that is the important factor for determining contour saliency (Hess & Field, 1999; Pettet, McKee, & Grzywacz, 1998). In addition, it has been suggested that some of the psychophysical results indicating higher sensitivity to concentric patterns using rotational glass patterns (Wilson et al., 1997; Wilson & Wilkinson, 1998) may have been influenced by stimulus windowing rather than concentric processing *per se* (Dakin & Bex, 2002), although this has been challenged in an ERP study (Pei et al., 2005). Finally, the patient deficient in concentric shape discrimination was also deficient in curvature perception (Gallant et al., 2000). Therefore, the key question that we address is: is this proposed concentric shape processing driven by concentric structure or more general image properties such as curvature?

Second, in their fMRI study, Wilkinson et al. (2000) only showed data limited to V1, V4 and a region particularly responsive to viewing of faces (fusiform face area; FFA; Kanwisher, McDermott, & Chun, 1997). A similar argument holds for the electrophysiological studies that are limited by the cortical sampling of neurons. Therefore, these previous studies do not establish whether any concentric shape processing is limited to V4. So the second aim of this study is to assess whether any specialization for processing concentric shape is limited to area V4.

We use fMRI and tightly controlled narrowband stimuli composed of Gabors (Achtman et al., 2003; Dumoulin & Hess, 2006) to address these issues. The Gabors were arranged to create either non-circular patterns or circular patterns. These patterns are matched both locally and globally in terms of total orientations and how orientations are distributed across space (orientation contrast and curvature) and thus allow us to address the as yet unanswered question of whether it is the orientation contrast/curvature or circularity that drives V4 responses.

2. Materials and methods

2.1. Subjects

Four experienced psychophysical observers were used as subjects (all male, mean age: 39, age range: 30–54). The subjects were instructed to fixate at a provided fixation-point and trained prior to the scanning session to familiarize them with the task. All observers had normal or corrected-to-normal visual acuity. All studies were performed with the informed consent of the subjects and were approved by the Montréal Neurological Institute Research Ethics Committee.

2.2. Visual stimuli

For a more detailed description of the stimuli see Dumoulin and Hess (2006). The visual stimuli were generated in the MatLab programming environment and displayed using the PsychToobox (Brainard, 1997; Pelli, 1997) on a Macintosh G4 Powerbook, and displayed on a LCD projector (NEC Multisync MT820). The visual display subtended 20 degrees (diameter).

The stimuli were constructed from 625 oriented Gabors, i.e. a 1D sine-wave enclosed in a 2D Gaussian envelope ($\lambda = 0.2$ and $\sigma = 0.1$ degrees), i.e. the spatial frequency content of the images was centered on 5 cycles/degree. The positions of the Gabors were jittered (-0.4 to 0.4 degrees) around a square grid centered on the image matrix (grid distance = 0.8 degrees). The contrast of each Gabor was randomly chosen from a uniform distribution (contrast range = 25–100%). The global orientation content was controlled to be isotropic between 0 and 360 degrees.

Two different stimuli types were used (see Fig. 1). In one stimulus type the Gabor array formed 10 circles with random centers (Fig. 1a), in the other the Gabors formed random arrays were the local orientation smoothness or contrast was constrained to be similar to the circular shapes (Fig. 1b; for more detail on the creation of these images see Appendix A). We will refer to these types of images as ''circle'' and ''flowfield'' images. The orientation difference of neighboring Gabors as a function of the Gabor euclidean distance was used to match the orientation gradient of the flowfield images to that of the circular images. The orientation gradient is identical between the two image types indicating that the stimuli have similar curvature (Fig. 1c). Therefore, the only difference between the stimulus conditions was the presence or absence of circular structure.

The different stimulus conditions were alternated in a block design (block duration 12 s). Each condition (block) was repeated at least five times giving a total duration of approximately 6 min per scan. The stimuli were presented time-locked to the acquisition of fMRI time-frames, i.e. every 3 s. To control for attention, the subjects continuously performed a two-interval forced-choice (2IFC) contrast-discrimination task. That is, a given stimulus presentation consisted of two intervals, both displaying a different image from the same condition either at full or reduced (0.7×) contrast. The subject indicated which interval contained the high contrast stimulus. Each image was presented for 500 ms and the inter-stimulus interval was 500 ms. In the remaining 1.5 s the subjects' responses were recorded. During mean luminance (blank) conditions an identical task was performed for the fixation dot. The subjects' performance was on average 75% correct.

2.3. Magnetic resonance imaging

The magnetic resonance images were acquired with a Siemens Sonata 1.5T MRI. The experiments were conducted with the subjects lying on their back with a surface-coil (circularly polarized, receive only) centered over their occipital poles. Head position was fixed by means of a foam head-rest and a bite-bar.