Vision Research 109 (2015) 107–121

Contents lists available at ScienceDirect

Vision Research

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

Functional and anatomical properties of human visual cortical fields

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ARTICLE INFO

Article history:
Received 7 March 2014
Received in revised form 29 December 2014
Available online 4 February 2015

Keywords:
Cortical surface
Visual cortical fields
Cortex
FA
MTR
T1/T2

ABSTRACT

Human visual cortical fields (VCFs) vary in size and anatomical location across individual subjects. Here, we used functional magnetic resonance imaging (fMRI) with retinotopic stimulation to identify VCFs on the cortical surface. We found that aligning and averaging VCF activations across the two hemispheres provided clear delineation of multiple retinotopic fields in visual cortex. The results show that VCFs have consistent locations and extents in different subjects that provide stable and accurate landmarks for functional and anatomical mapping. Interhemispheric comparisons revealed minor differences in polar angle and eccentricity tuning in comparable VCFs in the left and right hemisphere, and somewhat greater intersubject variability in the right than left hemisphere. We then used the functional boundaries to characterize the anatomical properties of VCFs, including fractional anisotropy (FA), magnetization transfer ratio (MTR) and the ratio of T1W and T2W images and found significant anatomical differences between VCFs and between hemispheres.

1. Introduction

Mapping the location and extent of the visual cortical fields (VCFs) is a prerequisite for precise neuroimaging studies of human visual cortex (Wandell, Dumoulin, & Brewer, 2007). The methods used to functionally define VCFs using retinotopic stimuli are well established and have been used in many previous studies (DeYoe et al., 1996; Dumoulin et al., 2003; Engel, Glover, & Wandell, 1997; Sereno et al., 1995; Sereno, McDonald, & Allman, 1994; Wandell, Brewer, & Dougherty, 2005; Warnking et al., 2002). Usually, VCF boundaries have been identified manually. Recently, several automatic methods have been proposed to define VCF borders objectively in order to support quantitative analysis (Dougherty et al., 2003; Dumoulin et al., 2003; Warnking et al., 2002). However, because VCFs vary in size (Dougherty et al., 2003) and precise anatomical location (Dumoulin et al., 2000) in individual subjects, the accuracy of analysis of VCF properties using boundaries defined in across-subject averages will be limited by the consistency of VCF anatomical locations and orientations across subjects.

In addition to VCF properties defined by functional data analysis, several recent MRI studies have combined retinotopic maps with anatomical information (Benson et al., 2012; Sereno et al., 2013). Benson et al. (2012) used standard T1-weighted anatomical images alone to predict the retinotopic organization of striate cortex and showed that higher-order cortical areas (e.g., V2) were more variable in anatomical locations than primary areas such as V1. Sereno et al. (2013) found that the borders of VCFs were associated with significant changes in quantitative relaxation rate ($R_1 = 1/T_1$). The addition of anatomical data may be particularly useful in defining VCFs, especially in light of the recent failures of BOLD functional imaging to detect certain kinds of visual cortical activity (Sirotin & Das, 2009; Swettenham, Muthukumaraswamy, & Singh, 2013). This suggests that functional neuroimaging alone may face limits in defining VCF boundaries and functional properties.

A reasonable starting point for examining the anatomical properties of VCFs is to focus on the analysis of myelin, because of the well-known line of Gennari, a dark band of heavily myelinated fibers that characterizes V1 (Hinds et al., 2009, 2008; Sanchez-Panchuelo et al., 2012). To this end we used three different MR sequences to analyze white matter properties: fractional anisotropy (FA), measured with diffusion tensor imaging (DTI), which is sensitive to the integrity and organization of axons

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http://dx.doi.org/10.1016/j.visres.2015.01.015
0042-6989/

(Le Bihan, 2003). The magnetization transfer ratio (MTR), estimated from magnetization transfer imaging (MTI), which is sensitive to the density of cell membranes and myelin (Bastin et al., 2009; Schiavone et al., 2009; Vrenken et al., 2010). Finally, the ratio of T1-weighted (T1W) and T2-weighted (T2W) images, T1/T2, which has been found to reflect the myelin content and areal boundaries of cortical sensory areas (Glasser & Van Essen, 2011). Thus, the combined use of FA, MTR and T1/T2 provides a relatively complete picture of white matter structure and tissue properties (Bastin et al., 2009; Kang, Herron, & Woods, 2011; Vrenken et al., 2010).

Surface-based analysis of human cerebral cortex increases the power and precision anatomical investigations (Anticevic et al., 2008; Van Essen et al., 1998), and enhances the magnitude and significance of functional activations (Argall, Saad, & Beauchamp, 2006; Hagler, Saygin, & Sereno, 2006; Jo et al., 2007; Van Essen, 2005). Aligning the anatomical and functional data to the gyral and sulcal structures of the cortical surface permits the visualization of the average organization of visual cortex (Cate et al., 2012; Van Essen & Dierker, 2007; Wandell & Winawer, 2011). FreeSurfer (Fischl et al., 1999) is a popular surface-based tool that inflates each hemispheric surface and aligns the inflated hemispheres to the templates of the left and right hemispheres. The left and right hemispheres can be further aligned to a hemispherically unified spherical coordinate system (Kang et al., 2012) through optimal rigid-body spherical transformation.

The use of a single coordinate system combined across hemispheres permits direct comparisons of the VCF properties of the two hemispheres. Previous studies (Benson et al., 2012; Dumoulin et al., 2003; Wandell, Dumoulin, & Brewer, 2007; Wu et al., 2012) have compared the interhemispheric anatomical or functional properties of VCFs using individual hemispheres' data, e.g., by making separate measurements of a field's extent or area in each hemisphere. Visualizing the average (or the difference) of two hemispheres' maps in the same global space allows the visualization of more complex interhemispheric difference that might not emerge by comparing scalar features such as extent or thickness. For example, hemispheric differences in thickness in a particular VCF may be non-uniform; e.g., concentrated in an anatomical subregion.

Anatomical studies of post-mortem brains have found minimal interhemispheric differences in the extent of V1. Rademacher et al. (1993) reported that area 17 generally showed close bilateral symmetry in area and extent. In 8 out of 10 brains, interhemispheric asymmetries in V1 size averaged less than 8%. A more recent MRI study of post-mortem brains (Hinds et al., 2008) reported differences in the parameters required to align V1 in the two hemispheres, and, more importantly, noted that the average V1 overlap across subjects was higher in the left hemisphere than in the right (70.6% vs. 58.5%). Using anatomical techniques, Amunts et al. (2000) found that the mean volume of area 17 did not differ between the hemispheres. In contrast, fMRI studies using retinotopic stimuli, have reported that V1 is larger in the left than in the right hemisphere (1578 vs. 1362 mm^2) (Dougherty et al., 2003). However, such interhemispheric differences may be influenced by methodological procedures. Although the location of functionally-defined V1 is closely reflected in patterns of cortical curvature (Benson et al., 2012), cortical-surface based coregistration methods apply modest amounts of areal distortion in order to align deep sulci like the calcarine sulcus (Kang et al., 2012). Therefore, to correct for distortion, we analyzed V1 areal asymmetries in native anatomical space using the functional boundaries that were defined on inflated cortical surfaces.

In the current manuscript, we used Mollweide (MW) projection maps (Feeman, 2000; Yang, Snyder, & Tobler, 2000) of the cortical surface to display functional and anatomical data, e. g. FA and MTR, etc., averaged over the left and right hemispheres on a flattened two-dimensional (2D) map. Such MW projections introduce less distortion than alternative projection methods (Kang et al., 2012). FA, MTR and T1/T2 were analyzed in VCFs defined individually from the visual field maps for each of 11 subjects, and the average of all subjects were displayed on the 2D MW projection map. These parameters were also analyzed to describe the anatomical properties in visual cortex fields on five surfaces around the gray matter (GM)/white matter (WM) boundary.

2. Materials and methods

2.1. Subjects and MR scans

We studied 11 young, right-handed subjects (5 females, ages 18–33 years, mean 24.2 years). All subjects had normal or corrected visual acuity. Ethics approval for the study was granted by Institutional Review Board of the Northern California Health Care System within the US Department of Veterans Affairs. Informed, written consent was obtained from all of the subjects, and subjects were paid for their participation.

All subjects underwent anatomical and functional scans on a 3 T Siemens Verio scanner (Syngo MR B17). The scans include: (1) two high-resolution MPRage images (TR = 3000 ms, TE = 1.62 ms, flip angle = 9°, voxel size $1 \times 1 \times 1$ mm); (2) high resolution T2W image (TR = 2000 ms, TE = 409 ms, variable flip angle, voxel size $1 \times 1 \times 1$ mm); (3) two sets of DTI scans (TR = 10700 ms, TE = 95 ms, flip angle = 15°, b = 1500 s/mm^2, 30 directions, 5 b = 0 images, voxel size $2 \times 2 \times 2$ mm, 1 field map) with the second DTI directions reversed to reduce the non-affine geometry distortions in plane (Shen et al., 2004); (4) two MTI scans with and without the MT pulse (TR = 2600 ms, TE = 13.3 ms, flip angle = 70°, voxels size $2 \times 2 \times 2$ mm; MT offset and amplitude); and (5) four sets of functional EPI scans with different stimuli (TR = 2510 ms, TE = 30 ms, flip angle = 90°, voxels size $3 \times 3 \times 4$ mm, 1 field map). Subjects' heads were stabilized with foam pads to reduce head motion.

2.2. Stimuli for EPI scans

Visual stimulus presentation and response collection were controlled by Presentation software (Version 15.1, Neurobehavioral Systems, Inc., Berkeley, CA). Stimuli were projected onto a screen located near the subjects' feet using a Sanyo PLC-XU116, XGA 3LCD 4500 lumen projector set outside the scanning room. Subjects viewed the screen through an angled mirror attached to the head coil at a viewing distance of 260 cm. The display was adjusted to be of maximal size viewable from the center of the scanner bore, with a field of view of 12.5° (horizontal) and 10.2° (vertical).

Retinotopic fields were measured by delivering standard rotating wedge and expanding ring stimuli (Fig. 1) that induce waves of neural activity in the visual cortex (Warnking et al., 2002). All the stimulus patterns were achromatic checkerboards flickering at 8 Hz with 97% contrast. The wedge and the maximal ring had the same radius (10° of visual angle). To measure the polar angle representation, a single wedge was rotated in (balanced) clockwise and counterclockwise directions around a fixation cross at the center of the display. The wedge spanned 60° and rotated at steps of 20°, remaining at each position for 2510 ms, i.e., at the repetition time (TR) of the scan sequence. Thus, the wedge completed a full rotation every 45.18 s. Eccentricity was mapped by using expanding or contracting rings completing a full expansion (or contraction) every 45.18 s. As with the wedge, the ring-stimulus expanded or contracted in 18 discrete steps (i.e., at each 2510 ms TR). During each imaging session, four runs of data were obtained: one run