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Radial asymmetries in population receptive field size and cortical magnification factor in early visual cortex

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ABSTRACT

Human visual cortex does not represent the whole visual field with the same detail. Changes in receptive field size, population receptive field (pRF) size and cortical magnification factor (CMF) with eccentricity are well established, and associated with changes in visual acuity with eccentricity. Visual acuity also changes across polar angle. However, it remains unclear how RF size, pRF size and CMF change across polar angle. Here, we examine differences in pRF size and CMF across polar angle in V1, V2 and V3 using pRF modeling of human fMRI data. In these visual field maps, we find smaller pRFs and larger CMFs in horizontal (left and right) than vertical (upper and lower) visual field quadrants. Differences increase with eccentricity, approximately in proportion to average pRF size and CMF. Similarly, we find larger CMFs in the lower than upper quadrant, and again differences increase with eccentricity. However, pRF size differences between lower and upper quadrants change direction with eccentricity. Finally, we find slightly smaller pRFs in the left than right quadrants of V2 and V3, though this difference is very small, and we find no differences in V1 and no differences in CMF. Moreover, differences in pRF size and CMF vary gradually with polar angle and are not limited to the meridians or visual field map discontinuities. PRF size and CMF differences do not consistently follow patterns of cortical curvature, despite the link between cortical curvature and polar angle in V1. Thus, the early human visual cortex has a radially asymmetric representation of the visual field. These asymmetries may underlie consistent reports of asymmetries in perceptual abilities.

Introduction

The representation of visual space in the cortical visual field maps influences how we see the world. As visual field eccentricity increases across a visual field map, neural receptive field (RF) and population receptive field (pRF) sizes increase, and cortical magnification factor (CMF) decreases (Dow et al., 1981; Duncan and Boynton, 2003; Harvey and Dumoulin, 2011; Hubel and Wiesel, 1974; Smith et al., 2001). Both increases in RF/pRF size and decreases in CMF imply a coarser neural representation of visual space. Indeed, visual acuity and other metrics of perceptual performance decrease with visual field eccentricity (Duncan and Boynton, 2003; Strasburger et al., 2011). Recent human fMRI studies have linked differences in perceptual performance to the large differences in pRF size and CMF across eccentricity (Duncan and Boynton, 2003) and between individuals (Song et al., 2015).

There is also behavioral evidence of smaller differences in visual perceptual performance for stimuli presented at the same eccentricity at different polar angles: above, below, left and right of fixation (for a review see (Karim and Kojima, 2010)). However, it remains unclear how RF/pRF size and CMF change with polar angle. Given these perceptual asymmetries, we hypothesize that there may be small variations in RF size and CMF across polar angle in early visual cortex. Here we set out to measure these variations using pRF modeling from fMRI data.

Several technical limitations have complicated neurophysiological investigation of this question. First, large differences in receptive field size and CMF across eccentricity can obscure smaller differences across

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polar angle. Differences across polar angle are difficult to resolve if comparing recordings made at different eccentricities, and it is very difficult to find pairs of individual neurons at the same eccentricity in single-unit recordings. Second, individual animals and humans differ considerably in RF size, pRF size and CMF (Dougherty et al., 2003; Harvey and Dumoulin, 2011; Van Essen et al., 1984), necessitating large numbers of measurements in the same individual. It is difficult to measure from large numbers of single neurons in a single visual field map of a single animal. FMRI measurements are well suited to analyze these changes across the visual field map because they distribute recording sites densely and evenly across cortex. Taking advantage of this technique, we can make paired comparisons between recording sites at different polar angles, but at the same eccentricity and in the same subject. Third, changes in CMF with polar angle differ between species and individual animals (Van Essen et al., 1984), so it is unclear how results from small numbers of primates would generalize to the human population. Here we used a larger number of human subjects.

Despite these complications, some neurophysiological studies have shown changes in CMF with polar angle in V1 (Adams and Horton, 2003; Tootell et al., 1988; Van Essen et al., 1984). However, these CMF differences may simply result from V1's strong relationships between polar angle and cortical folding, which could cause certain polar angles to cover larger areas of the surface (i.e. have larger CMF) (Dahlem and Tusch, 2012). Therefore, CMF differences may be a byproduct of anatomical constraints and have no functional consequence. On the other hand, these CMF differences may have functional consequences regardless of whether they result from cortical folding differences. These possibilities could be distinguished by examining changes in pRF size together with CMF: RF/pRF size and CMF differences between individuals and across eccentricity are closely related (Harvey and Dumoulin, 2011; Hubel and Wiesel, 1974). Furthermore, V1's relationships between cortical folding, available cortical surface area and polar angle would not apply to V2 and V3. However, functional properties of one visual field map are often mirrored in its neighbors. Therefore, we examine changes in pRF size as well as CMF across both polar angle and cortical curvature, and extend these measurements into V2 and V3.

With this approach, we revealed smaller pRFs and larger CMFs in the horizontal (left and right) than the vertical (upper and lower) visual field quadrants, implying a finer representation of the visual field in these quadrants. PRFs were also smaller and CMFs larger in the lower than upper quadrant in most visual field maps, and pRFs were smaller in the left than right quadrant in V2 and V3. These differences typically increased with eccentricity. They were not limited to the meridians or discontinuities in the visual field maps, but varied gradually with polar angle to reach maxima and minima at the meridians. These results demonstrate that the early human visual cortex does not have a radially symmetrical representation of the visual field. We speculate that these small asymmetries in the neural representation may underlie reports of asymmetries in perceptual performance in different parts of the visual field.

Materials and methods

The data acquisition and most of the analyses follow the protocols used in a previous study of the relationship between pRF size and CMF and across eccentricity (Harvey and Dumoulin, 2011). Here, we added eleven further subjects to our existing pool of eleven right-handed subjects, and added new analyses to examine changes in pRF size and CMF across polar angle.

Subjects

Twenty-two healthy right-handed subjects participated in this study (age range 22–46 years, 8 female). To restrict comparisons between left and right visual quadrants to subjects with the same dominant hemisphere, we excluded left-handed subjects using the Edinburgh handedness inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal visual acuity. Experiments were undertaken with the informed written consent of each subject. All experimental procedures were cleared by the ethics committee of University Medical Center Utrecht.

MRI acquisition

We acquired functional and anatomical MRI data on a Philips Achieva 3T scanner (Philips Medical Systems, Best, Netherlands) with a Quasar Dual gradient set. We acquired T1-weighted anatomical MRI data at $0.75 \times 0.75 \times 0.8$ mm spatial resolution. Flip angle was set to 8°, repetition time (TR) was 10.029 ms, and echo time (TE) was 4.6 ms. We acquired T2*-weighted functional 2D echo planar images at $2.5 \times 2.5 \times 2.5$ mm spatial resolution, with 24 slices. Flip angle was set to 70°, TR was 1500 ms, and TE was 30 ms. Each functional scan was 248 time frames (372 s) in duration, the first eight time frames (12 s) of which were discarded. We acquired seven to ten repeated scans within the same session for each subject.

Stimulus presentation setup

We back-projected visual stimuli onto a 101×76 cm screen viewed through a mirror attached to the MRI coil. The screen was 348 cm from the subject's eyes, via the mirror, and its resolution was 800×600 pixels. We constrained stimuli to a circular area filling the screen's vertical dimension. Any area outside this circle remained at constant mean luminance. The stimulus circle was 6.25° of visual angle in radius, from the subject's viewpoint.

Visual stimuli

We generated the visual stimuli using the PsychToolbox for Matlab (Brainard, 1997; Pelli, 1997). They consisted of drifting bar apertures at various orientations, which exposed a checkerboard pattern with 100% contrast moving parallel to the bar's orientation (Dumoulin and Wandell, 2008). Alternating rows of checks moved in opposite directions. The motion direction of the checks reversed at random intervals, with 4 s minimum between reversals. The bar width and the fundamental spatial frequency of the checks was 1.56°. The bar stepped across the stimulus aperture in 20 equally spaced steps of 0.625° each. The bar stepped at the start of each functional volume acquisition, so took 20 TRs (30 s) to cross the stimulus circle. In each scan, we showed 4 bar orientations each stepping in two opposite directions, making a total of 8 bar motion directions (upwards, downwards, left, and right, alternated with four diagonals). We displayed 30 s of mean luminance display with no bar after each horizontal or vertical bar orientation pass, at regularly spaced intervals through the scanning run.

Subjects fixated a dot in the center of the visual stimulus, which changed colors at random intervals between red and green. Subjects pressed a button on a response box every time the color changed to ensure attention and fixation were maintained. Color changes were every 3 s on average, with a minimum change interval of 1.8 s. We discarded any scan where detection performance dropped below 75% (2 scans of 1 subject).

Preprocessing of anatomical and functional images

We analyzed fMRI data in the mrVista software package for MATLAB, available at (http://white.stanford.edu/software/). For each subject, we resampled T1-weighted anatomical scans to 1 mm^3 resolution. We automatically segmented the resulting anatomical image using FSL (Smith et al., 2004), then hand-edited it to minimize segmentation errors (Teo et al., 1997). We reconstructed the cortical surface at the gray-white matter border. We rendered this as a smoothed 3D surface (Wandell et al., 2000). We measured and corrected for head movement and motion