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Systematic variation of population receptive field properties across cortical depth in human visual cortex

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ABSTRACT

Receptive fields (RFs) in visual cortex are organized in antagonistic, center-surround, configurations. RF properties change systematically across eccentricity and between visual field maps. However, it is unknown how center-surround configurations are organized in human visual cortex across lamina. We use sub-millimeter resolution functional MRI at 7 Tesla and population receptive field (pRF) modeling to investigate the pRF properties in primary visual cortex (V1) across cortical depth. pRF size varies according to a U-shaped function, indicating smaller pRF center size in the middle compared to superficial and deeper intra-cortical portions of V1, consistent with non-human primate neurophysiological measurements. Moreover, a similar U-shaped function is also observed for pRF surround size. However, pRF center-surround ratio remains constant across cortical depth. Simulations suggest that this pattern of results can be directly linked to the flow of signals across cortical depth, with the visual input reaching the middle of cortical depth and then spreading towards superficial and deeper layers of V1. Conversely, blood-oxygenation-level-dependent (BOLD) signal amplitude increases monotonically towards the pial surface, in line with the known vascular organization across cortical depth. Independent estimates of the haemodynamic response function (HRF) across cortical depth show that the center-surround pRF size estimates across cortical depth cannot be explained by variations in the full-width half maximum (FWHM) of the HRF.

Introduction

The visual cortex is organized at different spatial scales, ranging from microscopic (individual neurons) to mesoscopic (cortical columns and layers) and macroscopic (visual field maps and pathways) scales. Neurons within visual cortex process only a local extend of visual space: the classical receptive field (RF). The RFs are typically organized in an antagonistic fashion: the responses to stimulation in the classical RFs are modulated by stimulation in the extra-classical RF (or surround). These modulations can be excitatory or inhibitory and have been characterized in detail by electrophysiological and psychophysical studies (Hubel and Wiesel, 1968; Allman et al., 1985; Cavanaugh et al., 2002). Furthermore, RF properties change systematically along the various spatial scales of the visual hierarchy.

Human functional magnetic resonance imaging (fMRI) can segregate the cortex into regions that contain separate maps of the visual field (Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996). Recently, population receptive field (pRF) properties have been estimated using fMRI in humans (Dumoulin and Wandell, 2008; Kay et al., 2008). These pRF properties are estimated in degrees of visual angle and resemble those measured with neurophysiology, including suppressive surrounds (Zuiderbaan et al., 2012), and systematic changes within and between visual field maps (Dumoulin and Wandell, 2008; Amano et al., 2009; Winawer et al., 2010; Harvey and Dumoulin, 2011). Here we extend these measurements of antagonistic pRF properties to the mesoscopic scale using sub-millimeter resolution 7 Tesla fMRI and pRF modeling. Several recent studies investigated the laminar variation of blood-oxygenation-level-dependent (BOLD) signal in humans (Ress et al., 2007; Polimeni et al., 2010; Koopmans et al., 2010, 2011; Siero et al., 2011; Zimmermann et al., 2011; Olman et al., 2012; Chen et al., 2013; De Martino et al., 2013; Huber et al., 2014, 2015), non-human primates (Goense and Logothetis, 2006; Goense et al., 2007, 2012) and

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other mammals (Silva and Koretsky, 2002; Harel et al., 2006; Jin and Kim, 2008), but none of the aforementioned studies investigated the cortical depth dependence of pRF properties.

The cortex is divided into six functionally and structurally distinct layers. In primary visual cortex (V1), information arrives indirectly from the retina through afferents from the lateral geniculate nucleus (LGN), and enters the cortex mainly (but not exclusively) in layer 4 (granular layer, Sincich and Horton, 2005). After the first synapse in the granular layer, information rapidly spreads along cortical depth towards supra- and infra-granular layers (Self et al., 2013). The local neural circuitry across this layered structure underlies crucial stages in early visual processing, as the functions of extra-striate visual cortical areas receiving input from V1 are based on the patterns generated in V1 (Callaway, 1998).

It is unknown how the size of center-surround configurations is organized in human V1 across lamina. Using invasive neurophysiology, neural RF sizes vary across cortical layers in rat somatosensory and visual cortex (Chapin, 1986; Vaiceliunaite et al., 2013; Self et al., 2014). On the other hand, in macaque V1 how RF sizes vary across cortical layers is not as clear cut. Hubel and Wiesel (1972, 1977) point out that there is a correlation between complexity and layering, where the cells in layer IV tend to be least complex with smaller RFs. On the other hand, Sceniak et al. (2001) and Shushruth et al. (2009) report approximately constant RF sizes across lamina except for larger RF sizes in layer 6. Sceniak and colleagues also report surround suppression greatest in layer 4B and weakest in layer 6, whereas others report that far surrounds are larger outside input layer 4 (Shushruth et al., 2009; Angelucci et al., 2002).

Here we estimate the size of center-surround configurations across cortical depth in human V1. We demonstrate systematic and balanced center-surround changes across cortical depth. These changes cannot be explained by variations of the haemodynamic response properties. These results extend our knowledge on pRF properties in early visual cortex, showing that their change is not limited across eccentricity and visual field map hierarchy (Dumoulin and Wandell, 2008), but also extends across cortical depth, suggesting a balanced center-surround relationship within the laminar hierarchy.

Methods

Participants

Four males participated in the experiment (age range 30–40 years). Two participants were naïve to the experiment purpose. All participants have normal or corrected-to-normal visual acuity. All experimental procedures were conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki (most recently amended in 2008, Seoul), and cleared by the ethics committee of the University Medical Center Utrecht.

Visual stimuli setup

Visual stimuli were presented by back-projection onto a 15.0 × 7.9 cm screen inside the MRI bore. Participants viewed the display through prisms and mirrors, and the total distance from the participant's eyes (in the scanner) to the display screen was 35 cm. Display resolution was 1024 × 538 pixels. The stimuli were generated in Matlab (Mathworks, Natick, MA, USA) using the PsychToolbox (Brainard, 1997; Pelli, 1997).

V1 definition and pRF modeling at conventional resolution

The primary visual cortex field map was reconstructed using near-identical procedures as in previous studies (Dumoulin and Wandell, 2008; Amano et al., 2009; Winawer et al., 2010; Harvey and Dumoulin, 2011). Stimuli consisted of drifting bar apertures at four orientations, which exposed a checkerboard pattern moving parallel to the bar orientation (Dumoulin and Wandell, 2008). Alternating rows of checks moved in opposite directions, and orthogonally with respect to the bar orientation. The bar width (and width of alternating white and black checks) subtended one-quarter of the stimulus radius (1.56 degrees of visual angle). The bar moved across the stimulus aperture in 20 evenly spaced steps, each 0.625 degrees of visual angle, 1/20th of the stimulus window diameter. As there was one step at the start of each functional volume acquisition, each pass of the stimulus lasted for 20 acquisition repetitions (TRs), 30 s. Four bar orientations and two different motion directions for each bar were presented, giving a total of eight bar motion directions (upward, downward, left, right, and four diagonals) within each run (the same stimuli order was presented for each run). After each horizontal or vertical bar orientation pass, a 30 s of mean-luminance (zero contrast) stimulus was displayed. Four mean-luminance blocks were presented at regular intervals during the scan. Participants fixated on a dot in the center of the visual stimulus. The model estimates a pRF for every voxel using a method previously described (Dumoulin and Wandell, 2008). We used the position estimates of the pRF to define V1. Area V1 was defined on T1-weighted anatomical MRI data with a voxel size of 0.8 × 0.8 × 0.8 mm (resampled at 1 mm isotropic). Repetition time (TR) was 7 ms, echo time (TE) was 2.84 ms and flip angle was 8°. Functional T2*-weighted multi-slice echo-planar images (EPIs) were acquired using a Philips Achieva 7 T scanner (Best, Netherlands), a volume transmit coil for excitation and a 32-channel head coil for signal reception (Nova Medical, MA, USA). Acquisition parameters were: TR/TE: 1500/30 ms, flip angle: 70°, voxel size: 2 mm isotropic, and 24 coronal slices. Functional scans were each 248 time frames (372 s) in duration, and the first eight time frames were discarded to ensure that signal had reached steady state.

PRF estimation across cortical depth: Visual stimuli and imaging

Sub-millimeter functional imaging is characterized by relatively slow repetition time (TR = 4 s in our experiment, see methods below). This limited the number of time-points available in our time-series (72 time points for each time-series, see methods below). Due to this limitation, we aimed to keep the number of parameters estimated from each time-series at minimum, in order to maximize the number of degrees of freedom at the modeling stage. To this aim, the visual stimuli used to map pRF across cortical depth consisted of an expanding and a contracting ring aperture (Fig. 1A), which exposed a checkerboard pattern moving radially (Dumoulin and Wandell, 2008). Using this stimulus, for each ring step at a given eccentricity and TR, we stimulate all pRFs at that specific eccentricity. This allows us to estimate 3 main parameters: the optimal eccentricity, center pRF size and surround pRF size for each responsive voxel, instead of the 4 main parameters usually derived from pRF modeling: optimal × position, y position, center pRF size and surround pRF size.

Alternating rows of checks moved in opposite directions. The ring width subtended 0.5 degrees of visual angle and moved across the stimulus aperture in 12 evenly spaced steps, each 0.25 degrees of visual angle (Fig. 1A). Each pass of the stimulus lasted for 12 acquisition repetitions (TRs), 48 s. Two different ring directions were presented (expanding and contracting). After each expanding or contracting ring pass, 20 s of mean-luminance (zero contrast) stimulus was displayed. The stimulation sequence for each run was as follows: expanding ring–contracting ring–contracting ring–expanding ring, with each single part of the stimulation sequence intermixed with the baseline condition (Fig. 1B). Participants were asked to fixate a dot in the center of the visual stimulus and report colour changes; mean performance across runs and participants was 85%.

High resolution functional data were acquired using the 7 T scanner (Philips, Best, Netherlands), and the volume transmit coil for excitation