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A new method for estimating population receptive field topography in visual cortex

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ABSTRACT

We introduce a new method for measuring visual population receptive fields (pRF) with functional magnetic resonance imaging (fMRI). The pRF structure is modeled as a set of weights that can be estimated by solving a linear model that predicts the Blood Oxygen Level-Dependent (BOLD) signal using the stimulus protocol and the canonical hemodynamic response function. This method does not make *a priori* assumptions about the specific pRF shape and is therefore a useful tool for uncovering the underlying pRF structure at different spatial locations in an unbiased way. We show that our method is more accurate than a previously described method (Dumoulin and Wandell, 2008) which directly fits a 2-dimensional isotropic Gaussian pRF model to predict the fMRI time-series. We demonstrate that direct-fit models do not fully capture the actual pRF shape, and can be prone to pRF center mislocalization when the pRF is located near the border of the stimulus space. A quantitative comparison demonstrates that our method outperforms the direct-fit methods in the pRF center modeling by achieving higher explained variance of the BOLD signal. This was true for direct-fit isotropic Gaussian, anisotropic Gaussian, and difference of isotropic Gaussians model. Importantly, our model is also capable of exploring a variety of pRF properties such as surround suppression, receptive field center elongation, orientation, location and size. Additionally, the proposed method is particularly attractive for monitoring pRF properties in the visual areas of subjects with lesions of the visual pathways, where it is difficult to anticipate what shape the reorganized pRF might take. Finally, the method proposed here is more efficient in computation time than direct-fit methods, which need to search for a set of parameters in an extremely large searching space. Instead, this method uses the pRF topography to constrain the space that needs to be searched for the subsequent modeling.

Introduction

One of the great achievements of fMRI is the in-vivo characterization of the functional organization of the human visual cortex. Early methods for the retinotopic mapping of the visual cortex (DeYoe et al., 1996; Dougherty et al., 2003; Engel et al., 1994, 1997; Sereno et al., 1995) used ring and wedge stimuli, and reported a strong coherence between the blood oxygen level-dependent (BOLD) signal arising in a voxel and particular stimulus locations in the visual field. From these measurements, the eccentricity and azimuth visual angle of each voxel can be estimated and this information can be used to define the borders between early visual areas (Sereno et al., 1995; Wandell et al., 2007).

Recently, Dumoulin and Wandell (2008) introduced a new method to model population receptive fields (pRFs) and quantitatively assess their properties. This seminal approach allowed us for the first time to measure quantitatively, in vivo, basic population receptive field properties in human visual areas. Like any method, however, this approach also has its limitations. For example, it assumed that the pRF has an isotropic Gaussian topography while the potentially suppressive surround is not modeled. There have been subsequent approaches (Harvey and Dumoulin, 2011; Zuiderbaan et al., 2012) which have used the same principles with different pRF models, but in general any assumptions about the receptive field structure puts some *a priori* constraints on the ability to extract the pRF topography without necessarily strong experimental justification. Inaccurate assumptions about the pRF topography could lead to the wrong model and to potentially erroneous estimation of pRF characteristics such as location and size. It would therefore be useful to have a method that can provide information about pRF topography in an unbiased manner.

To overcome these problems, we propose a new data-driven method that estimates the structure of the pRF. Without assuming the pRF shape *a priori*, we model the pRF as a vector of weights which can be estimated

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from the fMRI time-series by solving a set of linear equations for each voxel. This approach is similar to linear reverse correlation methods applied in electrophysiology (Ringach, 2004; Simoncelli et al., 2004). By avoiding a-priori assumptions, our method enables us to visualize pRF features such as surround suppression, or the anisotropic shape of the pRF. Visual inspection of the pRF topography can then guide the development of more appropriate models for fitting the pRF weights. This is particularly important in regions where the pRF shape is unknown. Even in early visual cortex, exploring the pRF topography reveals that pRF centers would be best modeled by an anisotropic Gaussian, in contrast to prevailing methods (Dumoulin and Wandell, 2008; Harvey and Dumoulin, 2011; Zuiderbaan et al., 2012). This approach yields an estimate of the orientation and elongation of the pRF center in addition to an estimate of its location and size.

In order to evaluate the method we proposed, we compared its performance to that of direct pRF model fitting methods. Our method of estimating the pRF center outperforms the direct-fit isotropic Gaussian (DIG) (Dumoulin and Wandell, 2008), the direct-fit anisotropic Gaussian (DAG), and the direct-fit difference of isotropic Gaussians (DDoIG) (Harvey and Dumoulin, 2011; Zuiderbaan et al., 2012) models by i) explaining a larger part of the BOLD signal variance, and by ii) providing more accurate eccentricity maps. In addition, visualizing the pRF topography as proposed here can make the subsequent modeling more efficient in computation time by constraining the pRF shape prior to the modeling. In contrast, direct-fit methods need considerably longer computation time as they have to select the best set of parameters in a much larger searching space.

Material and methods

Subjects

FMRI data were acquired from 4 participants (2 females, ages 23–26). All participants had normal or corrected-to-normal visual acuity. Experiments were conducted with the informed written consent of each participant and were approved by the Ethical Committee of the Medical Faculty of the University of Tübingen.

Stimulus

While scanning, participants fixated a central spot (radius: 0.0375°; 2 pixels) while a moving bar aperture exposed a moving square-checkerboard pattern with 100% contrast travelling across the visual field. The checkerboard pattern aligned to the longitudinal axis of the bar aperture moved in orthogonal directions of the bar movement. The stimulus was presented only over the central part of the visual field within a circular disk with radius 11.25°. The bar was moved sequentially in 8 different directions according to the following sequence [0, 135, 270, 315, 180, 45, 90, 225°] (Fig. 1A), where angles are reported counter-clockwise from the horizontal (0°) direction of the right visual hemifield. The long axis of the bar was orthogonal to the drifting direction. In each direction, the bar drifted 24 steps with each moving step being 0.9375°. The bar width was 1.875°. The position of the bar was updated for every image volume acquisition. The visual stimuli were generated with an adaptation of an open toolbox (VISTADISP), and PsychToolbox (Brainard, 1997) in MATLAB (The Mathworks, Inc.). The stimuli were presented through an MR-compatible goggle system (VisuaStimDigital, Resonance Technology Inc., Northridge, CA, USA) with min luminance = 0.39 cd/m^2, mean luminance = 6.27 cd/m^2, and max luminance = 12.15 cd/m^2 (lower photopic vision).

Data acquisition and preprocessing

All subjects participated in scanning sessions to obtain T1-weighted anatomical volume and functional volume data. FMR and structural MR imaging were performed using a 3T whole body scanner (Trio Tim, Siemens, Erlangen, Germany) with a 12-channel head coil. Two T1-weighted anatomical volumes (T1 MPRAGE scan) were acquired for each subject and averaged to increase signal to noise ratio [matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm^3, 176 partitions, flip angle = 9°, TR = 1900 ms, TE = 2.26 ms, TI = 900 ms]. The structural data were used for segmentation of anatomical data into white and gray matter (Teo et al., 1997). Functional BOLD image volumes were acquired using gradient echo sequences of 28 contiguous 3 mm-thick slices covering the entire brain (repetition time [TR] = 2,000 ms, echo time [TE] = 40 ms, matrix size = 64 × 64, voxel size = 3 × 3 × 3 mm^3, flip angle = 90°).

We performed 5–9 identical scanning sessions. In each functional session, 195 image volumes were acquired, the first 3 of which were discarded to allow for signal stabilization. Motion artifacts within and between runs were corrected (Nestares and Heeger, 2000). The functional images were co-registered with the averaged anatomical image using a mutual information method (Maes et al., 1997). All these preprocessing steps were performed using VISTA software (http://white.stanford.edu/software/). After detrending fMRI data in each scan with a cut-off frequency of 1 cycle per scan, all functional images across scans were averaged to formulate a volume series of 192 images.

Estimation of pRF topography based on linear system analysis

To predict the fMRI signals, we used a linear model for the fMRI response (Birn et al., 2001; Boynton et al., 1996; Friston et al., 1995; Hansen et al., 2004; Worsley and Friston, 1995). As opposed to the pRF model which directly uses a Gaussian model with a single sigma (Dumoulin and Wandell, 2008) to fit the BOLD data, we first use the BOLD data to estimate a weight vector representing the detailed topography of the pRF. Then, in a second step, we select an appropriate model to fit the observed pRF structure. The "stimulus presentation space" corresponding to a circular disk in the visual field, is represented as M pixels with size of 0.0187 × 0.0187 degrees per pixel. The stimulus at time t is denoted as $\mathbf{s}(t)\in\Re^M$ and the pRF at voxel i is denoted as $\mathbf{p}_i\in\Re^M$. Under the linear model, the presentation of the effective stimulus to the pRF of voxel i causes the following response:

$$r(t) = p_i^T s(t) \tag{1}$$

After convolving with the canonical hemodynamic response function (HRF) $h(t)$, the prediction of the BOLD response $d_i(t)$ at voxel i and time t is obtained:

$$d_i(t) = h(t) * \left(p_i^T s(t)\right) \tag{2}$$

The convolution in Eq. (2) is reformulated into:

$$d_i = Kp_i = HSp_i \tag{3}$$

where $\mathbf{H}$ is a matrix form for the convolution of $h(t)$ and $\mathbf{S} = [\mathbf{s}(1),\cdots, \mathbf{s}(t),\cdots, \mathbf{s}(N)]^T$, (N: the number of volume instances). In our study, a two-gamma function (Friston et al., 1998; Glover, 1999; Worsley et al., 2002) with the default parameters in the VISTA software was used as the canonical HRF as follows:

$$h(t) = (t/d_1)^{\alpha_1}\exp(-(t-d_1)/\beta_1) - c(t/d_2)^{\alpha_2}\exp(-(t-d_2)/\beta_2), \tag{4}$$

where $d_1 = 5.4, \alpha_1 = 5.98, \beta_1 = 0.90, c = 0.35, d_2 = 10.8, \alpha_2 = 11.97$, and $\beta_2 = 0.90$.

Then, when the observed signal vector $\mathbf{y}_i$ at voxel i is given, the pRF $\mathbf{p}_i$ can be estimated via a least-square fit:

$$J_i = \|y_i - d_i\|^2 = \|y_i - Kp_i\|^2. \tag{5}$$