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Spatial specificity of the functional MRI blood oxygenation response relative to neuronal activity

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ABSTRACT

Previous attempts at characterizing the spatial specificity of the blood oxygenation level dependent functional MRI (BOLD fMRI) response by estimating its point-spread function (PSF) have conventionally relied on retinotopic spatial representations of visual stimuli in area V1. Consequently, their estimates were confounded by the width and scatter of receptive fields of V1 neurons. Here, we circumvent these limits by instead using the inherent cortical spatial organization of ocular dominance columns (ODCs) to determine the PSF for both Gradient Echo (GE) and Spin Echo (SE) BOLD imaging at 7 Tesla.

By applying Markov chain Monte Carlo sampling on a probabilistic generative model of imaging ODCs, we quantified the PSFs that best predict the spatial structure and magnitude of differential ODCs' responses. Prior distributions for the ODC model parameters were determined by analyzing published data of cytochrome oxidase patterns from post-mortem histology of human V1 and of neurophysiological ocular dominance indices. The average PSF full-widths at half-maximum obtained from differential ODCs' responses following the removal of voxels influenced by contributions from macroscopic blood vessels were 0.86 mm (SE) and 0.99 mm (GE). Our results provide a quantitative basis for the spatial specificity of BOLD fMRI at ultra-high fields, which can be used for planning and interpretation of high-resolution differential fMRI of fine-scale cortical organizations.

1. Introduction

Functional magnetic resonance imaging (fMRI) of the human brain is increasingly being used to investigate fine-scale structures such as cortical columns (Cheng et al., 2001; De Martino et al., 2015; Goncalves et al., 2015; Goodyear and Menon, 2001; Menon et al., 1997; Nasr et al., 2016; Shmuel et al., 2010; Tootell and Nasr, 2017; Yacoub et al., 2008, 2007; Zimmermann et al., 2011). To optimally plan high-resolution fMRI studies and to correctly interpret their results it is necessary to know the inherent limits of the fMRI spatial specificity relative to the sites where changes in neuronal activity occur.

The most commonly used fMRI approach relies on gradient echo (GE) blood oxygenation level dependent (BOLD) contrast (Bandettini et al., 1992; Kwong et al., 1992; Ogawa et al., 1990, 1992). GE BOLD is sensitive to the intra- and extravascular effects of activation-induced changes in the deoxy-hemoglobin content of blood. At standard magnetic field strengths (1.5 T, 3 T) the signal is dominated by contributions from large blood vessels. At higher magnetic field strengths, the strong intravascular component of these large blood vessels decreases, while the extravascular signal changes around capillaries and smaller vessels increase (Uludağ et al., 2009; Yacoub et al., 2001). Additional weighting towards the microvasculature can be achieved by using spin echo (SE) BOLD imaging, which suppresses extravascular signal contributions from large blood vessels (Uludağ et al., 2009; Yacoub et al., 2003).

The first study to quantify the spatial specificity of the BOLD response (Engel et al., 1997) used an elegant phase-encoding paradigm that induced traveling waves of retinotopic neural activity in the primary visual cortex (V1). Assuming a shift-invariant linear response, Engel et al. (1997) estimated the point-spread function (PSF), which represents the spatial response that would be elicited by a small point stimulus. They found the full-width at half-maximum (FWHM) of the GE BOLD PSF to be 3.5 mm at 1.5 T. Similar values (3.9 mm for GE BOLD and 3.4 mm for SE BOLD) have been reported at 3 T (Parkes et al., 2005) using a paradigm similar to that used in Engel et al. (1997). To estimate the GE BOLD PSF at 7 T, we previously measured the spatiotemporal spread of the fMRI response in gray matter regions around the V1 representation of edges of

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visual stimuli (Shmuel et al., 2007). To reduce contributions from macroscopic veins, we excluded voxels that showed vessel-like response features. The mean measured and estimated FWHMs were 2.34 ± 0.20 mm and <2 mm, respectively. The spatial specificity of SE BOLD fMRI at ultra-high magnetic fields has not yet been quantified.

All previous attempts at characterizing the spatial specificity of the BOLD fMRI response (Engel et al., 1997; Parkes et al., 2005; Shmuel et al., 2007) relied on an implicit assumption that neuronal responses to small visual stimuli are point-like. However, to estimate the spatial specificity of the BOLD response, these studies have conventionally relied on spatial representations of visual stimuli in area V1. Unlike the implicit assumption of point-like responses, the receptive fields of neurons in V1 have non-zero spatial extents (Hubel and Wiesel, 1968). In addition, electrode measurements in macaque V1, oriented orthogonally relative to the surface of cortex have demonstrated substantial scatter in the center of receptive fields (Hubel and Wiesel, 1974). Therefore, the pattern of neural activity parallel to the cortical surface is a blurred representation of the visual stimulus. This implies that receptive field size and scatter pose a lower limit on any BOLD fMRI PSF width that is estimated using spatial representations of visual stimuli in V1. Consequently, the previously computed estimates of the spatial specificity of the fMRI response were confounded by the width and scatter of receptive fields of V1 neurons. Such estimates are limited in that they solely measure the capacity of the BOLD response to resolve retinotopic representations; they do not measure its ability to resolve more fine-grained neuronal activity. Yet only this latter resolvability matters for functional imaging at the spatial scale of cortical columns.

Here, we estimate and compare the PSF widths of GE and SE BOLD imaging at 7 T using a novel approach. We circumvent the limits posed by the retinotopic representation of visual stimuli by instead using the inherent cortical spatial organization of ocular dominance columns (ODCs). To this end, we fit a model of ODCs imaging (Chaimow et al., 2011) to ODCs' responses acquired at 7 T (Yacoub et al., 2007) following the removal of voxels influenced by contributions from macroscopic blood vessels. The model's spatial BOLD response is modeled as a convolution of the neuronal response with a Gaussian PSF. We quantify the width of the PSF that best predicts the spatial structure and magnitude of differential ODC fMRI responses. Since we do not have access to the underlying anatomical ODC patterns and neurophysiological responses, we use a probabilistic modeling approach. We constrain the model ODC parameters by estimating features of real ODC patterns taken from post-mortem cytochrome oxidase (CO) maps of human ODCs (Adams et al., 2007) and neurophysiological response distributions in primates (Berens et al., 2008; Hubel and Wiesel, 1968). We then fit our model by Markov chain Monte Carlo (MCMC) sampling. Our results provide a quantitative basis for the spatial specificity of differential BOLD fMRI at ultra-high fields.

2. Theory: using a probabilistic model of imaging ODCs to estimate the BOLD PSF from real data

2.1. Model of imaging ODCs

In the current study, we build on a model of imaging ODCs, which we developed previously (2011). The first component of the model, i.e. the modeling of realistic neuronal ODCs (Fig. 1, top part of the Model box) followed (Rojer and Schwartz, 1990). It consists of band-pass filtering a random instantiation of a two-dimensional Gaussian white noise array. The filtering is followed by applying a sigmoidal point-wise non-linearity, which controls the smoothness of transitions between left and right eye preference regions. The statistical properties of the ODCs pattern (i.e. column spacing, regularity, branchiness and sharpness of transitions) are determined by parameters of the filter and the subsequent non-linearity (all parameters of the model as used in our current study are listed in Table 1).

In the next stage (Fig. 1, bottom part of the Model box), we modeled the spatial BOLD response as a convolution of the neuronal ODCs pattern with a Gaussian PSF, parameterized using its FWHM:

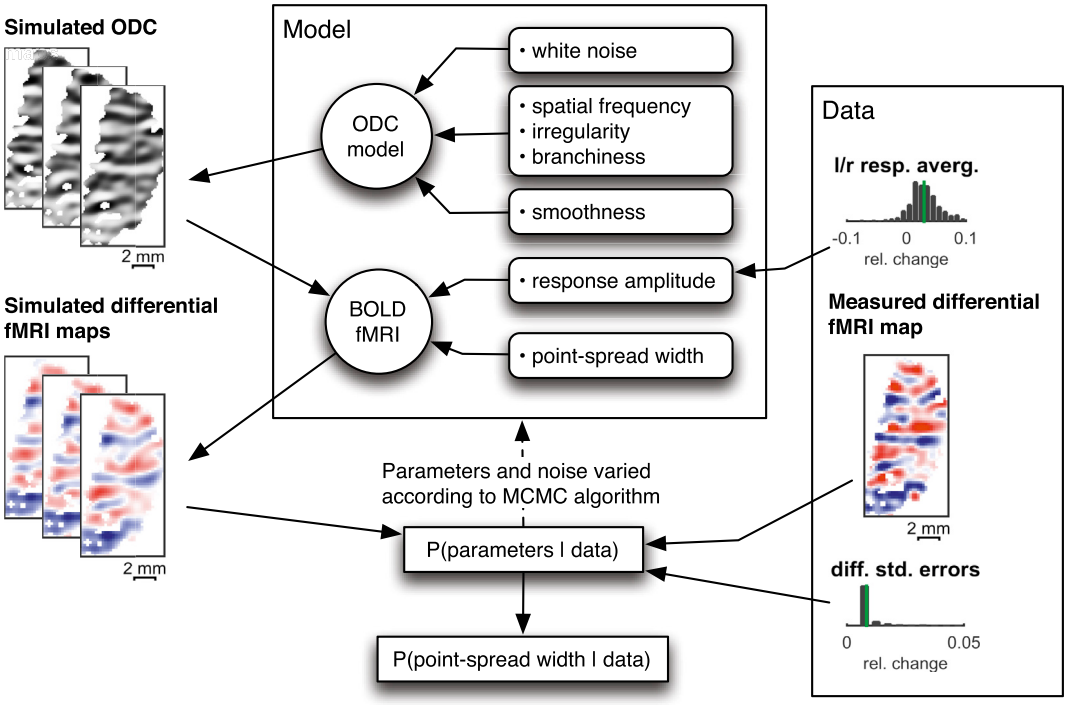

Fig. 1. Overview of Markov chain Monte Carlo fitting. The model was fitted to the fMRI data using Markov chain Monte Carlo (MCMC) sampling. For an arbitrary given set of parameters, the model generated a differential fMRI map (left). This map was compared to the measured fMRI map (right) and the likelihood of parameters given the data was calculated. The MCMC algorithm uses this likelihood together with parameter priors to further traverse the parameter space. After sufficiently many iterations the resulting parameter samples are distributed according to their joint posterior probability distribution.

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