NeuroImage 66 (2013) 376–384

Contents lists available at SciVerse ScienceDirect

NeuroImage

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

Connective field modeling

Koen V. Haak [a,b,c,*], Jonathan Winawer [d], Ben M. Harvey [e], Remco Renken [b], Serge O. Dumoulin [e], Brian A. Wandell [d], Frans W. Cornelissen [a,b]

[a] Laboratory for Experimental Ophthalmology, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands
[b] BCN Neuroimaging Center, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands
[c] Department of Psychology, University of Minnesota, Minneapolis, MN, United States
[d] Department of Psychology, Stanford University, Stanford, CA, United States
[e] Helmholtz Institute, Experimental Psychology, Utrecht University, Utrecht, The Netherlands

ARTICLE INFO

Article history:
Accepted 6 October 2012
Available online 27 October 2012

Keywords:
Visual cortex
fMRI
Functional connectivity
Connective field
Population receptive field

ABSTRACT

The traditional way to study the properties of visual neurons is to measure their responses to visually presented stimuli. A second way to understand visual neurons is to characterize their responses in terms of activity elsewhere in the brain. Understanding the relationships between responses in distinct locations in the visual system is essential to clarify this network of cortical signaling pathways. Here, we describe and validate connective field modeling, a model-based analysis for estimating the dependence between signals in distinct cortical regions using functional magnetic resonance imaging (fMRI). Just as the receptive field of a visual neuron predicts its response as a function of stimulus position, the connective field of a neuron predicts its response as a function of activity in another part of the brain. Connective field modeling opens up a wide range of research opportunities to study information processing in the visual system and other topographically organized cortices.

Introduction

The interpretation of visual neuroscience measurements made in different parts of the brain is unified by the receptive field concept. A measurement at any point in the visual pathway is usually summarized by referring to the stimulus properties (location, contrast, color, motion) that are most effective at driving a neural response. Stimulus-referred receptive fields provide a common framework for understanding the sequence of visual signal processing. The classic receptive field construct summarizes the entire set of signal processing steps from the stimulus to the point of measurement. This sequence of signal processing can be made explicit by modeling how the activity of one set of neurons predicts the responses in a distinct set of neurons. Characterizing the responses of a cortical neuron in terms of the activity of neurons in other parts of cortex can provide insights into the computational architecture of visual cortex. Such measurements are exceptionally difficult to achieve with single-unit recordings. The relatively large field of view in functional magnetic resonance imaging (fMRI) offers an opportunity to measure responses in multiple brain regions simultaneously, and thus to derive neural-referred properties of the cortical responses. These cortical response properties provide important information about how neuronal signals are transformed along the visual processing pathways. For example, stimulus-referred measurements in cortex show that visual space is sampled according to a compressive function (i.e., the V1 cortical magnification factor corresponds to a logarithmic compression of cortical space with eccentricity). Neural-referred measurements show that this compression is established at the earliest stages of vision; later visual field maps sample early maps uniformly and inherit the early compressive representation (Harvey and Dumoulin, 2011; Kumano and Uka, 2010; Motter, 2009).

A limitation in developing models of how fMRI responses in two parts of cortex relate to each other is that the problem is under-constrained. For example, there are many voxels in visual area V1, and there are many ways in which these responses could be combined to predict the response in a voxel in V2. Hence, any estimate requires imposing some kind of prior constraint on the set of possible solutions. Heinzle and colleagues (Heinzle et al., 2011), for example, used a support vector machine approach to reduce the dimensionality of the solution of V1 signals and predict responses in extrastriate cortex. Here, we take a different approach based on the idea that in retinotopic cortex connections are generally spatially localized. We build on a model-based population receptive field (pRF) analysis that was developed to estimate the stimulus-referred visual receptive field of a voxel (Dumoulin and Wandell, 2008). In the pRF analysis, the receptive field is modeled and fit to the fMRI signals elicited by visual field mapping stimuli. This is done by generating fMRI signal predictions from a combination of the receptive field model and the experimental stimuli. In the present

* Corresponding author at: Department of Psychology, University of Minnesota, Minneapolis, MN, United States.
E-mail address: koenhaak@gmail.com (K.V. Haak).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2012.10.037

analysis, fMRI signal predictions are generated from fMRI signals originating from the regions of cortex covered by a model of the inter-areal connective field (Angelucci et al., 2002; Lehky and Sejnowski, 1988; Sholl, 1953). Conceptually, this means that the localized activity in one cortical region acts as a stimulus for voxels in another region. We model the connective field as a two-dimensional, circular symmetric Gaussian that is folded to follow the cortical surface (Fig. 1). The assumption of a Gaussian connective field model is motivated by findings that the receptive fields of two extrastriate areas in the macaque, V4 and MT, can be described as two-dimensional, circularly symmetric, Gaussian sampling from the V1 map (Kumano and Uka, 2010; Motter, 2009). The Gaussian width parameter provides crucial information about the connective field, namely its size. Because the inter-areal connective field size is a measure of spatial integration, the analysis can be used to trace the extent of spatial integration as information moves from the primary visual cortex to higher visual areas.

Methods

Participants

Cortical responses were measured using 7 Tesla fMRI in subjects S1 and S2 with 1.6, 2.0 as well as 2.5 mm isotropic voxel sizes. S1 also participated in a 3 Tesla fMRI experiment with a 2.5 mm isotropic resolution. During all experimental sessions, the participants viewed high-contrast drifting bar stimuli interposed with mean luminance periods. Both subjects had normal visual acuity. All experiments were performed with the informed written consent of the subjects and approved by the UMCU Medical Ethics Board.

Stimulus presentation

The visual stimuli were generated in the Matlab programming environment using the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were displayed in one of two configurations. In both configurations, the participants viewed the display through an angled mirror. The first display configuration consisted of an LCD projecting the stimuli on a translucent display at the back of the magnet bore with a maximum stimulus radius of 5.5 degrees of visual angle. This configuration was used during the 7 T experiments. The second display configuration consisted of an LCD with a maximum stimulus radius of 6.25 degrees of visual angle. This configuration was used during the 3 T experiment.

Stimulus description

In both the 7 T and 3 T experiments, we measured responses to drifting bar apertures at various orientations that exposed a high-contrast checkerboard pattern (Dumoulin and Wandell, 2008; Harvey and Dumoulin, 2011; Zuiderbaan et al., 2012). Parallel to the

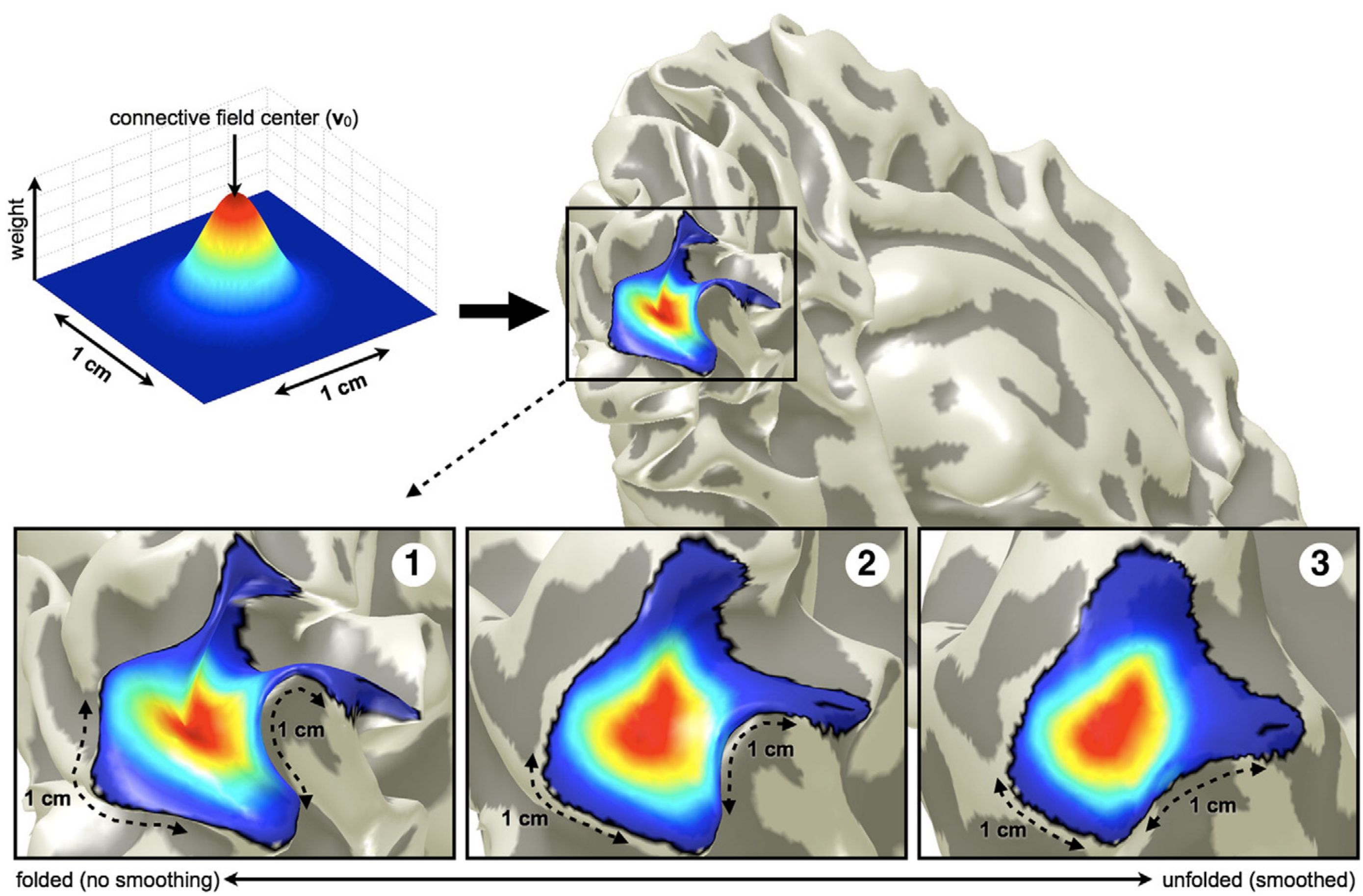

Fig. 1. Connective field models follow the curvature of the cortex. A two-dimensional, Gaussian connective field model (top-left) is defined as a function of Dijkstra's shortest path distance between pairs of vertices in a three-dimensional mesh representation of the original, folded cortical surface (top-right). The advantage of this approach is that the measurement of cortical distance avoids the distortions introduced if the Gaussian were projected onto a flattened, two-dimensional cortical surface representation. Panels 1, 2 and 3 (bottom) further illustrate the connective field model projection when the surface mesh is unfolded (smoothed).