

Model-based estimation of the population contrast response function in human visual cortex

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Contrast determines how strong visual stimuli drive neural responses and, in turn, how well we can see. This contrast-response relationship is nonlinear, with gain control mechanisms acting to compress responses to high-contrast stimuli, effectively setting the contrast range that neural responses are most sensitive to. Yet, capturing these saturating responses noninvasively in human functional magnetic resonance imaging (fMRI) has proven challenging. Here, we introduce a model-based fMRI approach to more flexibly and efficiently estimate saturating contrast responses: population contrast response function (CRF) mapping. To vet this technique, we benchmarked pCRF mapping against traditional deconvolved BOLD responses for stimuli presented with a fast event-related design. We found tight correspondence in parameter estimates between the deconvolution-derived CRF and pCRF estimates, validating the model-based approach. We then asked whether pCRF mapping could push beyond conventional paradigms by employing a continuous, highly condition-rich stimulation design that affords greater efficiency and flexibility but does not lend itself to traditional fMRI analyses. As predicted by the model-based approach, voxel-wise pCRF estimates could still be recovered from this unconventional design. In sum, we demonstrated that model-based pCRF mapping dissociates CRF estimation from strict design constraints and broadens the space of usable experimental paradigms while still capturing the saturating nonlinearities that are fundamental to neural population responses.

Introduction

Contrast governs how well we can see: the higher the contrast of a stimulus, the stronger its corresponding neural response, and the greater our brain's certainty about what we're seeing. Importantly, the relation between the contrast of a stimulus and the visual system's corresponding response is nonlinear, with gain control mechanisms believed to play a role in compressing responses to high contrast stimuli (Carandini & Heeger, 1994; Heeger, 1992). This saturating nonlinearity, referred to as the contrast response function (CRF), has long been observed in single-unit recordings of visual cortex in animal models (Albrecht & Hamilton, 1982; Bonds, 1991; Dean, 1981; Williford & Maunsell, 2006), and is well described by classic divisive normalization models of the visual system (Carandini & Heeger, 1997; Carandini & Heeger, 2012; Priebe & Ferster, 2012).

Although saturating nonlinearities have been commonplace in invasive measures of the CRF, capturing nonlinear CRFs in the human visual cortex has proven to be somewhat more challenging (Boynton, Engel, Glover, & Heeger, 1996; Boynton, Demb, Glover, & Heeger, 1999; Buracas, Fine, & Boynton, 2005; Buracas & Boynton, 2007; Hara & Gardner, 2014; Itthipuripat, Sprague, & Serences, 2019; Marquardt, Schneider, Gulban, Ivanov, & Uludağ, 2018; Murray, 2008; Pestilli, Carrasco, Heeger, & Gardner, 2011; Tootell et al., 1995; Tootell et al., 1998). Unlike single-unit recordings in animal models,

Citation: Vinke, L. N., Ling, S., & Bloem, I. M. (2026). Model-based estimation of the population contrast response function in human visual cortex. *Journal of Vision*, 26(9):7, 1–18, <https://doi.org/10.1167/jov.26.9.7>.



human experiments typically rely on non-invasive measures, such as functional magnetic resonance imaging (fMRI), which measure pooled activity across large heterogeneous populations of neurons. Pooling can be problematic for detecting nonlinearities, as averaging heterogeneous nonlinear responses can easily attenuate, or even effectively linearize, the aggregate response, even when individual neurons show saturating responses (Albrecht, Farrar, & Hamilton, 1984; Hara & Gardner, 2014). The same logic applies across spatial scales, whether it be pooling across participants, pooling responses across a visual area within a participant or even pooling across neural responses within a single voxel in a single visual area of a single participant.

One major source of this heterogeneity is that neural responses to a given contrast are not fixed, but instead exhibit complex temporal dynamics shaped by stimulus history through adaptation (Groen et al., 2022; Kohn, 2007; Ohzawa, Sclar, & Freeman, 1985; Sclar, Lennie, & DePriest, 1989). Single-unit recordings in visual cortex have shown that contrast response functions shift laterally along the contrast axis to match the visual environment, a form of contrast gain control that recenters neuronal sensitivity around recently experienced contrast levels (reviewed by Kohn, 2007). Crucially, this recentering builds progressively over time, rather than occurring instantaneously (Bao, Fast, Mesik, & Engel, 2013; Webster, 2015). This temporal dependence matters directly for how CRFs are measured with fMRI. In the long stimulus epochs typical of blocked fMRI designs, often 18–48 s, adaptation has substantial time to develop during the measurement itself. Given that the rate and magnitude of that adaptation depends upon stimulus contrast (Albrecht et al., 1984; Ohzawa et al., 1985), the response to any given contrast reflects an evolving, contrast-specific adaptation state. As higher- and lower-contrast stimuli each drive the system toward their own adapted state, the resulting responses grow more similar to one another over time, making the aggregate contrast response appear more linear across the full contrast range.

This issue is not eliminated simply by switching to an event-related design. Brief stimulus presentations reduce the amount of adaptation that can accumulate within a trial, but do not remove adaptation altogether. For example, even a 2 s stimulus, a duration typically used in event-related designs, is long relative to the timescale of neural adaptation, which begins to develop within tens of milliseconds and continues to build with increasing duration (Bao et al., 2013). Event-related designs do, however, make it possible to control the recent history more precisely, following a logic long used in psychophysical adaptation experiments. In such a paradigm an initial adapting stimulus first drives the visual system into a known state, which is then held in place with brief top-up presentations between trials

(Blakemore & Campbell, 1969; Greenlee, Georgeson, Magnussen, & Harris, 1991). Gardner et al. (2005) exploited this logic by imposing a controlled adaptation state and measuring responses with fMRI. They showed that contrast response functions in early visual cortex shift systematically and approximately recenter around the adapting contrast. Building on this, we recently showed more directly that the adaptation state itself is critical for recovering saturating CRFs with fMRI: leaving adaptation unconstrained failed to produce response saturation, whereas fixing adaptation at a known reference point revealed the expected nonlinear, saturating CRFs (Vinke, Bloem, & Ling, 2022).

Here, we introduce a novel model-based fMRI approach to estimating nonlinear contrast responses: population contrast response function (pCRF) mapping. The pCRF mapping gives experimenters the advantages of the adaptation-based neural homogenization protocol, allowing for voxel-wise measures of the nonlinear CRF, while also offering significantly more flexibility in experimental design. pCRF uses a model-based approach inspired by previous model-based neuroimaging methods that have been widely adopted to measure other properties of the visual system, including receptive field size (Aquil, Knapen, & Dumoulin, 2021; Benson, Kupers, Barbot, Carrasco, & Winawer, 2021; Dumoulin & Wandell, 2008; Kay, Winawer, Mezer, & Wandell, 2013; Kupers et al., 2021; Wandell & Winawer, 2015) and spatial frequency selectivity (Aghajari, Vinke, & Ling, 2020; Broderick, Simoncelli, & Winawer, 2022; Ha, Broderick, Kay, & Winawer, 2025; Ramirez, Wang, & Ling, 2025; Roelofzen, Daghljan, van Dijk, de Jong, & Dumoulin, 2025; Wiecek, Ramirez, Klimova, & Ling, 2026), among others (Groen et al., 2022; Harvey, Klein, Petridou, & Dumoulin, 2013; Zhou, Benson, Kay, & Winawer, 2019). In a nutshell, our pCRF mapping approach assumes that each voxel's response can be captured by a candidate underlying contrast response model, described concisely by a sigmoidal Naka-Rushton equation (Naka & Rushton, 1966). Given any sequence of visual stimuli varying in contrast over time, we were able to synthesize predicted neural (and hemodynamic) response time series for each voxel, and compare that predicted time series to the measured fMRI BOLD time series. Candidate model outputs are then iteratively fit with the measured BOLD time series, to find the best underlying pCRF model parameters, per voxel.

To vet this model-based pCRF mapping approach, we conducted two experiments, demonstrating the validity and versatility of the pCRF approach in measuring nonlinear CRFs, under less restrictive experimental designs. In Experiment 1, we validate the pCRF method, demonstrating that pCRF yields results similar to conventional fMRI measurements, when using a traditional event-related experimental design with imposed contrast adaptation. In Experiment 2,

we showcase the versatility of the pCRF modeling approach by comparing the modeling results achieved with an effectively continuous stimulus presentation design against the previous Experiment 1 modeling results. Rather than relying on an explicit adapting stimulus and top-up presentations to impose and maintain a fixed adaptation state, Experiment 2 instead leverages the recent history of contrasts inherent to the continuous stimulus stream itself, allowing adaptation state to emerge naturally from the ongoing sequence of presented contrasts. Crucially, we are able to successfully recover voxel-wise pCRF estimates using this continuous stimulus presentation—a design that is more experimentally-flexible, yet does not lend itself to typical deconvolution or GLM analysis approaches, demonstrating one of the many ways the pCRF approach can broaden design choices available to the investigator, while successfully capturing the saturating nonlinearities inherent in neural population responses.

Material and methods

Participants

Eight participants (seven female, between the ages 24 to 37) participated in two experiments. Data for Experiment 1 (Vinke et al., 2022) included 10 participants. For the present analyses, only data from the eight participants who also participated in Experiment 2 were used. All participants reported normal or corrected-to-normal visual acuity. Participants were recruited from Boston University and the surrounding community, were provided written informed consent before study enrollment, and were screened for any MRI-related contraindications. Participants were reimbursed for volunteering their time. All aspects of the study were approved by the Boston University Institutional Review Board.

Methods were largely similar to those previously published in Vinke et al. (2022). Below we summarize the stimuli and general paradigm.

Visual stimuli

Participants were presented with stimuli generated using MATLAB (2015b) and the Psychophysics MATLAB toolbox (Brainard, 1997), which were displayed via back-projection onto a screen set within the MRI scanner bore, using a VPixx Technologies PROPixx DLP LED projector (maximum luminance: 306 cd/m²). The linear gamma of the projector was confirmed using photometer measurements (LS-100; 1 DAC step = 1.2 cd/m²; Konica Minolta, Tokyo, Japan).

Throughout the majority of each experimental fMRI run, participants viewed a stimulus display containing an arrangement of five concentric ring patterns radiating out from fixation (Figure 1a). Each concentric ring was composed of eight circular apertures equally-spaced along the entire ring circumference, with the polar angle positioning of each set of apertures per ring alternating with a 22.5° offset, to maximize overall stimulus spatial density throughout the visual field. Each aperture contained a sinusoidal grating stimulus at a fixed spatial frequency oriented in a radial fashion relative to fixation to promote maximal responsivity, as has been previously reported when stimuli have a radial orientation bias (Sasaki et al., 2006). In Experiment 1, the luminance contrast of all apertures varied in tandem between nine different contrast intensities, spaced above and below 16% contrast in octaves (2.7%, 4%, 5.3%, 8%, 16%, 32%, 48%, 64%, and 96% Michelson contrast). Aperture spatial frequency was optimized for relative spatial frequency preference using a cortical magnification function (multiplicative inverse function, (Polimeni, Balasubramanian, & Schwartz, 2006)). Specifically, the cortically-magnified spatial frequencies were 9.38, 6.81, 4.67, 3.07, and 1.95 cycles-per-degree corresponding respectively to apertures centered at 0.9°, 1.5°, 2.5°, 4.2°, and 7° of eccentricity logarithmically-spaced out from fixation. Correspondingly, aperture size (radius) also increased logarithmically across each successive ring going from parafovea (0.35°; innermost ring) out to the periphery (2.56°; outermost ring). Furthermore, a Gaussian roll off was imposed to smooth the boundaries between the stimulus edge and the mean luminance background ($\sigma = 30$). The inner bound of the innermost aperture ring was 0.64° of visual angle from fixation, while the outer bound of the outermost aperture ring was 9.17°, resulting in a total stimulation area spanning 8.53° (Figure 1a). Last, to maintain vigorous cortical stimulation during stimulus presentation, and to minimize retinal afterimages, the phase of the gratings in all apertures was randomly shifted at a rate of 10 Hz.

In Experiment 2, the intended model-based analysis approach made it possible to relax the constraints regarding multiple observations of fixed contrast levels. Thus the luminance contrast of all apertures again varied in tandem, but with the specific contrast being sampled from a mixed uniform and Gaussian distribution centered on 16% Michelson contrast, see Figure 6b. The resulting distribution spanned 0% (blank) plus 49 nonzero contrast levels linearly spaced between 4% and 100% Michelson contrast. The sampling probabilities followed a Gaussian profile centered at 16% contrast with a standard deviation of 6% contrast (maximum sampling probability 11.8%, minimum 0.29%). The decision to use an adapter stimulus of 16% Michelson contrast was based on the presence of saturating fMRI-based contrast responses

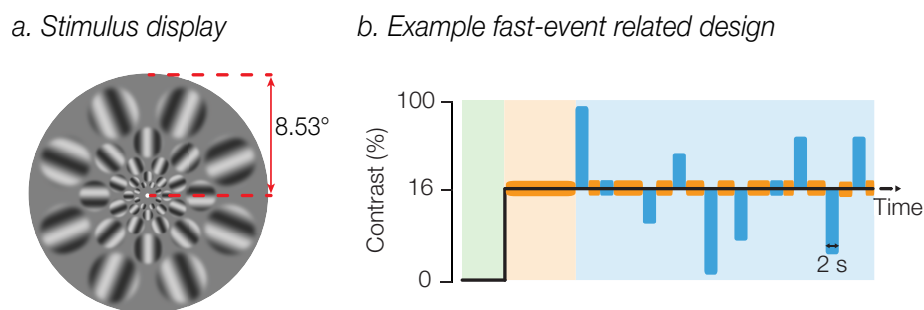


Figure 1. **(a)** Cortically magnified stimulus. Experimental stimulus composed of gratings with radial orientations (relative to fixation) and cortically magnified spatial frequency (actual stimulus spatial frequency not depicted). **(b)** Example fast event-related fMRI run. Timeline and organization of typical fMRI run for Experiment 1, consisting primarily of fast event-related stimulus presentations (2 s duration) at one of 9 Michelson contrast levels, interleaved with the 16% contrast adapter stimulus to maintain adaptation throughout the entirety of each run. Each run began with a 30 s blank fixation baseline period (highlighted in green), followed by a 60 s sustained adaptation period (highlighted in orange) to promote contrast response homogeneity.

reported previously by [Gardner and colleagues \(2005\)](#), wherein lower contrast adapter states in general allowed for stronger saturation to evolve at higher contrast levels. Additionally, using a 16% anchor contrast allowed for four equally log-spaced contrast levels above and below to be presented in Experiment 1. However, it is important to emphasize that a 16% Michelson contrast adapter in particular is not necessary for the application of the model-based approach being proposed here.

Experimental design

This study consisted of two fMRI experiments, both designed to measure visually evoked contrast response functions in human visual cortex, but using distinct experimental designs. In both experiments, each run began with a 30-second baseline, a 60-second adaptation, and concluded with a 16-second baseline period.

Experiment 1 used a traditional paradigm designed for a deconvolution analysis approach using a finite-impulse response (FIR) model ([Figure 2](#)) ([Dale, 1999](#); [Glover, 1999](#)). In this experiment, each run included a 60 second adaptation period at 16% Michelson contrast, after which fixed contrast levels were presented for two seconds (twice the TR length), interleaved with “top-up” adaptation periods (minimum 4 sec; maximum 17 sec; 16% Michelson contrast) between contrast stimulus presentations (54 events per run; total run time 510 seconds).

Experiment 2 introduced a nonstandard experimental design to highlight the versatility of our model-based approach. In this experiment, the contrast levels were randomly sampled from a distribution that combined a Gaussian and uniform component. Stimuli were presented at a shorter duration (0.5 seconds, half the TR

length), with the same baseline and initial adaptation (16% Michelson contrast) periods ([Figure 6a](#)). Notably, no interleaved “top-up” adaptation periods were used, resulting in a continuous sequence of contrast events (388 contrast events per run; total run time 300 seconds). By biasing sampling towards the adapter contrast, while preserving coverage of the entire contrast range, this approach maintained adaptation around the adapter contrast, while eliminating the need for time-consuming “top-up” adaptation periods. Crucially, although the continuous nature of Experiment 2 is more efficient and opens up more experimental flexibility, it would not lend itself to standard deconvolution or GLM-based analysis approaches.

For all fMRI experiments, participants fixated on a red dot at central fixation (diameter: 0.11°), while being engaged in a rapid serial visual presentation (RSVP) task also located at fixation. The RSVP task consisted of a rapid sequential presentation of letters, with target letters appearing with a 30% probability every 250 ms, after a minimum of 10 non-target letters following the last target letter presentation. An MR-compatible response box was used to record behavioral responses to the RSVP task. Participants maintained above-chance performance across all runs in all experiments.

A third additional fMRI session was dedicated to collecting anatomical images, and data for population receptive field (pRF) mapping using standard techniques and stimuli ([Dumoulin & Wandell, 2008](#); [Kay, Naselaris, Prenger, & Gallant, 2013](#); [Kriegeskorte et al., 2008](#)).

MRI data acquisition

All anatomical and functional MRI data was collected using a research-dedicated Siemens Prisma 3T scanner with a 64-channel head coil. Whole-brain

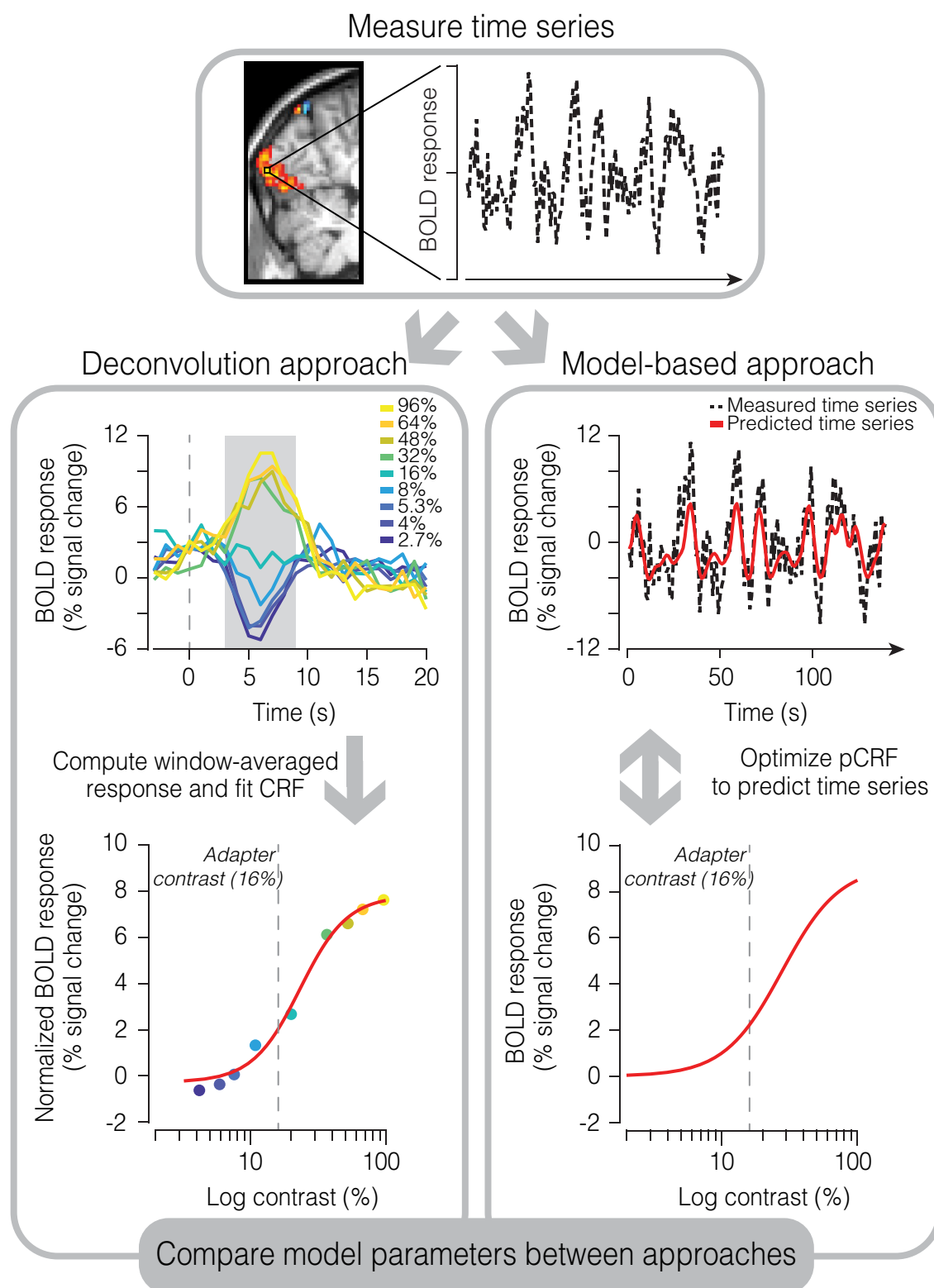


Figure 2. Comparison of a traditional deconvolution approach and a model-based approach for estimating pCRFs. Both approaches start from the measured BOLD response time series from an individual voxel from a representative participant. Left panel: In the deconvolution approach, a FIR model is used to estimate a time course for each contrast level individually. A window-averaged response is computed per contrast level, yielding a voxel wise CRF. The contrast responses shown have been baseline-corrected by subtracting the mean of the first three contrast levels, anchoring the curve around 0% signal change. Right panel: For the model-based approach, pCRF parameters are optimized to predict the entire measured BOLD time series directly. Subsequently, the model parameters can be compared between the two approaches.

anatomical data was acquired using a T1-weighted multi-echo MPRAGE 3D sequence (1 mm³; FOV = 256 × 256 × 176 mm; FA = 7°; TR = 2530 ms; TE = 1.69 ms) (van der Kouwe, Benner, Salat, & Fischl, 2008). All functional neuroimaging data (main experiments and pRF mapping) was acquired using a T₂*-weighted in-plane simultaneous multi-slice imaging sequence (multi-band factor: 3) (Moeller et al., 2010; Xu et al., 2013), with the field of view oriented perpendicular to the calcarine sulcus (2 mm³; FOV = 60 × 112 × 172 mm; FA = 80°; TR = 1000 ms; TE = 35 ms).

Anatomical data analysis

The T1-weighted whole-brain anatomical MRI data was analyzed using the Freesurfer cortical surface reconstruction pipeline (Fischl, 2012), generating subject-specific cortical surface models, whole-brain segmentations, and cortical parcellations. Cortical surface models facilitated surface-based registration between structural and functional MRI volumes, permitting pRF retinotopic information to be transformed to native functional volume space.

Functional data analysis

EPI distortion correction was applied to all fMRI BOLD time-series data using a reverse phase-encoding method (Andersson, Skare, & Ashburner, 2003) implemented in FSL (Smith et al., 2004). All fMRI preprocessing steps were completed with FS-FAST (Fischl, 2012), including standard motion-correction procedures, Siemens slice timing correction, and boundary-based registration (Greve & Fischl, 2009) between functional and anatomical volumetric spaces. To facilitate voxel-wise analyses, no volumetric spatial smoothing was performed (FWHM = 0 mm). Precise volumetric alignment of experimental condition data across and within all neuroimaging sessions was achieved using cross-run within-modality robust rigid registration (Reuter, Rosas, & Fischl, 2010), with the middle time-point of the first run (first session) serving as the target volume, and the middle time-point of each subsequent run in session 1, and all session 2 runs, serving as the movable volume used for alignment. Before converting BOLD time-series data to units of percent signal change, time-points corresponding to the initial adaptation period (60 frames) were excluded. Data collected during the separate pRF mapping session was analyzed using the analyzePRF toolbox (Kay et al., 2013). Only voxels located within the cortical ribbon of the occipital lobe were designated for pRF modeling, which were identified using a visual area network label generated using an intrinsic functional connectivity atlas (Yeo et al., 2011).

Voxel selection

The results from the pRF mapping were used to determine voxel selection within each region-of-interest (ROI). The pRF results were used to define the boundaries of all early visual areas (V1–V3), and identify candidate voxels within each visual area having eccentricity preferences bounded by stimulus dimensions (inner diameter = 0.7°, outer diameter = 9.1°). ROI labels were further constrained by excluding voxels with poor pRF modeling goodness-of-fit ($r^2 < 20\%$), and unreasonably small population receptive field sizes (RF < 0.1°). Subsequently, for each participant within each experiment, the ROI-averaged deconvolution time-course (FIR function) for the highest contrast condition (96%) was fit with a four-parameter Gaussian function for each early visual area (V1–V3). The mean and standard deviation of the residual sum of squares when fitting the highest contrast condition with the Gaussian function was equivalent across adaptation (V1: 0.21 ± 0.08 ; V2: 0.15 ± 0.07 ; V3: 0.13 ± 0.08) conditions. The best-fitting Gaussian function describing the ROI-averaged FIR function was then adjusted using linear regression (unbounded y-intercept and amplitude scalar parameters) to best match the FIR function of each individual voxel contained within the ROI (96% contrast condition only). At the conclusion of this fitting procedure, the voxel-wise goodness-of-fit (r^2 coefficient) was then used to create a metric ranging from 0 (worst fit) to 1 (best fit) for all voxels in each ROI. Voxels within each ROI were ranked according to their goodness-of-fit metric, with the top 40% selected for further analysis. Importantly, voxels with a high goodness-of-fit metric solely indicates that these particular voxels had a strong stimulus evoked response to the highest contrast level which was well described by a Gaussian function. This metric does not take into account the evoked responses at any other contrast level (< 96%), thus it serves as a voxel selection method that is agnostic to the overall qualitative shape of the contrast response function. Last, any voxels with a maximal BOLD response exceeding 10% signal change were excluded in an effort to only include voxels with responses not attributable to draining vein hemodynamics, which are known to be significantly delayed in time relative to cortical gray matter (Lee, Glover, & Meyer, 1995) and are mainly expected to occur at the foveal confluence (Winawer, Horiguchi, Sayres, Amano, & Wandell, 2010). On average this exclusion constituted less than 2% of all voxels across all participants. The total number of voxels (mean ± SEM across participants) that survived these selection criteria, after combining across left and right hemispheres, were as follows: V1: 209.6 ± 26.4 ; V2: 217.0 ± 20.6 ; V3: 207.8 ± 13.0 . The specific percentage of included voxels did not

affect our results, as confirmed by applying a more stringent voxel selection threshold (Supplementary Fig. S1).

Deconvolution-based contrast response estimation

The deconvolution analysis was conducted using a finite-impulse response (FIR) modeling approach (window size = 24 s, prestimulus delay = 4 s; Dale, 1999). This FIR approach makes no assumptions about the shape of the hemodynamic response. Instead, it estimates the BOLD response time course empirically by fitting a set of temporally ordered basis functions (one per time bin per condition) directly to the measured BOLD response across all runs. This yields a set of 24 beta-weight parameters per voxel for each contrast level, describing the time course of the BOLD response within this window. An average response amplitude was extracted by averaging the beta weights over a fixed averaging window (3–9 s post-stimulus onset), yielding a voxel-wise contrast response. To anchor the curve around 0% signal change we applied a baseline correction by subtracting the mean response across the first three contrast levels for each voxel.

Contrast response function

The BOLD responses to stimulus contrasts C were modeled using the Naka-Rushton equation (Albrecht & Hamilton, 1982; Naka & Rushton, 1966):

$$CRF = R_{max} * \frac{C^n}{C^n + C_{50}^n},$$

where R_{max} is the maximum response, C_{50} a semi-saturation contrast (the contrast at which the response reaches half the R_{max}), and n is an exponent controlling the steepness of the sigmoid.

The pCRF model

The pCRF model predicts a BOLD time series by modeling a neural response as a nonlinear function of the stimulus contrast time series followed by a convolution with a hemodynamic response function. For each voxel, a single hemodynamic impulse response function (HIRF) was estimated jointly across all contrast levels. The predicted neural response was convolved with the HIRF:

$$\begin{aligned} HIRF(p, w, \tau) \\ = \text{gampdf}(t, p, \tau) - w \cdot \text{gampdf}(t, 2p, \tau), \end{aligned}$$

here, t represents time, p a shape factor affecting the positive and negative components of the temporal profile, w is the relative weight of the negative gamma, and τ is a scale factor fixed at 1. The HIRF was normalized to unit sum prior to convolution.

The predicted BOLD time series was obtained by convolving the neural response with the HIRF and adding a constant β :

$$\text{pred} = CRF * HIRF + \beta.$$

Model parameters (R_{max} , C_{50} , n , p , w , β) were estimated by minimizing the sum of squared error (SSE) between the predicted and measured BOLD time series using `fmincon` (MATLAB).

Quantifying CRF agreement

To quantify the similarity between the two modeling approaches in their characterization of the contrast response function, we compared the CRF profiles derived from each method on a voxel-wise basis. Each approach yields the three Naka–Rushton parameter estimates per voxel, obtained independently through the deconvolution and pCRF pipelines.

Profile agreement was then quantified using an R^2 metric, treating the deconvolution CRF as the reference and the pCRF-reconstructed CRF as the prediction:

$$R^2 = 1 - \frac{\sum (\text{deconCRF} - \text{pCRF})^2}{\sum (\text{deconCRF} - \overline{\text{deconCRF}})^2}$$

An R^2 of 1 would indicate perfect agreement between the two approaches, whereas lower values reflect differences in the pCRF profile compared to the deconvolution-based CRF, arising from the combined influence of all three parameters comprising the CRF profile.

Results

We have previously shown that using a traditional fast-event related design, we can estimate nonlinear contrast response functions. Inspired by previous model-based neuroimaging methods that have been widely adopted to measure properties of the visual system (Aghajari et al., 2020; Aqil et al., 2021; Broderick et al., 2022; Dumoulin & Wandell, 2008; Harvey et al., 2013; Kay et al., 2013; Kim, Kupers, Lerma-Usabiaga, & Grill-Spector, 2024; Kupers et al., 2021; Ramirez et al., 2025; Roelofzen et al., 2025; Wandell & Winawer, 2015; Wiecek et al., 2026; Zhou et al., 2019), we developed a model-based framework that fits a parametric pCRF directly to

the measured BOLD time series. By benchmarking the model-based approach on our published dataset (Vinke et al., 2022), we directly compared whether both analysis approaches provide comparable parameter estimates (Figure 2).

Our original analysis utilized a deconvolution approach to estimate a voxel-wise BOLD response time course for each contrast level, from which a single amplitude was extracted using a post-stimulus averaging window. These contrast responses were fit with a Naka-Rushton equation, optimizing its parameters to describe response saturation ($R_{\max}$), the semi-saturation point (C_{50}) where the response reaches half the response saturation, and the steepness of the sigmoidal function (n) (Figure 2 left panel).

Introducing model-based pCRF mapping

The model-based pCRF method takes a more direct approach to estimate the contrast response function. Rather than summarizing responses to fixed conditions post hoc, the model-based approach captures the contrast response by optimizing the Naka-Rushton parameters to directly predict the entire BOLD response time series (concatenated across individual runs). Importantly, this model-based approach allows for a greater flexibility in experimental design, as model optimization is not dependent on condition repetitions, stimulus duration, and even spacing between subsequent stimulus presentations (Figure 2 right panel). Indeed, traditional fMRI experimental designs typically set out to summarize BOLD responses for each experimental condition. To do so, stimulus presentations need to be sufficiently temporally spaced or orthogonalized by jittering blank periods to minimize overlap of the hemodynamic response, allowing GLMs or deconvolution approaches to estimate these condition specific responses. However, this introduces an artificial temporal structure on stimulus presentations, reducing flexibility in the experimental design and placing a limit on the total number of repetitions per condition that can be presented within a scan. Our pCRF approach circumvents these design constraints.

In Figure 3 we describe the flow of the model-based framework. The analysis takes a stimulus time series as input. This stimulus time series is a temporal sequence indicating when each contrast intensity (or other relevant stimulus property) was presented. The stimulus time series is then transformed by the pCRF model to simulate a neural response time course. This is subsequently convolved with a hemodynamic impulse response function (HIRF), resulting in a predicted BOLD response time series. For every iteration, the pCRF parameters are optimized to minimize the SSE

between the predicted and measured BOLD response time course, yielding for each voxel an estimate of the pCRF parameters that include the contrast response parameters ($R_{\max}$, C_{50} , n), 2 HRF parameters, and a baseline parameter, which simply offsets the predicted time series (see Methods).

The pCRF produces comparable results to conventional analysis approaches

We first set out to evaluate whether pCRF mapping produces results that are similar to traditional fMRI analysis approaches (such as GLM or deconvolution). Using the same voxel selection and ROI definitions as in the original study (Vinke et al., 2022), we fit the model-based pCRF to the BOLD time series of individual voxels, and compared the resulting contrast response parameters ($R_{\max}$, C_{50} , n) to those obtained from fitting a Naka-Rushton equation with the same functional form to the window-averaged responses.

Parameter estimates derived from the model-based pCRF analysis closely tracked those from the deconvolution method (Figure 4). For each participant, ROI and parameter we quantified the voxel-wise relationship between the two methods by computing a pairwise Spearman correlation. The individual participant correlations were Fisher- z transformed and at the group level tested whether there is a consistent linear relationship (two-sided t -test on the Fisher- z transformed correlations). The voxel-wise parameter maps showed strong correspondence between the two methods for the semi-saturation point C_{50} (V1: $t(7) = 5.83$; $p < 0.001$, $r = 0.49$; V2: $t(7) = 4.07$; $p = 0.005$, $r = 0.37$; V3: $t(7) = 6.43$; $p < 0.001$, $r = 0.42$), the maximum response $R_{\max}$ (V1: $t(7) = 21.98$; $p < 0.001$, $r = 0.76$; V2: $t(7) = 19.51$; $p < 0.001$, $r = 0.64$; V3: $t(7) = 13.30$; $p < 0.001$, $r = 0.61$), and transducer (V1: $t(7) = 3.37$; $p = 0.01$, $r = 0.30$; V2: $t(7) = 5.66$; $p < 0.001$, $r = 0.29$; V3: $t(7) = 4.07$; $p = 0.005$, $r = 0.26$). Complementing these voxel-wise correlations, paired t -tests revealed that the median $R_{\max}$, C_{50} and transducer ROI parameter estimates did not differ between the two analysis methods (all $t(7) < 1.75$, all $p > 0.12$). Despite this overall correspondence, the model-based approach yielded a somewhat more compressed range of C_{50} estimates relative to the deconvolution approach (Figure 4).

We next quantified the overall similarity of the CRF profile between the two methods (capturing differences in response gain, semi-saturation contrast, and slope) by computing a voxel-wise coefficient of determination (Figure 5a). To obtain these voxel-wise predictions, we used the parameter estimates from the deconvolution method and the model-based approach to evaluate each model at the same nine contrast conditions, resulting

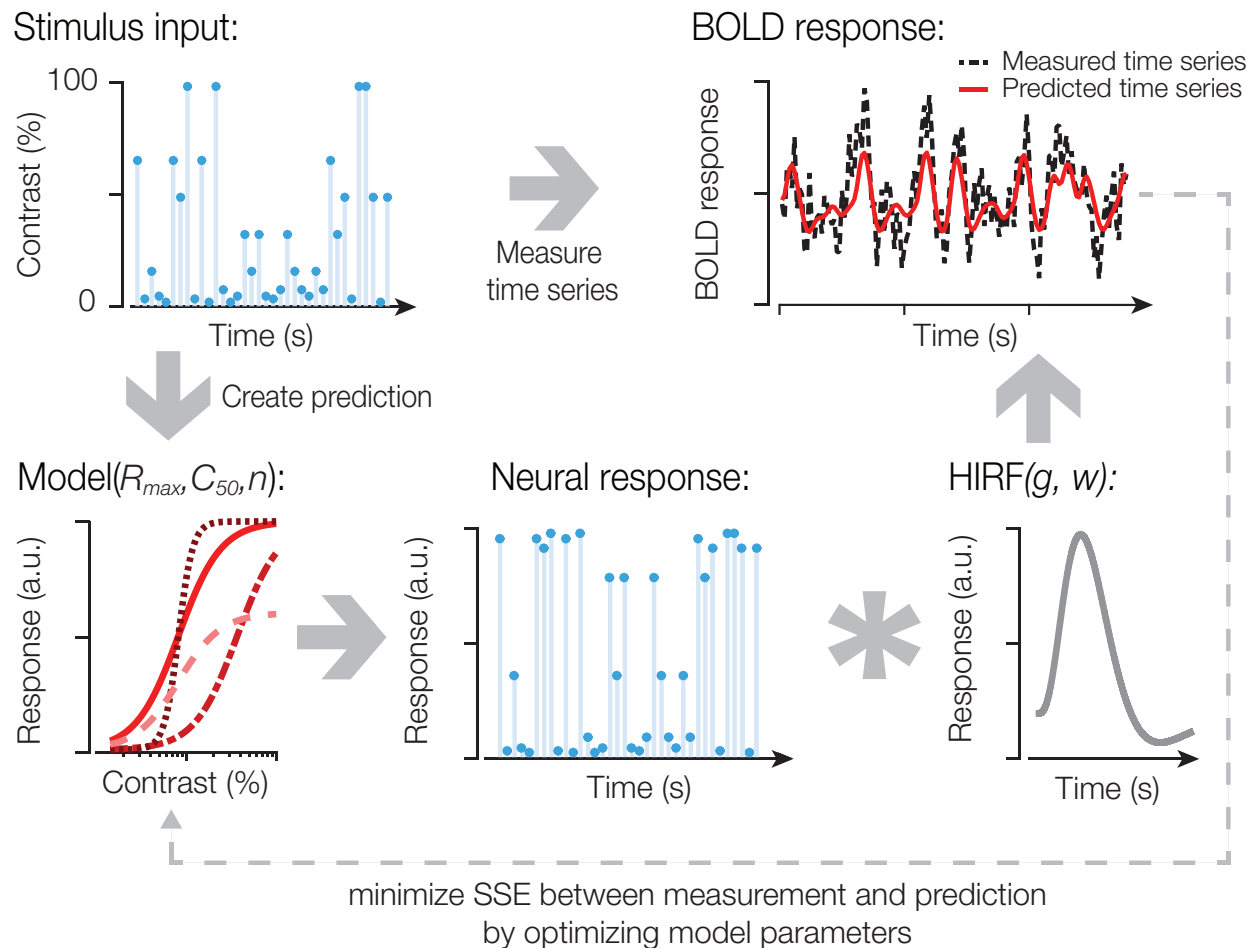


Figure 3. Schematic of the model-based approach for estimating population contrast response functions. The experimental stimulus input sequence (top left) reflects when each contrast level was presented within a run. This sequence is used to generate a simulated neural response (bottom middle), based on the Naka-Rushton model (bottom left). Different colored lines illustrate the influence of each parameter on the CRF profile. Here, the red solid line is the “standard” CRF, the light red dashed line a decrease in R_{max} , the dark red dot dashed line an increase in C_{50} , and the dotted dark line an increase in n . The simulated neural response is convolved with a hemodynamic impulse response function (HIRF; two parameters, bottom right) and combined with a baseline offset to generate a predicted time series (top right, red line) which is compared against the measured BOLD time series (top right, black dashed line). The pCRF model parameters (R_{max} , C_{50} , n , two HRF parameters, and offset) are optimized by minimizing the SSE between the predicted and measured time series. If the formation of a percept by the visual cortex were a Lego model, of all the many pieces that go into the construction of the percept, contrast is the one piece you absolutely don’t want to lose under the couch. This model-based approach effectively allows you to lift up said couch.

in a predicted CRF for each method that could be directly compared (see Figure 5b for a representative participant). Voxels with either negligible CRF variance or extreme misfit were excluded (on average 5.5 voxels in V1, 14 voxels in V2, and 21 voxels in V3). For each participant and ROI, we then summarized the remaining values by taking the median R^2 across voxels and averaged these medians across participants to obtain a group-level estimate of CRF profile agreement. This analysis revealed robust correspondence in early visual cortex (V1: group mean $R^2 = 0.72$ V2: 0.57; V3: 0.41; t -test against 0, all $p < 0.005$; Figure 5a).

Model-based approach overcomes limitations of traditional experimental approaches

Next, we designed an experiment to test how durable the model-based pCRF framework is when applied to a nonstandard, highly efficient experimental design that would be incompatible with traditional GLM or deconvolution analyses. To do so, we measured BOLD responses in participants while they viewed stimuli of rapidly varying contrasts: each contrast level was shown for only 500 ms, with no interstimulus interval, allowing for a much higher density of contrast

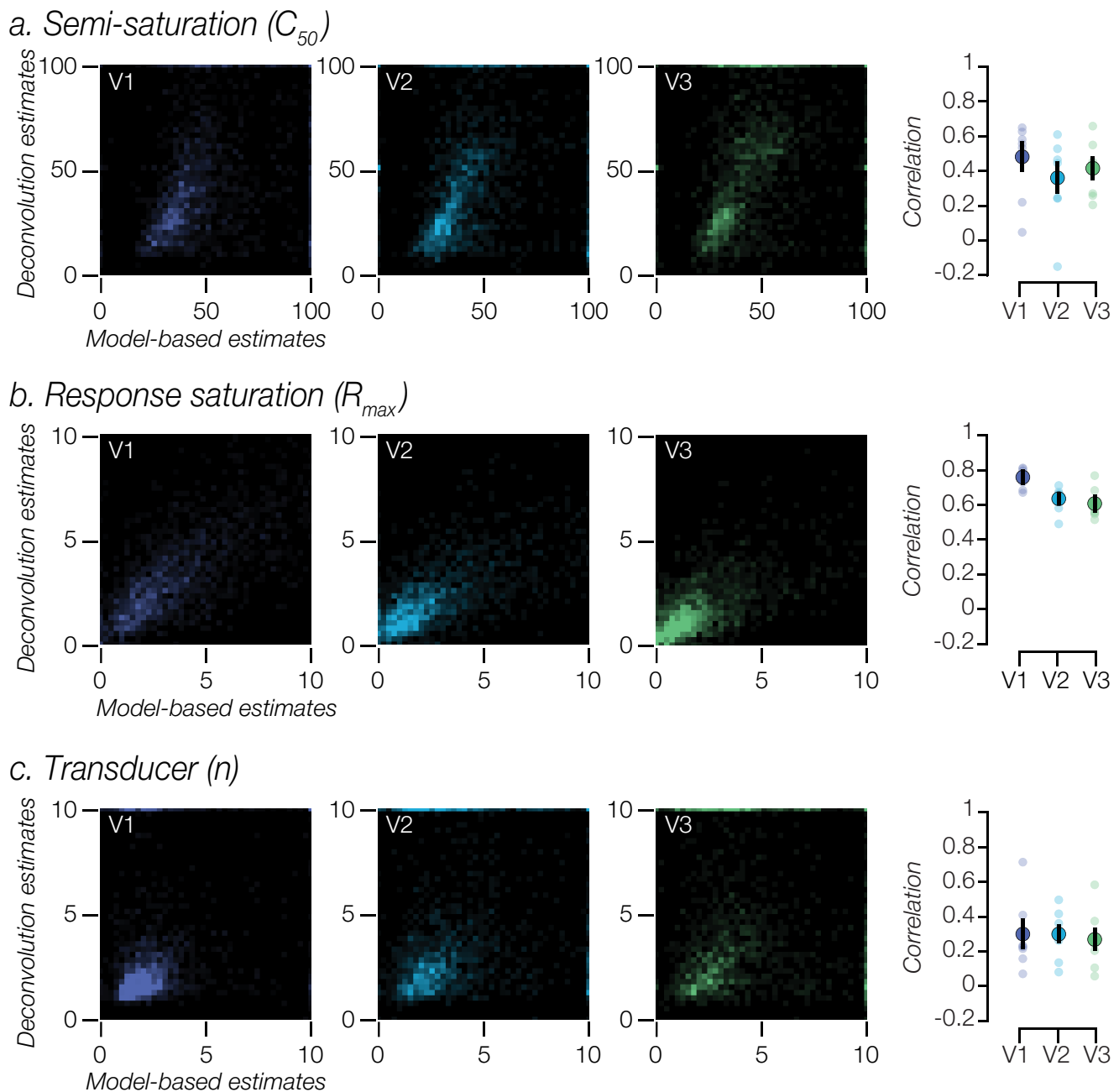


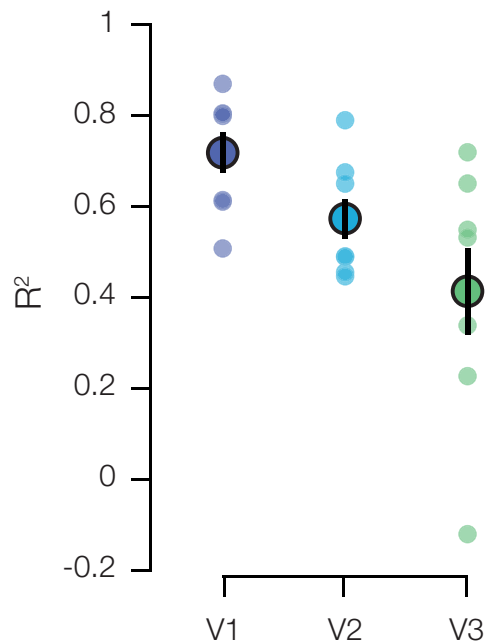
Figure 4. CRF parameter comparison between the deconvolution and model-based approaches. **(a)** Semi-saturation parameter. **(b)** Response saturation parameter. **(c)** Transducer parameter. Columns indicate V1 (purple), V2 (teal), V3 (green). D. Scatter plots illustrating the voxel-wise correlation between the approaches for each parameter per ROI. Large points depict the group-average, small dots individual participants, and the error bars represent the *SEM*.

events within a run (Figure 6a). To maintain a stable adapted state throughout the run, these contrast values were sampled from a biased mixture of a uniform and Gaussian distribution centered at 16% Michelson contrast (Figure 6b).

Although this continuous stimulus design would be problematic for conventional fMRI analyses, the pCRF model can be fit directly to the measured time

series (Figure 3). We quantified model performance using a voxel-wise cross-validated R^2 (cvR^2) computed for each participant, ROI and experiment using a leave-one-run-out scheme. For each fold, the model was fit on all but one run and used to predict the left-out run; we then assembled predictions across held-out runs and computed cvR^2 between the predicted and measured time series, yielding one cvR^2

a. CRF profile comparison



b. Representative participant

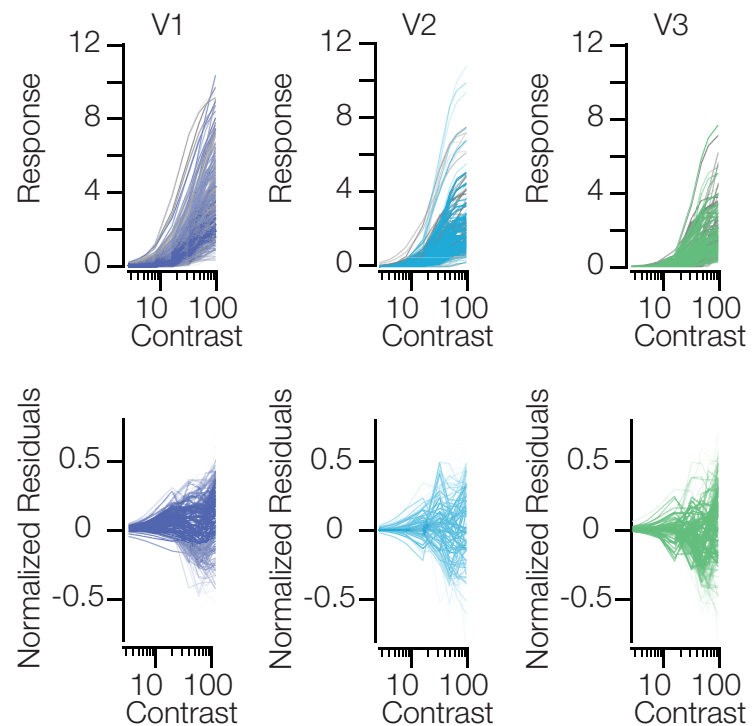


Figure 5. Contrast response profile agreement. (a) Voxel-wise goodness of fit R^2 when using the pCRF model to predict the deconvolution-based CRF profile. (b) Representative participant CRF curves for individual voxels within V1–V3; gray lines show deconvolution-based CRFs, colored lines show pCRF model prediction. Line opacity is scaled with R^2 . Bottom panels show residuals between the two methods, normalized by the maximum response of deconvolution-based CRF.

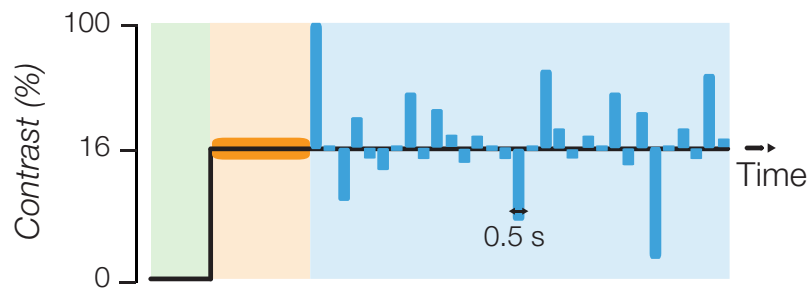
per voxel, for each experiment and participant. To focus on voxels that were robustly captured by the model in both experimental designs, we applied a combined cvR^2 threshold across the event-related and continuous experiments (V1: $cvR^2 > 0.05$, V2: $cvR^2 > 0.033$, V3: $cvR^2 > 0.167$; see Figure 6c). We used this voxel selection for the subsequent analysis. Within this voxel set, the event-related experiment (Experiment 1) yielded mean cvR^2 of about 0.12 in V1, 0.07 in V2, and 0.05 in V3 (all $p < 0.001$, two-sided t -tests), indicating that even for voxels that are well captured by the model, cross-validated fits to the full BOLD time series remain relatively modest. The continuous design (Experiment 2) produced lower but still reliably positive mean cvR^2 (approximately 0.08 in V1, 0.05 in V2, and 0.03 in V3; all $p < 0.001$), demonstrating that the pCRF model maintains above-chance predictive power under a more demanding, continuous stimulation protocol within the same set of voxels.

To evaluate whether the model-based pCRF still captured meaningful contrast tuning under the continuous design, we compared the fit to a stimulus-shuffled null. For each of 100 null iterations, we randomly shuffled the contrast order within each run and tested whether the pCRF model still explained

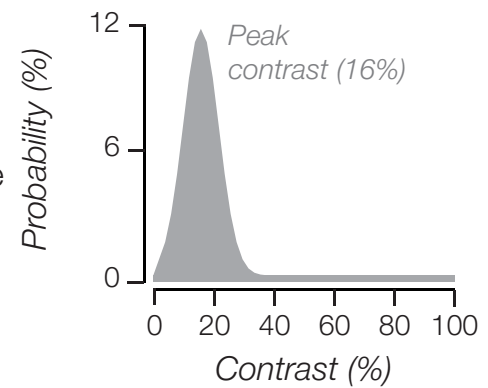
meaningful variance when the model input no longer matched the actual stimulus sequence. Model fit was quantified using the resulting SSE, yielding a null distribution of SSE values. For the actual (unshuffled) data, we computed a normalized improvement score per ROI, which is positive when the model outperforms the null (Figure 6d, first panel). In all three ROIs, these normalized SSE values were reliably greater than 0 (V1: mean improvement = 9.55%, 95% CI = [7.32, 11.79], $t(7) = 10.10$, $p < 0.001$; V2: mean improvement = 6.50%, 95% CI = [5.13, 7.88], $t(7) = 11.21$, $p < 0.001$; V3: mean improvement = 4.04%, 95% CI = [3.35, 4.74], $t(7) = 13.76$, $p < 0.001$), indicating that the pCRF explains substantially more variance than expected by chance under the stimulus-shuffled null.

The ROI average pCRF parameters showed the expected relative differences across the visual hierarchy. $R_{\max}$ decreased from V1 to V3, consistent with larger response amplitudes in earlier visual areas and slope tended to steepen. These hierarchical trends closely matched those obtained from the deconvolution-based CRFs, reinforcing that pCRF recovers plausible contrast-response properties under both the traditional and continuous designs.

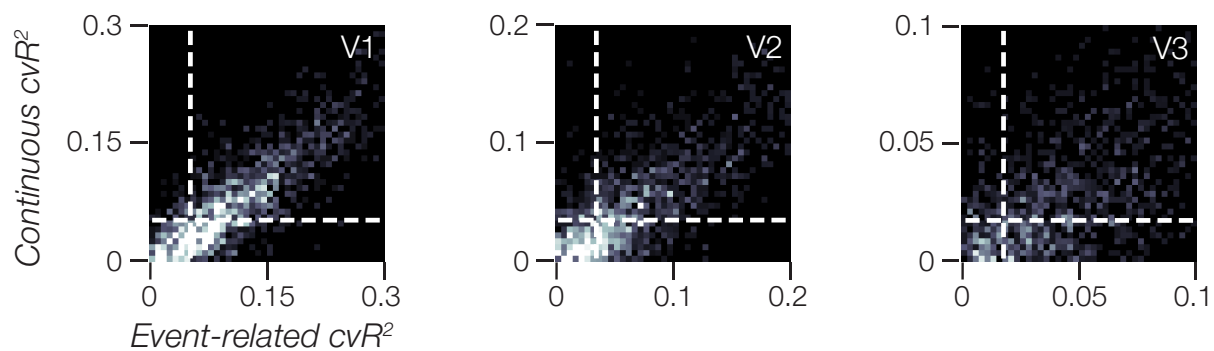
a. Example continuous design



b. Contrast distribution



c. Comparison of model performance



d. Model-based estimates

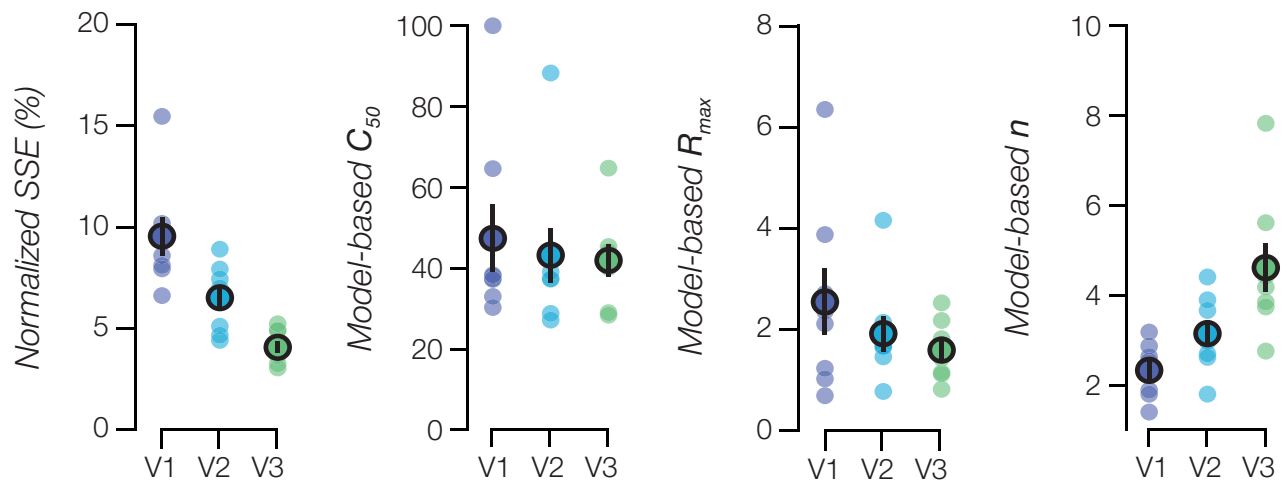
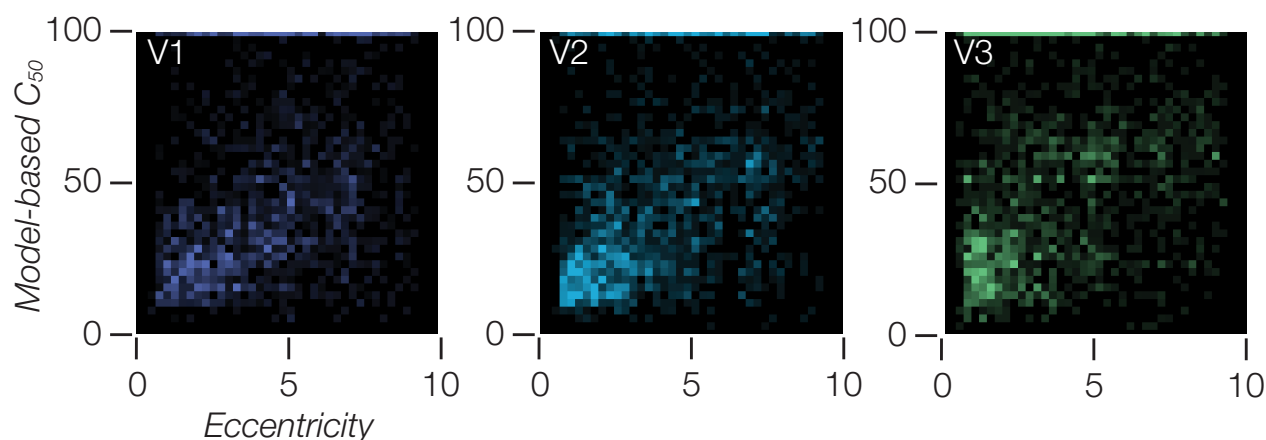


Figure 6. Continuous experimental design and model-based approach parameter estimates. **(a)** Experimental design with shaded regions depicting different phases. An initial 30-second baseline period (green), preceded a 60-second adaptation period (orange), with the remainder of the run dedicated to continuous contrast stimulus presentation at 0.5-second intervals. **(b)** Stimulus contrast levels were sampled from a biased distribution. This biased distribution was titrated to present a majority of contrasts around the adapter (here, 16% contrast), while additionally supplying the model ample instance of higher-contrast stimuli to better capture saturation. **(c)** Group-averaged 2D histograms to compare cross-validated R^2 between the event-related and continuous experimental designs. Dashed white lines indicate the cvR^2 cutoff we used for voxel selection for each ROI (V1–V3). **(d)** Estimates obtained using the continuous stimulus presentation design for the overall model goodness-of-fit improvement assessed by normalizing the SSE of the model by the SSE obtained after shuffling contrast stimulus levels, creating a conservative null comparison ($(SSE_{null} - SSE_{model}) / SSE_{null}$), and semi-saturation, response saturation, and transducer parameters, respectively. Large dots indicate the group average, the error bar denotes the SEM, and smaller dots individual participants.

a. Event-related dataset (Experiment 1)



b. Continuous dataset (Experiment 2)

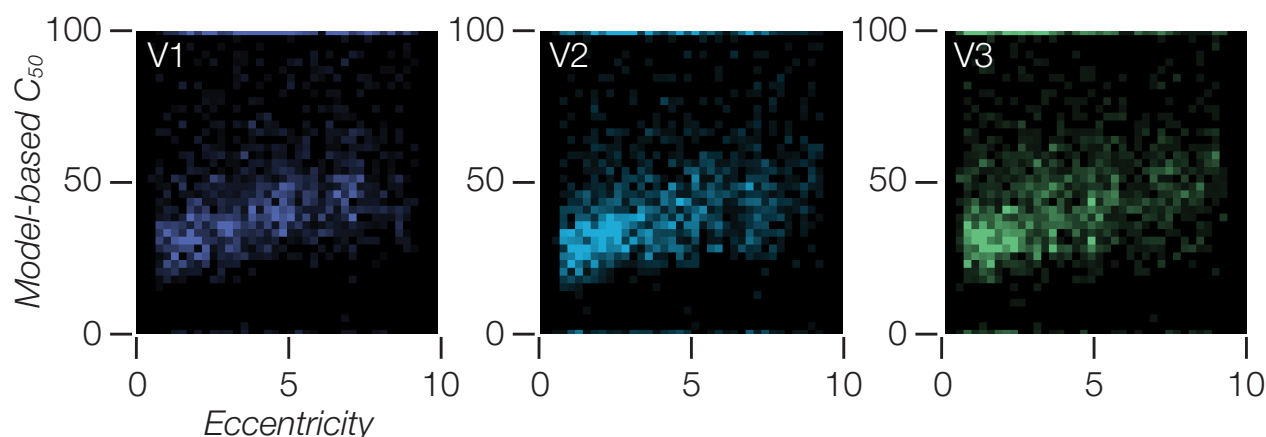


Figure 7. Voxel-wise correspondence between eccentricity and semi-saturation contrast. Group-average 2D histograms across visual areas V1-3. (a) Event-related dataset. (b) Continuous dataset. Brighter colors indicate a higher density of voxels.

Voxelwise patterns

Summarizing CRF parameter estimates across a whole ROI can obscure meaningful within region variability. Voxels within an ROI differ systematically in their preferred stimulus features, for example more peripheral voxels have larger receptive fields and prefer lower spatial frequencies (Aghajari et al., 2020; Broderick et al., 2022; Wiecek et al., 2026). Although the stimulus display was cortically magnified to account for these eccentricity driven preferences, CRF parameter estimates remain inherently constrained by the stimulus design. For instance, voxels with receptive fields near the outer edge of the stimulus display might be poorly driven by the stimulus, potentially influencing the profile of the CRF.

To examine within-ROI variability, we assessed the voxel-wise agreement between eccentricity (obtained from a separate pRF mapping session) and semi-

saturation estimates for both experiments (Figure 7). Consistent with findings from the event-related dataset (Vinke et al., 2022), both experimental designs revealed a positive correlation between eccentricity and C_{50} , where voxels with more peripheral receptive fields tend to have higher semi-saturation contrasts. This relationship was significant across participants in V1 and V2 for both datasets (event-related: V1 $r = 0.35$, V2 $r = 0.42$, V3 $r = 0.29$; continuous: V1 $r = 0.36$, V2 $r = 0.32$; all $p < 0.01$) and reached a trend level in V3 for the continuous dataset ($r = 0.21$, $p = 0.054$).

Discussion

Compressive nonlinearities, such as the contrast response function, are foundational towards understanding the bridge between brain and behavior

(Boynton et al., 1996; DiCarlo, Zoccolan, & Rust, 2012; Shapley & Victor, 1978). And yet, our ability to measure these nonlinear interactions noninvasively in human visual cortex had, until recently, proven surprisingly elusive (Boynton et al., 1996, 1999; Buracas et al., 2005; Buracas & Boynton, 2007; Hara & Gardner, 2014; Itthipuripat et al., 2019; Marquardt et al., 2018; Murray, 2008; Pestilli et al., 2011; Tootell et al., 1995; Tootell et al., 1998), particularly for population measures such as fMRI.

Here, we introduce a new technique, pCRF mapping, that can efficiently capture these nonlinear population response profiles, by coupling a forward model-based approach (Aghajari et al., 2020; Aqil et al., 2021; Broderick et al., 2022; Dumoulin & Wandell, 2008; Groen et al., 2022; Harvey et al., 2013; Himmelberg, Kwak, Carrasco, & Winawer, 2025; Kay et al., 2013; Kupers et al., 2021; Ramirez et al., 2025; Wandell & Winawer, 2015; Wiecek et al., 2026; Zhou et al., 2019) with an adaptation protocol that homogenizes nonlinear population responses (Gardner et al., 2005; Vinke et al., 2022). We first vetted this approach by demonstrating that model parameter recovery using pCRF squared nicely with those derived from more conventional approaches that use adaptation paired with a fast-event-related design. We then showcase the experimental flexibility of pCRF, demonstrating that we can carry out pCRF estimation of fMRI data even with an ultrarapid, stochastic stimulus design wherein there are little-to-no repeats of any particular stimulus condition—designs that do not lend themselves to conventional fMRI analysis approaches. This pCRF approach can be leveraged for a number of potential experiments, down the road. For instance, it can be used to recover the population contrast response properties of voxels while individuals view naturalistic videos or stimuli (Allen et al., 2022; Hedger, Naselaris, Kay, & Knapen, 2026; Kay et al., 2008), or it can allow for a more seamless port between neuroimaging measures and behavioral tasks, which often are more rapid, complex, and more stochastic than conventional analyses can typically withstand.

Of course, there are limitations to this approach. For instance, the variance explained by the pCRF model is low. Although this isn't that unusual for model-based fMRI approaches applied to individual voxel BOLD time series without averaging across voxels or runs, such as pRF and pSFT, it is certainly an area for further development. Notably, correspondence between the two approaches was strongest for $R_{\max}$, whereas C50 and n , which jointly determine the profile of the rising portion of the CRF, showed comparatively greater variability between methods, suggesting that resolving the finer structure of the response function's dynamic range remains more sensitive to differences in how each approach handles noise and estimation. One limitation

in the approach is that, in our ultra rapid, continuous design, we assume that there are no fluctuations in visual adaptation state. Our model assumes that the neural populations have settled on a steady state intensity driven by the rolling average of the presented contrast sequence. However, moment-to-moment fluctuations in adaptation state are likely (Heckman et al., 2007; Tring, Dipoppa, & Ringach, 2024; Tring, Moosavi, Dipoppa, & Ringach, 2024). A growing body of work suggests that adaptation and contrast normalization are not separate mechanisms, but rather different facets of the same temporally extended computation (Groen et al., 2022; Zhou et al., 2019). Under this view, the rapidly varying contrast stimuli feed into a shared history-dependent normalization pool, such that the adaptation state itself is continuously disturbed rather than held fixed. The continuous design in Experiment 2 partially guards against this, as centering the contrast distribution around the adapter contrast keeps the rolling normalization pool near a stable state on average. Nonetheless, the static pCRF model cannot represent these moment-to-moment interactions. Future work in model development could take the dynamic nature of adaptation into consideration, by including history-dependent gain control.

Although we fit a parametrized double-gamma HRF jointly with the pCRF parameters (see Supplementary Fig. S2 for parameter estimates), there is evidence to suggest that the HRF itself changes shape with contrast, potentially due to neurovascular coupling (Chen et al., 2021). Incorporating such contrast-dependent HRF dynamics would add further complexity to the model-based approach, but could increase the model's ability to capture systematic variance in the BOLD response.

Contrast adaptation is a process that is constantly unfolding as we perceive moment-to-moment changes in our visual environment. In this study, despite focusing on a single adaptation contrast level throughout both experiments, we demonstrate the utility of temporarily clamping down the contrast adaptation variation in the interest of repeatably measuring the same contrast responses over the course of the neuroimaging session, highlighting an important consideration that should be paid to rapid event-related fMRI experimental designs. Specifically, whether (contrast) adaptation is a potential confound to be controlled for (as we demonstrate) or intentionally left to unfold naturally within or across experimental conditions-of-interest. In either case the model-based approach presented here provides a useful testbed for evaluating the effectiveness of chosen rapid event-related fMRI design.

Like most model-based fMRI approaches, pCRF is unidimensional, only accounting for changes in stimulus contrast. While each visuocortical subpopulation we record from is multiplexed in its selectivity (e.g., orientation, spatial frequency,

luminance), our approach does not attempt to capture all these properties at once. Specifically, we use the Naka-Rushton model to demonstrate how this data-driven modeling approach can be applied. More broadly, the same framework could incorporate any neural response model, unidimensional or multiplexed, depending on the experimental design and stimuli used. Additional follow-up work could improve how much variance is captured by implementing multiplexed models, per voxel, across multiple feature dimensions. However, for such an approach to be successful, it is crucial to select an appropriate neural response model and to characterize input stimulus intensity and timing dynamics as accurately as possible, noting all incongruencies between experimental conditions. Taken together, these results suggest that pCRF mapping offers a flexible and extensible framework for characterizing nonlinear population responses, opening the door to studying gain control mechanisms under the complex, naturalistic, and rapidly changing conditions that better approximate real-world visual experience.

Keywords: *adaptation, divisive normalization, gain control, fMRI, vision, visual cortex*

Acknowledgments

Supported by National Institutes of Health Grants EY028163, EY035640 & EY037358 to S. Ling. This research was carried out in part at the Boston University Cognitive Neuroimaging Center, which is supported by the NSF Major Research Instrumentation Program through grant number 1625552. We thank Randolph Blake for imprinting the joy of science, and ourselves for providing meaningful feedback and comments on this project. Also, surfing, synthesizers and shark movies.

Author contributions: L.N.V., S.L., and I.M.B. conceived and designed this study; L.N.V. and I.M.B. acquired the data; L.N.V. and I.M.B. performed data analyses; L.N.V., S.L. and I.M.B. wrote and edited the manuscript.

Data and code availability: All preprocessed fMRI data sets reported in this study, as well as all MATLAB code used for stimulus presentation and data analysis, are available at <https://osf.io/p9q3u>.

Commercial relationships: none.

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