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Report

Reconstructing Visual Experiences from Brain Activity Evoked by Natural Movies

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Summary

Quantitative modeling of human brain activity can provide crucial insights about cortical representations [1, 2] and can form the basis for brain decoding devices [3–5]. Recent functional magnetic resonance imaging (fMRI) studies have modeled brain activity elicited by static visual patterns and have reconstructed these patterns from brain activity [6–8]. However, blood oxygen level-dependent (BOLD) signals measured via fMRI are very slow [9], so it has been difficult to model brain activity elicited by dynamic stimuli such as natural movies. Here we present a new motion-energy [10, 11] encoding model that largely overcomes this limitation. The model describes fast visual information and slow hemodynamics by separate components. We recorded BOLD signals in occipitotemporal visual cortex of human subjects who watched natural movies and fit the model separately to individual voxels. Visualization of the fit models reveals how early visual areas represent the information in movies. To demonstrate the power of our approach, we also constructed a Bayesian decoder [8] by combining estimated encoding models with a sampled natural movie prior. The decoder provides remarkable reconstructions of the viewed movies. These results demonstrate that dynamic brain activity measured under naturalistic conditions can be decoded using current fMRI technology.

Results

Many of our visual experiences are dynamic: perception, visual imagery, dreaming, and hallucinations all change continuously over time, and these changes are often the most compelling and important aspects of these experiences. Obtaining a quantitative understanding of brain activity underlying these dynamic processes would advance our understanding of visual function. Quantitative models of dynamic mental events could also have important applications as tools for psychiatric diagnosis and as the foundation of brain machine interface devices [3–5].

Modeling dynamic brain activity is a difficult technical problem. The best tool available currently for noninvasive measurement of brain activity is functional magnetic resonance imaging (fMRI), which has relatively high spatial resolution [12, 13]. However, blood oxygen level-dependent (BOLD) signals measured using fMRI are relatively slow [9], especially when compared to the speed of natural vision and many other mental processes. It has therefore been assumed that fMRI data would not be useful for modeling brain activity evoked during natural vision or by other dynamic mental processes.

Here we present a new motion-energy [10, 11] encoding model that largely overcomes this limitation. The model separately describes the neural mechanisms mediating visual motion information and their coupling to much slower hemodynamic mechanisms. In this report, we first validate this encoding model by showing that it describes how spatial and temporal information are represented in voxels throughout visual cortex. We then use a Bayesian approach [8] to combine estimated encoding models with a sampled natural movie prior, in order to produce reconstructions of natural movies from BOLD signals.

We recorded BOLD signals from three human subjects while they viewed a series of color natural movies ($20^\circ \times 20^\circ$ at 15 Hz). A fixation task was used to control eye position. Two separate data sets were obtained from each subject. The training data set consisted of BOLD signals evoked by 7,200 s of color natural movies, where each movie was presented just once. These data were used to fit a separate encoding model for each voxel located in posterior and ventral occipitotemporal visual cortex. The test data set consisted of BOLD signals evoked by 540 s of color natural movies, where each movie was repeated ten times. These data were used to assess the accuracy of the encoding model and as the targets for movie reconstruction. Because the movies used to train and test models were different, this approach provides a fair and objective evaluation of the accuracy of the encoding and decoding models [2, 14].

BOLD signals recorded from each voxel were fit separately using a two-stage process. Natural movie stimuli were first filtered by a bank of neurally inspired nonlinear units sensitive to local motion-energy [10, 11]. L1-regularized linear regression [15, 16] was then used to fit a separate hemodynamic coupling term to each nonlinear filter (Figure 1; see also Supplemental Experimental Procedures available online). The regularized regression approach used here was optimized to obtain good estimates even for computational models containing thousands of regressors. In this respect, our approach differs from the regression procedures used in many other fMRI studies [17, 18].

To determine how much motion information is available in BOLD signals, we compared prediction accuracy for three different encoding models (Figures 2A–2C): a conventional static model that includes no motion information [8, 19], a nondirectional motion model that represents local motion energy but not direction, and a directional model that represents both local motion energy and direction. Each of these models was fit separately to every voxel recorded in each subject, and the test data were used to assess prediction accuracy for each model. Prediction accuracy was defined as the correlation between predicted and observed BOLD signals. The averaged accuracy across subjects and voxels in early visual areas (V1, V2, V3, V3A, and V3B) was 0.24, 0.39, and 0.40 for the static, nondirectional, and directional encoding models, respectively (Figures 2D and 2E; see Figure S1A for subject- and area-wise comparisons). This

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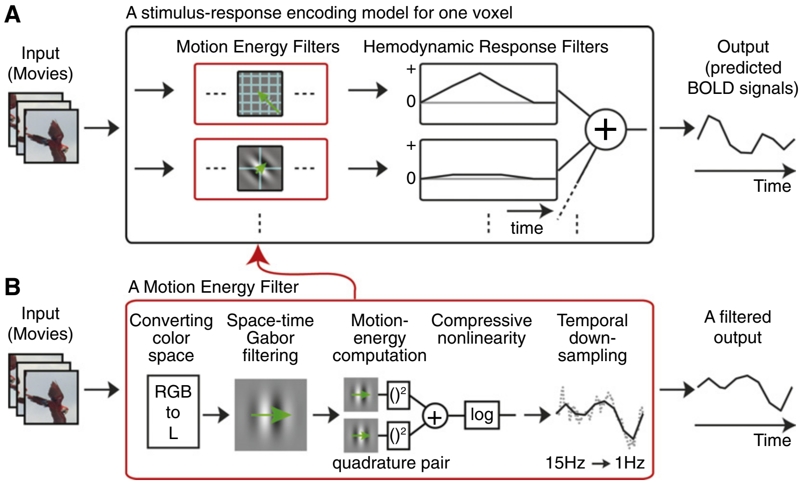

Figure 1. Schematic Diagram of the Motion-Energy Encoding Model

(A) Stimuli pass first through a fixed set of nonlinear spatiotemporal motion-energy filters (shown in detail in B) and then through a set of hemodynamic response filters fit separately to each voxel. The summed output of the filter bank provides a prediction of BOLD signals.
(B) The nonlinear motion-energy filter bank consists of several filtering stages. Stimuli are first transformed into the Commission Internationale de l'Éclairage L*A*B* color space, and the color channels are stripped off. Luminance signals then pass through a bank of 6,555 spatiotemporal Gabor filters differing in position, orientation, direction, spatial, and temporal frequency (see Supplemental Experimental Procedures for details). Motion energy is calculated by squaring and summing Gabor filters in quadrature. Finally, signals pass through a compressive nonlinearity and are temporally down-sampled to the fMRI sampling rate (1 Hz).

difference in prediction accuracy was significant ($p < 0.0001$, Wilcoxon signed-rank test). An earlier study showed that the static model tested here recovered much more information from BOLD signals than had been obtained with any previous model [8, 19]. Nevertheless, both motion models developed here provide far more accurate predictions than are obtained with the static model. Note that the difference in prediction accuracy between the directional and nondirectional motion models, though significant, was small (Figure 2E; Figure S1A). This suggests that BOLD signals convey spatially localized but predominantly nondirectional motion information. These results show that the motion-energy encoding model predicts BOLD signals evoked by novel natural movies.

To further explore what information can be recovered from these data, we estimated the spatial, spatial frequency, and temporal frequency tuning of the directional motion-energy encoding model fit to each voxel. The spatial receptive fields of individual voxels were spatially localized (Figures 2F and 2G, left) and were organized retinotopically (Figures 2H and 2I), as reported in previous fMRI studies [12, 19–23]. Voxel-based receptive fields also showed spatial and temporal frequency tuning (Figures 2F and 2G, right), as reported in previous fMRI studies [24, 25].

To determine how motion information is represented in human visual cortex, we calculated the optimal speed for each voxel by dividing the peak temporal frequency by the peak spatial frequency. Projecting the optimal speed of the voxels onto a flattened map of the cortical surface (Figure 2J) revealed a significant positive correlation between eccentricity and optimal speed: relatively more peripheral voxels were tuned for relatively higher speeds. This pattern was observed in areas V1, V2, and V3 and for all three subjects ($p < 0.0001$, t test for correlation coefficient; see Figure S1B for subject- and area-wise comparisons). To our knowledge, this is the first evidence that speed selectivity in human early visual areas depends on eccentricity, though a consistent trend has been reported in human behavioral studies [26–28] and in neurophysiological studies of nonhuman primates [29, 30]. These results show that the motion-energy encoding model describes tuning for both spatial and temporal information at the level of single voxels.

To further characterize the temporal specificity of the estimated motion-energy encoding models, we used the test data to estimate movie identification accuracy. Identification accuracy [7, 19] measures how well a model can correctly associate an observed BOLD signal pattern with the specific stimulus that evoked it. Our motion-energy encoding model could identify the specific movie stimulus that evoked an observed BOLD signal 95% of the time (464 of 486 volumes) within ± one volume (1 s; subject S1; Figures 3A and 3B). This is far above what would be expected by chance (<1%). Identification accuracy (within ± one volume) was >75% for all three subjects even when the set of possible natural movie clips included 1,000,000 separate clips chosen at random from the internet (Figure 3C). This result demonstrates that the motion-energy encoding model is both valid and temporally specific. Furthermore, it suggests that the model might provide good reconstructions of natural movies from brain activity measurements [5].

We used a Bayesian approach [8] to reconstruct movies from the evoked BOLD signals (see also Figure S2). We estimated the posterior probability by combining a likelihood function (given by the estimated motion-energy model; see Supplemental Experimental Procedures) and a sampled natural movie prior. The sampled natural movie prior consists of ~18,000,000 s of natural movies sampled at random from the internet. These clips were assigned uniform prior probability (and consequently all other clips were assigned zero prior probability; note also that none of the clips in the prior were used in the experiment). Furthermore, to make decoding tractable, reconstructions were based on 1 s clips (15 frames), using BOLD signals with a delay of 4 s. In effect, this procedure enforces an assumption that the spatiotemporal stimulus that elicited each measured BOLD signal must be one of the movie clips in the sampled prior.

Figure 4 shows typical reconstructions of natural movies obtained using the motion-energy encoding model and the Bayesian decoding approach (see Movie S1 for the corresponding movies). The posterior probability was estimated across the entire sampled natural movie prior separately for each BOLD signal in the test data. The peak of this posterior distribution was the conventional maximum a posteriori (MAP) reconstruction [8] for each BOLD signal (see second row in Figure 4). When the sampled natural movie prior contained clips similar to the viewed clip, the MAP reconstructions were good (e.g., the close-up of a human speaker shown in Figure 4A). However, when the prior contained no clips similar to the viewed clip, the reconstructions are poor (e.g., Figure 4B). This likely reflects both the limited size of the sampled natural movie prior and noise in the fMRI measurements. One way to

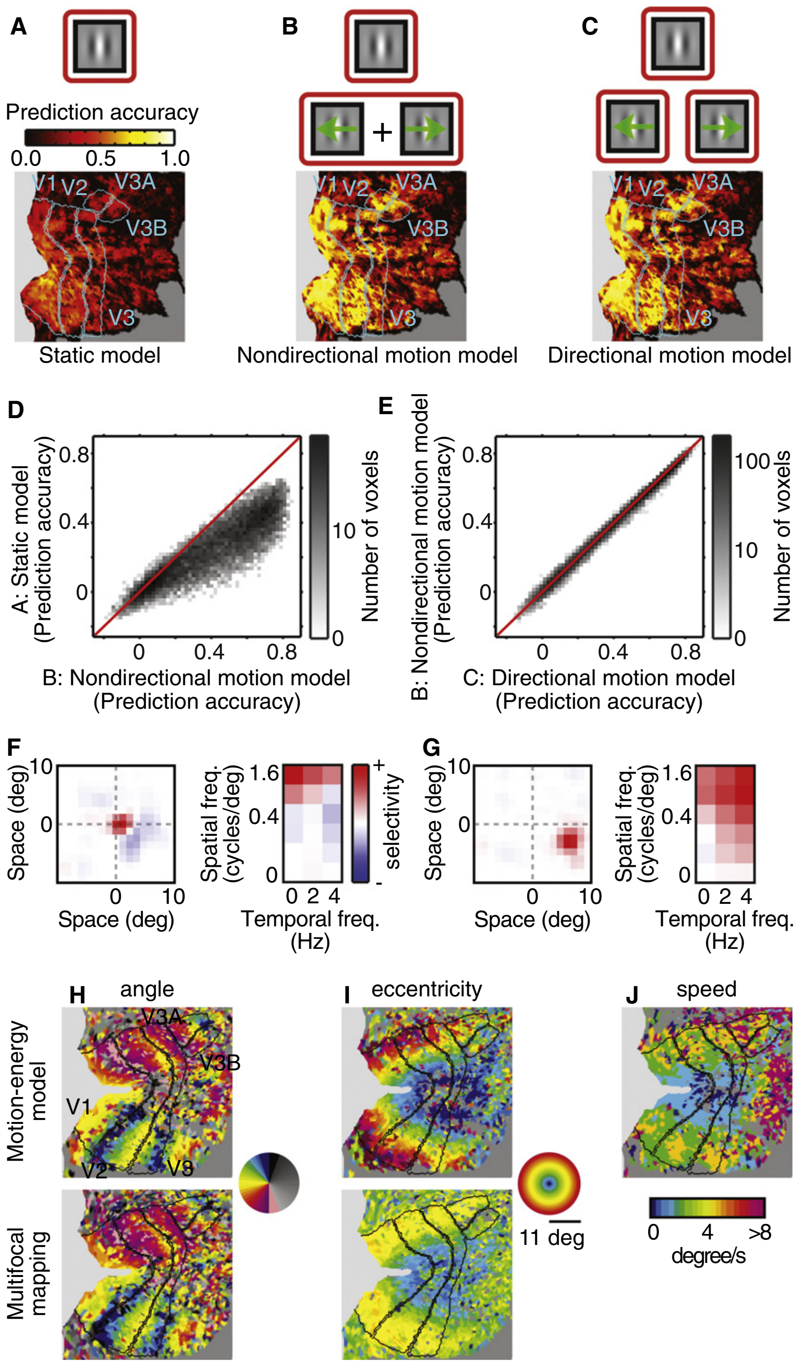

Figure 2. The Directional Motion-Energy Model Captures Motion Information

(A) Top: the static encoding model includes only Gabor filters that are not sensitive to motion. Bottom: prediction accuracy of the static model is shown on a flattened map of the cortical surface of one subject (S1). Prediction accuracy is relatively poor.

(B) The nondirectional motion-energy encoding model includes Gabor filters tuned to a range of temporal frequencies, but motion in opponent directions is pooled. Prediction accuracy of this model is better than the static model.

(C) The directional motion-energy encoding model includes Gabor filters tuned to a range of temporal frequencies and directions. This model provides the most accurate predictions of all models tested.

(D and E) Voxel-wise comparisons of prediction accuracy between the three models. The directional motion-energy model performs significantly better than the other two models, although the difference between the nondirectional and directional motion models is small. See also Figure S1 for subject- and area-wise comparisons.

(F) The spatial receptive field of one voxel (left) and its spatial and temporal frequency selectivity (right). This receptive field is located near the fovea, and it is high-pass for spatial frequency and low-pass for temporal frequency. This voxel thus prefers static or low-speed motion.

(G) Receptive field for a second voxel. This receptive field is located lower periphery, and it is band-pass for spatial frequency and high-pass for temporal frequency. This voxel thus prefers higher-speed motion than the voxel in (F).

(H) Comparison of retinotopic angle maps estimated using the motion-energy encoding model (top) and conventional multifocal mapping (bottom) on a flattened cortical map [47]. The angle maps are similar, even though they were estimated using independent data sets and methods.

(I) Comparison of eccentricity maps estimated as in (H). The maps are similar except in the far periphery, where the multifocal mapping stimulus was coarse.

(J) Optimal speed projected on to a flattened map as in (H). Voxels near the fovea tend to prefer slow-speed motion, whereas those in the periphery tend to prefer high-speed motion. See also Figure S1B for subject-wise comparisons.

achieve more robust reconstructions without enlarging the prior is to interpolate over the sparse samples in the prior. We therefore created an averaged high posterior (AHP) reconstruction by averaging the 100 clips in the sampled natural movie prior that had the highest posterior probability (see also Figure S2; note that the AHP reconstruction can be viewed as a Bayesian version of bagging [31]). The AHP reconstruction captures the spatiotemporal structure within a viewed clip even when it is completely unique (e.g., the spreading of an inkblot from the center of the visual field shown in Figure 4B).

To quantify reconstruction quality, we calculated the correlation between the motion-energy content of the original movies and their reconstructions (see Supplemental Experimental Procedures). A correlation of 1.0 indicates perfect reconstruction of the spatiotemporal energy in the original movies, and a correlation of 0.0 indicates that the movies and their reconstruction are spatiotemporally uncorrelated. The results for both MAP and AHP reconstructions are shown in Figure 4D. In both cases, reconstruction accuracy was significantly higher than chance ($p < 0.0001$, Wilcoxon rank-sum test; see Supplemental Experimental Procedures). Furthermore, AHP reconstructions were significantly better than MAP reconstructions ($p < 0.0001$, Wilcoxon signed-rank test). Although still crude (motion-energy correlation ~ 0.3), these results validate our general approach to reconstruction and demonstrate that the AHP estimate improves reconstruction over the MAP estimate.

Discussion

In this study, we developed an encoding model that predicts BOLD signals in early visual areas with unprecedented accuracy. By using this model in a Bayesian framework, we

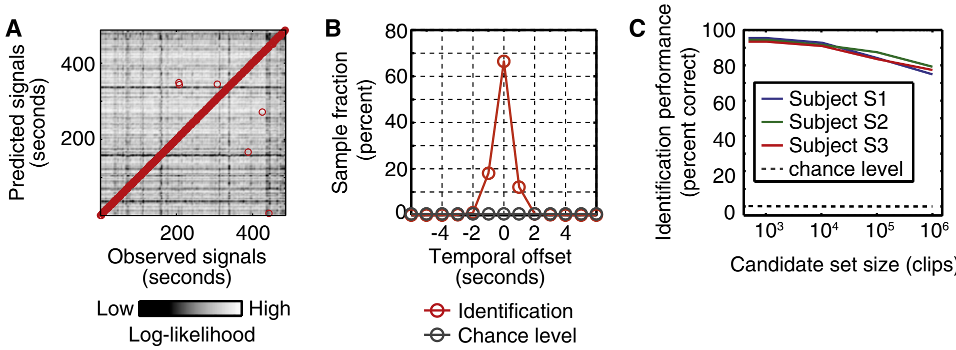

Figure 3. Identification Analysis

(A) Identification accuracy for one subject (S1). The test data in our experiment consisted of 486 volumes (s) of BOLD signals evoked by the test movies. The estimated model yielded 486 volumes of BOLD signals predicted for the same movies. The brightness of the point in the *m*th column and *n*th row represents the log-likelihood (see Supplemental Experimental Procedures) of the BOLD signals evoked at the *m*th second given the BOLD signal predicted at the *n*th second. The highest log-likelihood in each column is designated by a red circle and thus indicates the choice of the identification algorithm.

(B) Temporal offset between the correct timing and the timing identified by the algorithm for the same subject shown in (A). The algorithm was correct to within ± one volume (s) 95% of the time (464 of 486 volumes); chance performance is <1% (3 of 486 volumes; i.e., three volumes centered at the correct timing).

(C) Scaling of identification accuracy with set size. To understand how identification accuracy scales with size of stimulus set, we enlarged the identification stimulus set to include additional stimuli drawn from a natural movie database (which was not actually used in the experiment). For all three subjects, identification accuracy (within ± one volume) was >75% even when the set of potential movies included 1,000,000 clips. This is far above chance (gray dashed line).

provide the first reconstructions of natural movies from human brain activity. This is a critical step toward the creation of brain reading devices that can reconstruct dynamic perceptual experiences. Our solution to this problem rests on two key innovations. The first is a new motion-energy encoding model that is optimized for use with fMRI and that aims to reflect the separate contributions of the underlying neuronal population and hemodynamic coupling (Figure 1). This encoding model recovers fine temporal information from relatively slow BOLD signals. The second is a sampled natural movie prior that is embedded within a Bayesian decoding framework. This approach provides a simple method for reconstructing spatio-temporal stimuli from the sparsely sampled and slow BOLD signals.

Our results provide the first evidence that there is a positive correlation between eccentricity and optimal speed in human early visual areas. This provides a functional explanation for previous behavioral studies indicating that speed sensitivity

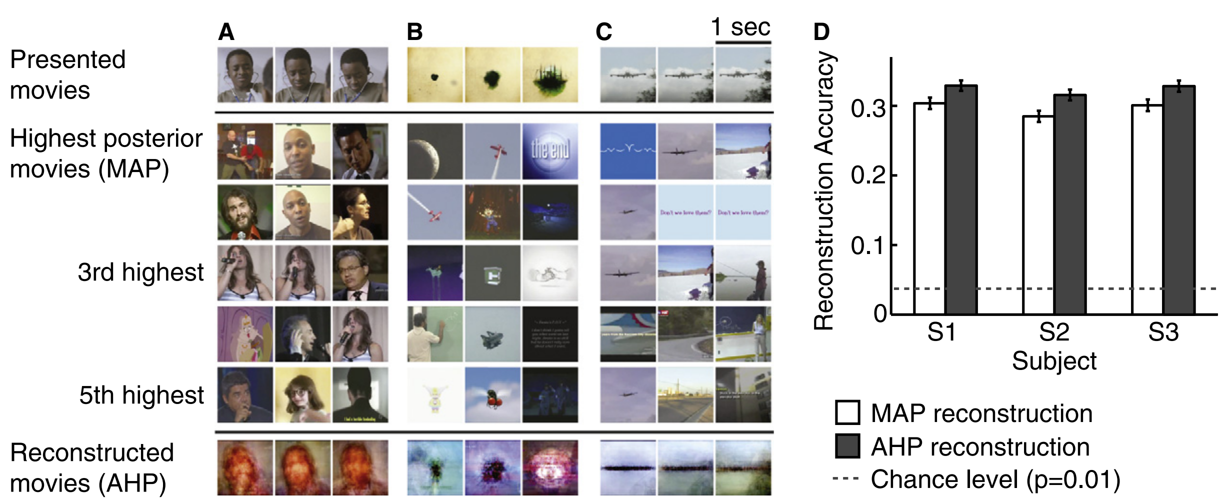

Figure 4. Reconstructions of Natural Movies from BOLD Signals

(A) The first (top) row shows three frames from a natural movie used in the experiment, taken 1 s apart. The second through sixth rows show frames from the five clips with the highest posterior probability. The maximum a posteriori (MAP) reconstruction is shown in the second row. The seventh (bottom) row shows the averaged high posterior (AHP) reconstruction. The MAP provides a good reconstruction of the second and third frames, whereas the AHP provides more robust reconstructions across frames.

(B and C) Additional examples of reconstructions, in the same format as (A).

(D) Reconstruction accuracy (correlation in motion-energy; see Supplemental Experimental Procedures) for all three subjects. Error bars indicate ±1 standard error of the mean across 1 s clips. Both the MAP and AHP reconstructions are significant, though the AHP reconstructions are significantly better than the MAP reconstructions. Dashed lines show chance performance (p = 0.01). See also Figure S2.

depends on eccentricity [26–28]. This systematic variation in optimal speed across the visual field may be an adaptation to the nonuniform distribution of speed signals induced by selective foveation in natural scenes [32]. From the perspective of decoding, this result suggests that we might further optimize reconstruction by including eccentricity-dependent speed tuning in the prior.

We found that a motion-energy model that incorporates directional motion signals was only slightly better than a model that does not include direction. We believe that this likely reflects limitations in the spatial resolution of fMRI recordings. Indeed, a recent study reported that hemodynamic signals were sufficient to visualize a columnar organization of motion direction in macaque area V2 [33]. Future fMRI experiments at higher spatial or temporal resolution [34, 35] might therefore be able to recover clearer directional signals in human visual cortex.

In preliminary work for this study, we explored several encoding models that incorporated color information explicitly. However, we found that color information did not improve the accuracy of predictions or identification beyond what could be achieved with models that include only luminance information. We believe that this reflects the fact that luminance and color borders are often correlated in natural scenes ([36, 37], but see [38]). (Note that when isoluminant, monochromatic stimuli are used, color can be reconstructed from evoked BOLD signals [39].) The correlation between luminance and color information in natural scenes has an interesting side effect: our reconstructions tended to recover color borders (e.g., borders between hair versus face or face versus body), even though the encoding model makes no use of color information. This is a positive aspect of the sampled natural movie prior and provides additional cues to aid in recognition of reconstructed scenes (see also [40]).

We found that the quality of reconstruction could be improved by simply averaging around the maximum of the posterior movies. This suggests that reconstructions might be further improved if the number of samples in the prior is much larger than the one used here. Likelihood estimation (and thus reconstruction) would also improve if additional knowledge about the neural representation of movies was used to construct better encoding models (e.g., [41]).

In a landmark study, Thirion et al. [6] first reconstructed static imaginary patterns from BOLD signals in early visual areas. Other studies have decoded subjective mental states, such as the contents of visual working memory [42], or whether subjects are attending to one or another orientation or direction [3, 43]. The modeling framework presented here provides the first reconstructions of dynamic perceptual experiences from BOLD signals. Therefore, this modeling framework might also permit reconstruction of dynamic mental content such as continuous natural visual imagery. In contrast to earlier studies that reconstruct visual patterns defined by checkerboard contrast [6, 7], our framework could potentially be used to decode involuntary subjective mental states (e.g., dreaming or hallucination), though it would be difficult to determine whether the decoded content was accurate. One recent study showed that BOLD signals elicited by visual imagery are more prominent in ventral-temporal visual areas than in early visual areas [44]. This finding suggests that a hybrid encoding model that combines the structural motion-energy model developed here with a semantic model of the form developed in previous studies [8, 45, 46] could provide even better reconstructions of subjective mental experiences.

Experimental Procedures

Stimuli

Visual stimuli consisted of color natural movies drawn from the Apple QuickTime HD gallery (http://trailers.apple.com/) and YouTube (http://www.youtube.com/; see the list of movies in Supplemental Experimental Procedures). The original high-definition movies were cropped to a square and then spatially downsampled to 512 × 512 pixels. Movies were then clipped to 10–20 s in length, and the stimulus sequence was created by randomly drawing movies from the entire set. Movies were displayed using a VisuaStim LCD goggle system (20° × 20° at 15 Hz). A colored fixation spot (4 pixels or 0.16° square) was presented on top of the movie. The color of the fixation spot changed three times per second to ensure that it was visible regardless of the color of the movie.

MRI Parameters

The experimental protocol was approved by the Committee for the Protection of Human Subjects at University of California, Berkeley. Functional scans were conducted using a 4 Tesla Varian INOVA scanner (Varian, Inc.) with a quadrature transmit/receive surface coil (Midwest RF). Scans were obtained using T2*-weighted gradient-echo EPI: TR = 1 s, TE = 28 ms, flip angle = 56°, voxel size = 2.0 × 2.0 × 2.5 mm^3, FOV = 128 × 128 mm^2. The slice prescription consisted of 18 coronal slices beginning at the posterior pole and covering the posterior portion of occipital cortex.

Data Collection

Functional MRI scans were made from three human subjects, S1 (author S.N., age 30), S2 (author T.N., age 34), and S3 (author A.T.V., age 23). All subjects were healthy and had normal or corrected-to-normal vision. The training data were collected in 12 separate 10 min blocks (7,200 s total). The training movies were shown only once each. The test data were collected in nine separate 10 min blocks (5,400 s total) consisting of 9 min movies repeated ten times each. To minimize effects from potential adaptation and long-term drift in the test data, we divided the 9 min movies into 1 min chunks, and these were randomly permuted across blocks. Each test block was thus constructed by concatenating ten separate 1 min movies. All data were collected across multiple sessions for each subject, and each session contained multiple training and test blocks. The training and test data sets used different movies.

Additional methods can be found in Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes two figures, Supplemental Experimental Procedures, and one movie and can be found with this article online at doi:10.1016/j.cub.2011.08.031.

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