

# Predicting the Stream of Consciousness from Activity in Human Visual Cortex

John-Dylan Haynes<sup>1,2,\*</sup> and Geraint Rees<sup>1,2</sup>

<sup>1</sup>Wellcome Department of Imaging Neuroscience

Institute of Neurology

University College London

12 Queen Square

London WC1N 3BG

United Kingdom

<sup>2</sup>Institute of Cognitive Neuroscience

University College London

Alexandra House

17 Queen Square

London WC1N 3AR

United Kingdom

## Summary

Can the rapid stream of conscious experience be predicted from brain activity alone? Recently, spatial patterns of activity in visual cortex have been successfully used to predict feature-specific stimulus representations for both visible [1, 2] and invisible [2] stimuli. However, because these studies examined only the prediction of static and unchanging perceptual states during extended periods of stimulation, it remains unclear whether activity in early visual cortex can also predict the rapidly and spontaneously changing stream of consciousness [3]. Here, we used binocular rivalry [4] to induce frequent spontaneous and stochastic changes in conscious experience without any corresponding changes in sensory stimulation, while measuring brain activity with fMRI. Using information that was present in the multivariate pattern of responses to stimulus features, we could accurately predict, and therefore track, participants' conscious experience from the fMRI signal alone while it underwent many spontaneous changes. Prediction in primary visual cortex primarily reflected eye-based signals, whereas prediction in higher areas reflected the color of the percept. Furthermore, accurate prediction during binocular rivalry could be established with signals recorded during stable monocular viewing, showing that prediction generalized across viewing conditions and did not require or rely on motor responses. It is therefore possible to predict the dynamically changing time course of subjective experience with only brain activity.

## Results

When dissimilar images are presented to the two eyes, they compete for perceptual dominance so that each image is visible in turn for a few seconds while the other is suppressed. This phenomenon is known as binocular rivalry [4]. Because perceptual transitions between each monocular view occur spontaneously without any change in physical stimulation, neural re-

sponses associated with conscious perception can be distinguished from those due to sensory processing. We measured brain activity while participants viewed a novel binocular rivalry stimulus (see [Figure 1](#) and [Experimental Procedures](#)) that consisted of two co-rotating orthogonal gratings ([Figure 1A](#)). This stimulus was specially devised to ensure relatively long perceptual dominance periods while strongly driving neuronal activity in early visual cortex ([Figures 1B](#) and [1C](#)). Responses from multiple concurrently recorded voxels in early visual cortex were jointly analyzed with multivariate pattern recognition applied directly to the raw BOLD signal ([Figure 2](#); see the [Supplemental Data](#) available with this article online). The cortical BOLD response pattern at each time point was assigned to one of two groups, depending on the dominant percept at the time it was acquired ([Figure 2A](#); [Figures S2](#) and [S3](#)). One part of the data was then used to train a pattern classifier (on a per-participant basis) to distinguish between the population responses during dominance of either of the two percepts ([Figure 2B](#)). In a second step, these trained classifiers were applied to *independently* acquired test volumes to determine whether the time course of rivalrous perception during their acquisition could be predicted. Note that the data used for training and testing were *independent* time series collected at different times.

## Response Patterns Reflect Dynamics of Perceptual Dominance

We found that the detailed time course of rivalrous perception could be predicted with remarkably high accuracy from brain activity in each scanning run ([Figure 3A](#)). Moreover, classification accuracy improved as patterns of activity across larger numbers of voxels in V1 were taken into account and reached an asymptotic value for around 20 voxels ([Figure 3B](#)). Activity from V1 was sufficient to predict with up to ~80% accuracy which of two possible rivalrous percepts a participant was experiencing at any one time. There were no differences in predictive accuracy among signals from V1, V2, or V3, but accuracy slightly increased to 85 percent when signals from V1, V2, and V3 were combined. The striking precision with which the detailed temporal dynamics of conscious perception were captured can be seen in [Figure 3C](#), which compares true and predicted perceptual time courses for all participants. We examined the output of our classifier around the time of perceptual transitions, and we found that when one of the two percepts became perceptually dominant, the associated pattern response was not transient, but instead was elevated for a prolonged period ([Figures 4A](#) and [4B](#)). This indicates that the pattern signal represented the dominant monocular percept in a sustained fashion and did not reflect only the transitions between perceptual phases. This is consistent with previous studies that have suggested that signals in V1 can reflect perceptual dominance during rivalry in a sustained fashion

\*Correspondence: haynes@fil.ion.ucl.ac.uk

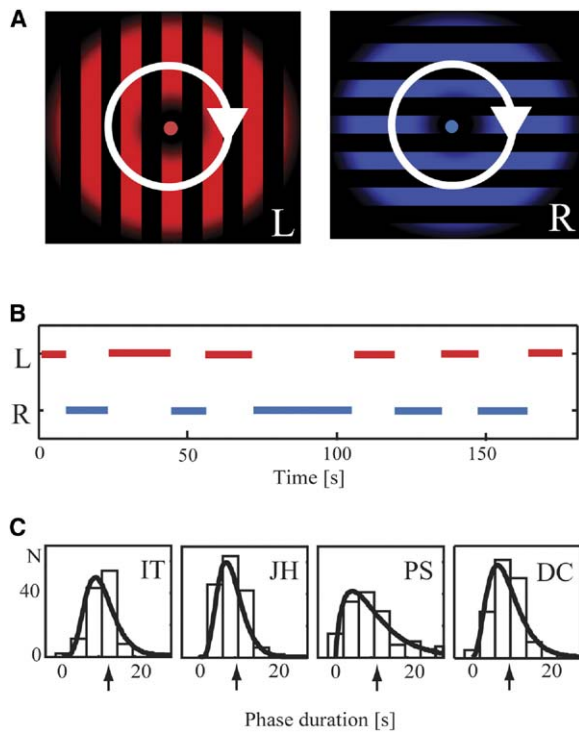


Figure 1. Rotating Binocular Rivalry Stimulus

(A) Stimuli comprised superimposed orthogonal red and blue gratings, both rotating clockwise. They were viewed through red/blue anaglyph glasses, so that the rotating blue grating was visible to the right eye and the rotating red grating to the left eye.

(B) Participants used response buttons to continuously indicate during each 180 s period of scanning whether they currently perceived either the red or blue grating. The stimulus induced binocular rivalry during which perception alternated between the two monocular views.

(C) As with previous studies on rivalry, the distribution of phase durations (shown here for all participants, collapsed across red and blue percepts) showed a skewed unimodal distribution that was well approximated with a  $\gamma$  function (solid lines). The mean phase duration (indicated by the vertical arrow on the abscissa) was  $\sim 10$  s.

[5]. In contrast to our successful predictions in early visual cortex, prediction based on signals from voxels in V5/MT was near chance level (Figure 3A). Prediction with two more-conventional analysis techniques was also very poor (see Figure 3A, “combined mean” and “differential mean”).

To further investigate the predictive pattern responses, we computed for each voxel an index of how much its response differed between the two perceptual dominance phases (for the training data sets). In many voxels, the average fMRI signal intensity exhibited a small but significant bias toward one of the two percepts (Figure S1). This is in accord with recent studies showing that fMRI can be used to measure selective processing for features, such as orientation, that are represented at a subvoxel scale [1, 2]. This probably reflects a biased sampling by individual voxels of feature-selective cells that are spatially distributed in an anisotropic fashion [1, 2]. Our rotating monocular stim-

uli differed in at least three featural properties: their ocularity, color, and relative phase. Both color and ocularity are represented by neuronal activity in a spatially distributed fashion in early visual cortex, and this distribution has slight anisotropies [6, 7] that could give rise to analogous sampling biases.

### Consequences of “Eye Swapping”

To investigate the nature of such sampling biases, we conducted a second “eye-swapping” experiment. Two subjects were exposed to rivalrous stimulation as before, but now the eyes to which the monocular colored stimuli were presented on each successive scanning run were reversed. This resulted in two complementary data sets: one in which a red grating was presented to the left eye and a blue grating to the right and one in which a blue grating was presented to the left eye and a red grating to the right. We trained classifiers with odd runs and tested their ability to predict perception on even runs in which the eye of stimulus origin had been swapped (see Supplemental Data). If classification was based on color alone, we reasoned that accuracy should be little changed in comparison to classifying and testing on the same data set because only the eye to which each stimulus was presented had been swapped and not its perceived color. However, if prediction depends on ocularity, then classification accuracy should reverse from above-chance to below-chance performance when eye swapping occurred. Intermediate outcomes could reflect a balance of color and ocularity biases. For V1, classification accuracy did indeed reverse when testing and training data sets were from different stimulated eyes, indicating that training signals predicted perceptual dominance on the basis of the eye of origin (Figure S4). In contrast, prediction accuracy in V3 remained significantly above chance after eye swapping, suggesting that prediction was based on perceived color (Figure S4). V2 showed an intermediate pattern of responses. These findings are consistent with the macroscopic organization of V1 into ocular dominance columns [7] and with the presence of color preferences in the majority of V3 cells, which, unlike V1, do not show strong monocular preferences [8].

### Prediction of Binocular Rivalry from Monocular Passive Viewing

Our data could be taken to represent a simple form of “mind reading,” in which brain responses were sufficient to predict dynamic changes in conscious perception in the absence of any behavioral clues. However, so far our method has only accomplished mind reading in the narrowest sense because we did not demonstrate generalization across different designs, stimuli, and subjects. As a first step toward such generalization, we hypothesized that it might be possible to predict perception during rivalry on the basis of pattern signals acquired during stable presentation of monocular images alone, in the absence of any rivalry. We performed a third experiment, during which two participants experienced rivalry alternating with stable pas-

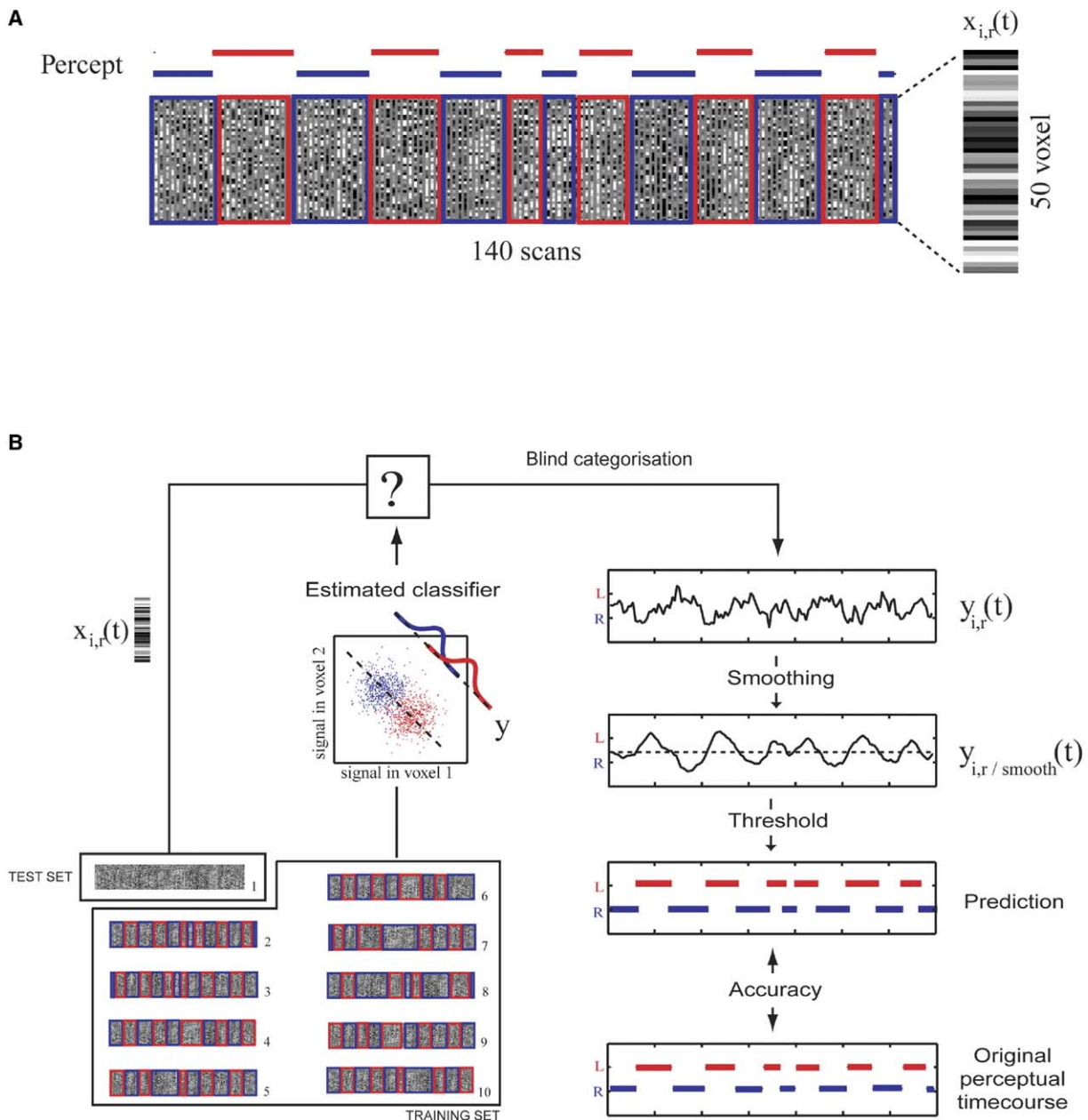


Figure 2. Full Description of Analysis Steps

(A) From each visual area ( $r$ ) (V1, V2, V3, and V5/MT) and each run ( $i$ ) we extracted activity from 50 voxels (defined as the 50 voxels most strongly activated by a localizer stimulus; see Supplemental Data) to yield an activation vector for each time point (volume),  $x_{i,r}(t)$ . For each scanning run, 140 whole-brain fMRI volumes were used. This panel shows the gray-scale-coded fMRI raw signal for each of the 140 volumes of one run ( $x$  axis) for each of the 50 voxels entering the analysis ( $y$  axis; data from V1 of subject PS). The top row shows the perceptual time course time delayed to account for the hemodynamic response function (for full details of this correction, see Figures S2 and S3). Each vertical section (equivalent to data  $x_{i,r}(t)$  from 1 time point) was labeled according to the percept that was dominant at the time it was recorded (red = left eye, blue = right eye; see Figures S2 and S3).

(B) The data from nine runs were used to train a pattern classifier that found the projection  $m$  from the 50-dimensional space onto a single dimension that maximally separated the responses to both categories (illustrated here with data from two voxels). This projection  $m$  was then used for a blind categorization of data from an independent test run for which the labels were unknown. This yielded a graded measure of categorization  $y_{i,r}(t)$  that indicated for each time point how closely the test data  $x_{i,r}(t)$  matched the blue or red exemplars. The graded categorization measure is then smoothed and thresholded to yield a predicted time course ("prediction"), after which it was determined how closely it matches the original perceptual time course. The example here shows the striking similarity between the predicted time course and the true perceptual time course as indicated by the participant.

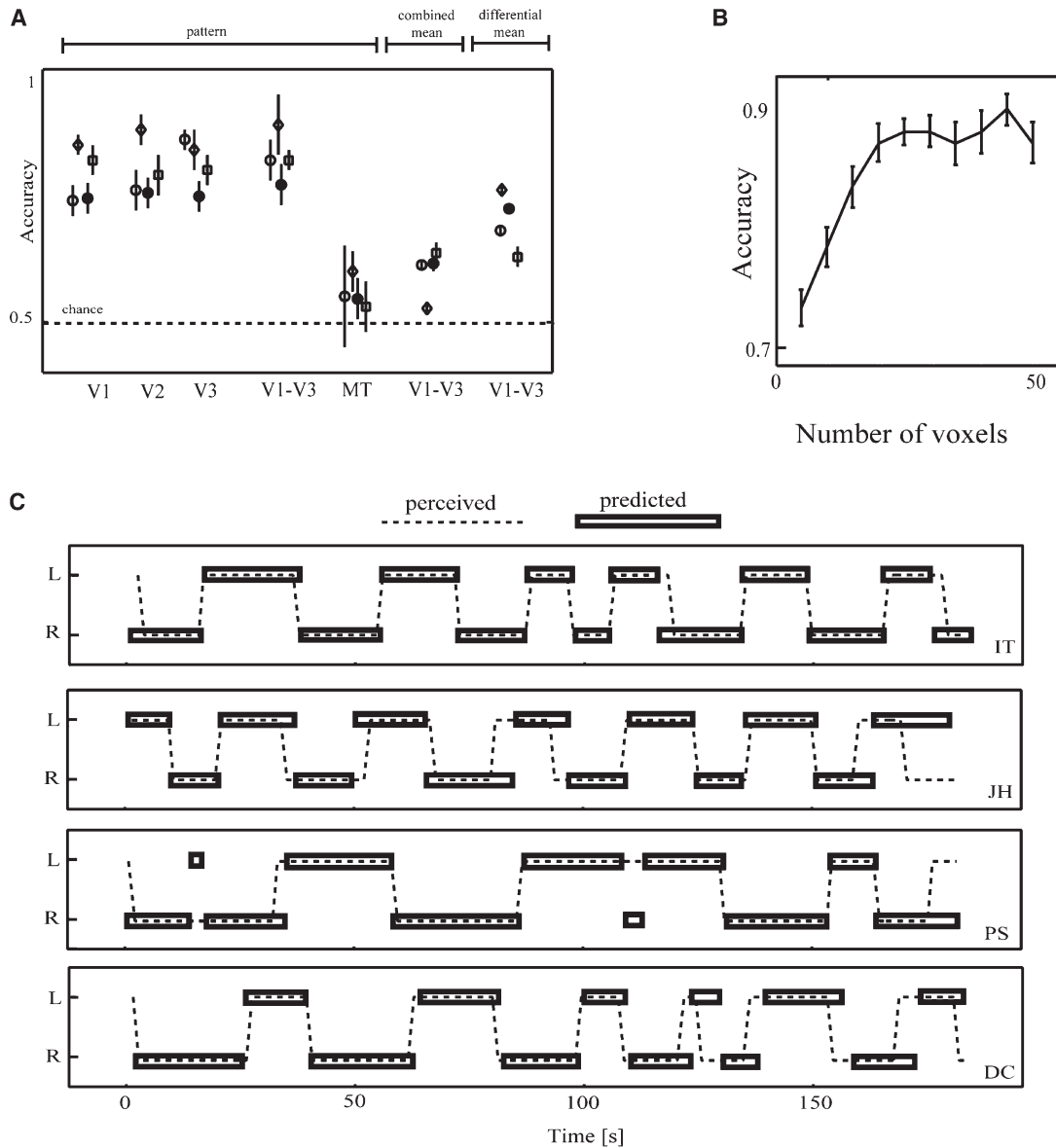


Figure 3. Prediction of Perceptual Time Courses from Signals in Different Areas of Visual Cortex

(A) Classification was very accurate when based upon the multivariate spatial pattern of response areas V1, V2, or V3 (see left, “pattern”; symbols encode the participants: circle = P.S., square = J.H., diamond = I.T., and filled circle = D.C.). Classification was even slightly better when signals from all three early areas V1, V2, and V3 (“V1–V3”) were included. Classification based on the pattern of responses in V5/MT was poor and barely exceeded chance level (dashed line). The figure also shows accuracy of prediction when classification was based on the signal averaged across all stimulus-driven voxels in V1, V2, and V3 (“combined mean”), revealing that accuracy of prediction was very low when the spatial pattern of responses was not taken into account (as would be the case for conventional voxel-based or region-of-interest-based fMRI analyses). Accuracy was considerably better when signals were differentially averaged for all red-preferring and all blue-preferring voxels (“differential mean”) and then entered into a 2-dimensional discriminant analysis. However, this did not reach the level of the full multivariate classification. This is presumably because in contrast to the differential mean analysis, multivariate pattern recognition takes the covariance between voxels into account and differentially weights each voxel by taking into account its “signal to noise” (SNR) level, whereas the differential mean analysis can be adversely affected by strong contributions from low-SNR (i.e., low-discriminating) voxels. All error bars represent the SEM.

(B) Prediction accuracy for signals combined from V1 to V3 (solid line) as a function of number of voxels used (averaged across participants; error bars represent the SEM). Accuracy increased for up to ~20 voxels and asymptotes at a level of around 85%.

(C) Comparison of *predicted* (red/blue) and *true* (dashed line) perceptual time courses for all participants with signals pooled across V1, V2, and V3. The similarity between prediction and true perceptual time courses is striking, even across a time course as long as 180 s.

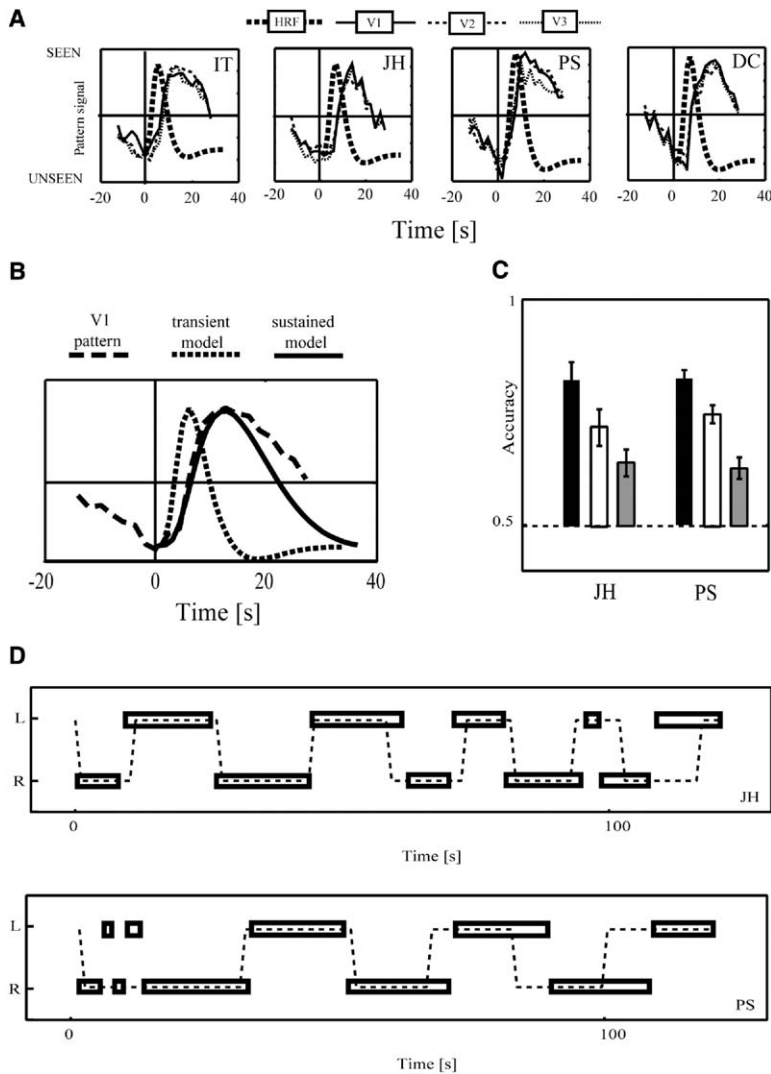


Figure 4. Event-Related Pattern Responses and Generalization of Prediction

(A) Event-related pattern signal for each subject and visual area. The raw unsmoothed pattern signal  $y_{i,r}(t)$  (see Figure 2B and Experimental Procedures) was averaged time locked to perceptual changes (occurring at 0 s), with inverted polarity for red-blue and blue-red transitions. The different visual areas are shown in different colors (V1 = red, V2 = green, and V3 = blue). The dashed line shows a canonical *transient* BOLD response to a single event at the time of reversal. The pattern response switches polarity in a sustained fashion, indicating that it is a correlate of perceptual states rather than of perceptual changes.

(B) This becomes clear by comparing the pattern signal (shown here for V1, averaged across subjects, red line) to the time course of a canonical transient BOLD response (dashed black line). The transient model is much shorter in comparison to the change in the pattern signal. In contrast, a sustained model (thick black line) more closely resembles the temporal profile of the pattern response. This model shows the expected response if the signal reflected states rather than changes (the sustained model was obtained here by convolving the phase distributions shown in Figure 1C with a canonical hemodynamic response function, HRF, whereas the transient model was computed by convolving a delta-function at  $t = 0$  s with the same HRF).

(C) Prediction in a third experiment (see Supplemental Data) with “cross training” that used stable (monocular) stimuli that do not require behavioral responses for training of the pattern classifier. Average prediction (across 4 runs) is plotted for each participant for training and test on rivalry stimuli (black bars), training on passively viewed stable stimuli, and test on rivalry stimuli (white bars), and for training and test on rivalry stimuli recorded on two different days (gray; error bars are one standard error). Prediction was still comfortably and significantly above chance even for cross training on different days (Figure S6 shows why this can be expected).

(D) Example time courses from the two participants were obtained with training on stable and test on rivalrous stimuli and plotted with the same conventions as for Figure 3C.

sive monocular viewing of each stimulus in successive runs. Remarkably, this “cross training” procedure was highly effective. Pattern responses to stable stimuli were able to accurately predict the perceptual time course elicited by subsequent presentation of rivalrous dichoptic stimuli, with only slightly lower accuracy than for classifiers trained on rivalrous stimuli alone (Figures 4C and 4D). There was also a close correlation between the stimulus preference of individual voxels under stable viewing and rivalry conditions (Figure S5). This suggests that our successful prediction was based on perceptual (not motor) signals. Moreover, it may also in principle permit the new possibility of prediction of fluctuations in perception associated with binocular rivalry in cases in which behavioral indicators of conscious perception are difficult or even impossible to obtain, for example in animals [9] or in patients suffering from

locked-in syndrome [10]. Finally, we investigated the stability of prediction over time. When training and test data sets were from the same subject scanned on different days, prediction accuracy was considerably lower than for within-session training and test. However, accuracy was still significantly above chance (Figure 4C), indicating that generalization over time is possible (see Figure S6 for why this can be expected).

## Discussion

In humans, signals from visual cortex distinguish between different dominant percepts during rivalry, suggesting that the contents of visual consciousness are reflected in the activity of visual cortex [5, 11–13]. However, these studies have relied on averaging samples from different spatial locations (voxels) and across

many individual measurements to improve signal quality. This ignores any information that is present in the spatial *pattern* of responses in individual samples of brain activity [1, 2, 14–17]. Importantly, by discarding time-dependent information, these conventional procedures could not predict the rapid dynamics with which conscious states spontaneously change over time. Recently, however, it has been shown that multivariate pattern recognition [1, 2, 14–17] applied to signals from early visual cortex can be successfully used to predict feature-specific stimulus representations for both visible [1, 2] and invisible orientation stimuli [2]. However, these studies examined only static and unchanging perceptual states during extended periods of stimulation, so it has remained unclear whether activity in early visual cortex can also predict the dynamic and stochastically changing stream of conscious perception [3]. Our new data show that taking the full spatial pattern of brain responses into account, it is possible to provide a fully automated algorithm that predicts the dynamically changing contents of conscious perception on a moment-by-moment basis, even under unchanging visual-stimulation conditions, such as during binocular rivalry.

Conceptually, our study is perhaps closest to the observation that the interocular difference in amplitude of the visually evoked potential can be correlated with perceptual alternations in rivalry [18]. However, this intriguing observation unfortunately does not provide information on the cortical sources of the underlying signals. Our finding significantly extends these results by demonstrating that there is enough information present in the response patterns in specific early visual areas (V1 to V3) to allow a highly precise reconstruction of the time course of conscious perception from brain signals alone. Similarly, a human observer can predict the content of some single visual imagery trials from fMRI measurements of brain activity in ventral visual areas [19], but this study did not address the dynamic aspects of conscious perception investigated here.

### Implications for Binocular Rivalry

In addition to demonstrating that brain activity alone can be used to predict the time course of conscious perception, our findings also shed some light on the biological mechanisms underlying binocular rivalry. Our novel rivalry stimulus engendered phase durations that were substantially longer than in previous studies [5, 11, 12]. This allowed us to demonstrate that rivalry-associated activity in early visual cortex can reflect sustained representations [5]. Thus, responses even in early visual areas could play a role in sustained encoding of certain low-level aspects of perception under rivalry in humans. Although we could predict dynamic changes in rivalrous perception with early visual cortical activity alone, our data do not determine the ultimate cause of these fluctuations. For example, top-down influences from areas outside visual cortex may give rise to such perceptual fluctuations [20, 21] through influencing activity in early visual areas. Interestingly, however, we found no clear increase in predictive accuracy for brain activity taken from V1, V2, or V3. Our findings are compatible with a large and growing literature

demonstrating clear modulations of early visual cortex by perceptual state during rivalry in humans [5, 11, 12]. In monkeys, in contrast, only weak effects of perceptual state are seen in V1, with stronger effects in higher visual areas [22]. This discrepancy may reflect the stronger correlation of BOLD activity measured with fMRI with local field potentials rather than spiking activity [23]. However, it is noteworthy that we found that accurate prediction from V1 activity reflected the eye of origin of the stimulus rather than the percept. This may suggest a reconciliation of monkey and human data if rivalry-related signals in V1 were not *directly* related to conscious perception, but to eye-specific control of visual input, for example by attenuating input from the nondominant eye [24]. In contrast, we found that prediction in V3 was dominated by the color of the percept, which might in turn point toward a stronger involvement of higher visual areas in encoding our conscious perceptual experience [22].

### Experimental Procedures

#### Participants and Experimental Design

Four healthy volunteers 30–34 years old gave written informed consent to participate in the experiments, which were approved by the local ethics committee. In the first experiment, four subjects viewed rivaling red and blue grating stimuli (see Figure 1; see Supplemental Data for full methods) presented continuously for 180 s during each run. In the second experiment (Figure S4), we again presented rivalry stimuli to two of our subjects, but we now switched the eye to which each stimulus was presented on successive scanning runs. In the third experiment (Figures 4C and 4D), we presented rivalry and stable viewing stimuli in alternating runs.

#### fMRI Acquisition

A Siemens Allegra 3T scanner with Nova Medical occipital surface coil was used to acquire functional MRI EPI volumes with 20 slices at an isotropic resolution of  $3 \times 3 \times 3$  mm (TR = 1300 ms; echo time [TE] = 30 ms; flip angle =  $60^\circ$ ). In the first experiment, we acquired 10 runs of 145 functional MRI volumes, in the second (“eye swapping”), we acquired 8 runs of 125 volumes (4 rivalry with left eye red, right eye blue, 4 with the opposite ocularity), and in the third (“cross training”), we acquired 8 runs of 125 volumes (4 rivalry, 4 stable). We also acquired a stimulus localizer, a motion localizer, and retinotopic mapping data for each subject (see Supplemental Data).

#### Data Analysis

To identify stimulus-driven cortical regions, we modeled the data from the *localizer* runs voxel-wise with a general linear model [25]. V1, V2, and V3 were identified from the retinotopic mapping data according to standard definitions [26] together with segmentation and cortical flattening in MrGray [27, 28]. Area V5/MT was identified with a standard motion localizer. The pattern recognition was performed without SPM with linear discriminant analysis based on the *raw fMRI signal* from every voxel and every scan. For full Experimental Procedures, see Figure 2 and Supplemental Data.

#### Supplemental Data

Detailed Experimental Procedures and several supplemental figures are available at <http://www.current-biology.com/cgi/content/full/15/14/1301/DC1/>.

#### Acknowledgments

The Wellcome Trust funded this work. We thank Will Penny, Nikolaus Weiskopf, Karl Friston, and Chris Frith for very helpful comments and advice, and Elliot Freeman for advice on the stimuli.

Received: March 23, 2005

Revised: June 8, 2005

Accepted: June 9, 2005

Published: July 26, 2005

## References

1. Kamitani, Y., and Tong, F. (2005). Decoding the subjective contents of the human brain. *Nat. Neurosci.* 8, 679–685.
2. Haynes, J.D.H., and Rees, G. (2005). Predicting the orientation of invisible stimuli from activity in primary visual cortex. *Nat. Neurosci.* 6, 686–696.
3. James, W. (1890). *The Principles of Psychology* (New York: Henry Holt).
4. Blake, R., and Logothetis, N.K. (2002). Visual competition. *Nat. Rev. Neurosci.* 3, 13–21.
5. Polonsky, A., Blake, R., Braun, J., and Heeger, D.J. (2000). Neuronal activity in human primary visual cortex correlates with perception during binocular rivalry. *Nat. Neurosci.* 3, 1153–1159.
6. Landisman, C.E., and Ts'o, D.Y. (2002). Color processing in macaque striate cortex: Electrophysiological properties. *J. Neurophysiol.* 87, 3138–3151.
7. Obermayer, K., and Blasdel, G.G. (1993). Geometry of orientation and ocular dominance columns in monkey striate cortex. *J. Neurosci.* 13, 4114–4129.
8. Gegenfurtner, K.R., Kiper, D.C., and Levitt, J.B. (1997). Functional properties of neurons in macaque area V3. *J. Neurophysiol.* 77, 1906–1923.
9. Leopold, D.A., Maier, A., and Logothetis, N.K. (2003). Measuring subjective visual perception in the nonhuman primate. *J. Consciousness Studies* 10, 115–130.
10. Bauer, G., Gerstenbrand, F., and Rimpl, E. (1979). Varieties of the locked-in syndrome. *J. Neurol.* 221, 77–91.
11. Tong, F., Nakayama, K., Vaughan, J.T., and Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron* 21, 753–759.
12. Tong, F., and Engel, S.A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411, 195–199.
13. Lee, S.H., Blake, R., and Heeger, D.J. (2005). Traveling waves of activity in primary visual cortex during binocular rivalry. *Nat. Neurosci.* 8, 22–23.
14. Cox, D.D., and Savoy, R.L. (2003). Functional magnetic resonance imaging (fMRI) “brain reading”: Detecting and classifying distributed patterns of fMRI activity in human visual cortex. *Neuroimage* 19, 261–270.
15. Duda, O.R., Hart, P.E., and Stork, D.G. (2001). *Pattern Classification* (New York: Wiley).
16. Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., and Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430.
17. Carlson, T.A., Schrater, P., and He, S. (2003). Patterns of activity in the categorical representation of objects. *J. Cogn. Neurosci.* 15, 704–717.
18. Brown, R.J., and Norcia, A.M. (1997). A method for investigating binocular rivalry in real-time with the steady-state VEP. *Vision Res.* 37, 2401–2408.
19. O’Craven, K.M., and Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *J. Cogn. Neurosci.* 12, 1013–1023.
20. Lumer, E.D., Friston, K.J., and Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science* 280, 1930–1934.
21. Lumer, E.D., and Rees, G. (1999). Covariation of activity in visual and prefrontal cortex associated with subjective visual perception. *Proc. Natl. Acad. Sci. USA* 96, 1669–1673.
22. Leopold, D.A., and Logothetis, N.K. (1996). Activity changes in early visual cortex reflect monkeys’ percepts during binocular rivalry. *Nature* 379, 549–553.
23. Logothetis, N.K., Pauls, J., Augath, M., Trinath, T., and Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412, 150–157.
24. Wales, R., and Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Percept. Psychophys.* 8, 827–835.
25. Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.P., Frith, C.D., and Frackowiak, R.S.J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Hum. Brain Mapp.* 2, 189–210.
26. Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R., and Tootell, R.B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268, 889–893.
27. Teo, P.C., Sapiro, G., and Wandell, B.A. (1997). Creating connected representations of cortical gray matter for functional MRI visualization. *IEEE Trans. Med. Imaging* 16, 852–863.
28. Wandell, B.A., Chial, S., and Backus, B.T. (2000). Visualization and measurement of the cortical surface. *J. Cogn. Neurosci.* 12, 739–752.