



## Decoding eye-of-origin outside of awareness

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### ABSTRACT

In the primary visual cortex of many mammals, ocular dominance columns segregate information from the two eyes. Yet under controlled conditions, most human observers are unable to correctly report the eye to which a stimulus has been shown, indicating that this information is lost during subsequent processing. This study investigates whether eye-of-origin information is available in the pattern of electrophysiological activity evoked by visual stimuli, recorded using EEG and decoded using multivariate pattern analysis. Observers ( $N=24$ ) viewed sine-wave grating and plaid stimuli of different orientations, shown to either the left or right eye (or both). Using a support vector machine, eye-of-origin could be decoded above chance at around 140 and 220 ms post stimulus onset, yet observers were at chance for reporting this information. Other stimulus features, such as binocularity, orientation, spatial pattern, and the presence of interocular conflict (i.e. rivalry), could also be decoded using the same techniques, though all of these were perceptually discriminable above chance. A control analysis found no evidence to support the possibility that eye dominance was responsible for the eye-of-origin effects. These results support a structural explanation for multivariate decoding of electrophysiological signals – information organised in cortical columns can be decoded, even when observers are unaware of this information.

### Introduction

Signals from the left and right eyes remain anatomically segregated throughout the early stages of visual processing. In the primary visual cortex of most primates, cells that preferentially respond to signals from one or other eye are organised into ocular dominance columns (Adams et al., 2007; Horton and Hocking, 1996; Hubel and Wiesel, 1969). This striking columnar structure is lost at later stages of processing, when signals are combined binocularly to give a cyclopean percept of the world. When a visual stimulus is presented to only one eye under controlled conditions, humans generally lack explicit conscious awareness of which eye was stimulated ('utrocular discrimination', or more properly 'utrocular identification'; Ono and Barbeito, 1985). This loss of information is distinct from other visual cues, such as spatial position and orientation, that are also segregated anatomically, yet remain perceptually available to conscious awareness.

Recently, studies using electro- and magneto-encephalography (EEG and MEG) have shown that both simple (Cichy et al., 2015; Ramkumar et al., 2013; Wardle et al., 2016) and more complex (Carlson et al., 2011, 2013; Cichy et al., 2014; Coggan et al., 2016; Nemrodov et al., 2016) image properties can be decoded from the pattern of electromagnetic activity evoked by a visual stimulus. One study investigating orientation decoding (Cichy et al., 2015) has suggested that any information encoded in cortical columns should

produce distinct spatial patterns of electrical activity that can be recovered using machine learning algorithms (multivariate pattern classifiers). Given the columnar representation of eye-of-origin in the early stages of cortical processing, this should extend to information about which eye (or combination of eyes) was stimulated, as has been demonstrated using fMRI (Schwarzkopf et al., 2010). Conversely, another recent study (Wardle et al., 2016) has claimed that the more perceptually distinct two stimuli are, the more easily their evoked responses can be dissociated using the same analysis techniques. This account would predict that eye-of-origin information should not be available in the electrophysiological evoked response, since it cannot be perceptually discriminated.

Here, sine-wave grating and plaid stimuli were presented to the left or right eye, as well as to both eyes together, whilst evoked responses were measured using EEG. For comparison with previous work, stimulus orientation was also manipulated, and conditions involving interocular conflict were included to probe the mechanisms of interocular suppression. To test the predictions of the two accounts of neural encoding described above, a support vector machine algorithm was trained to discriminate between the responses evoked by different combinations of the stimuli. The classifier achieved above-chance decoding accuracy for ocularity, orientation and pattern type, a finding not inconsistent with the idea that the cortical columnar structure for these cues results in different spatial patterns of evoked response that

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are apparent at the scalp. Observers were able to accurately report orientation, but not eye-of-origin, demonstrating that perceptual discriminability does not predict decoding accuracy across these ocular and spatial cues.

## Methods

### Observers

Written informed consent was obtained from 24 adults (8 male) with normal binocular vision. All observers wore their normal optical correction during testing if required. Experimental procedures were approved by the ethics committee of the Department of Psychology at the University of York.

### Apparatus and stimuli

Stimuli were constructed from patches of sine-wave grating with a contrast of 50%, a spatial frequency of 2c/deg and a diameter of 10°. Stimuli were in sine phase with the centre of the display. Two orientations ( $\pm 45^\circ$ ) were presented either in isolation, or superimposed to form a plaid pattern. All stimuli were spatially windowed by a raised cosine envelope and had a small hole (1° in diameter) in the centre that was also blurred by a cosine ramp. Example stimuli are shown in Fig. 1.

Stimuli were presented using a gamma corrected ViewPixx 3D display (VPixx Technologies, Canada). Binocular separation with minimal crosstalk was achieved by synchronising the refresh rate of the display with the toggling of a pair of active stereo shutter goggles (Nvidia Corp., California, USA) using an infra-red signal. The monitor refresh rate was 120 Hz, meaning that each eye was updated at 60 Hz.

EEG signals were recorded from 64 scalp locations from the 10–20 system using a WaveGuard cap and the ASALab system (ANT Neuro, Netherlands). The ground was placed posterior to electrode FPz, and all channels were referenced to a whole-head average. Eye-blinks were recorded using vertical electro-oculogram electrodes. Stimulus onset was recorded on the EEG trace via low-latency digital triggers from the display device. Electrode impedances were typically kept below 10 k $\Omega$  during testing, and signals were recorded at 1 kHz and then stored for offline analysis.

### Procedures

Stimuli were presented in 5 blocks, each comprising 220 trials (20 repetitions for each of the 11 conditions illustrated in Fig. 1), and taking around 6 min. The stimulus duration was 100 ms, and stimulus order was randomly determined in each block for each observer. After each stimulus presentation, observers indicated their percept using a two-button mouse, according to one of five different tasks (one task per block). In the first block, observers reported the stimulus orientation (tilted left or right). In the second block, they reported whether they saw one stimulus component (i.e. a single grating) or two components (i.e. a plaid or interocular conflict stimulus). In the third block, they reported whether they had seen the interocular conflict stimulus or another stimulus. In the final two blocks, observers were asked to indicate whether they believed one or two eyes had been stimulated (block four), and whether they believed the left or right eye had been stimulated (block five). Most observers found these final two tasks very difficult, and subsequently indicated that they were largely guessing throughout these blocks. In addition, they were instructed to guess when the stimulus did not clearly map onto the task (i.e. reporting the orientation of a plaid). Following each response, there was a variable length blank period (mean duration 1000 ms, SD of 200 ms) before the next stimulus was displayed. A central fixation cross was presented throughout.

EEG data were analysed offline. The data from each block were

bandpass filtered between 0.01 and 30 Hz, and trials were aggregated across blocks for each of the 11 conditions (see Fig. 1; 100 trials per condition per observer). To calculate the ERPs in Figs. 1 and 2, waveforms in the first 500ms following stimulus onset were normalized by the mean voltage in the 200ms time window before stimulus onset, and then averaged across ten occipito-parietal electrodes (Oz, O1, O2, POz, PO3-8), and then across trials and observers. No downsampling or artifact rejection was performed.

A support vector machine algorithm with a radial basis function kernel (Chang and Lin, 2011) was then trained to discriminate between the spatial patterns (i.e. the pattern of voltages across electrodes) of EEG response evoked by different combinations of stimuli, independently at each time point and for each observer. The classifier was trained on averages of random subsets of trials (means across 50 trials) from conditions of interest (see Figs. 2 and 3), and its discrimination performance tested on the average of the remaining trials not included in the training. There were at least three examples for each condition in a comparison (depending on the total number of conditions included in that comparison), and one example per condition for testing. The procedure was repeated 1000 times for each comparison (using different subsets of trials each time). The discrimination performance was then averaged across observers, and 95% confidence intervals were derived using bootstrap resampling to produce the timecourses in Fig. 3b–d. The classifier was also trained and tested using the waveform across a time window (either 100–300 ms in Fig. 4, or in 100 ms epochs for Fig. S1) at each electrode independently to produce the scalp distributions in Fig. 4.

A non-parametric cluster correction procedure (Maris and Oostenveld, 2007) was applied to determine significant clusters (either across time or across scalp locations) whilst controlling for multiple comparisons. For comparing ERP waveforms, summed  $t$ -values (from paired  $t$ -tests) across consecutive time points or adjacent electrode locations were compared with a null distribution generated by switching the condition labels for half of the observers. For assessing classifier accuracy, one-sample  $t$ -tests were used to compare accuracy to baseline (50% correct), and the null distribution was generated by reflecting half of the data points about the baseline (a procedure equivalent to changing the condition labels in a paired  $t$ -test). The cluster forming threshold was  $t > 2.069$ , and the cluster significance threshold was  $p < 0.0083$  (i.e.  $p < 0.05$ , Bonferroni corrected across the six comparisons under investigation). The entire cluster correction procedure was repeated for 1000 resampled data sets to derive confidence intervals for the onset and offset of significant clusters. Where resampled clusters did not overlap with significant clusters from the main data set they were discarded. Where multiple resampled clusters corresponded to a single original cluster, the onset of the first resampled cluster and the offset of the last resampled cluster were included in the resampled populations.

## Results

All stimulus arrangements produced typical event-related potentials. Examples averaged across ten occipito-parietal electrodes (Oz, O1, O2, POz, PO3-8) are shown in Fig. 1 for each condition, along with depictions of the stimulus arrangements. There were slight differences in the evoked potential across different conditions, with plaids (blue traces) producing earlier negative deflections than individual gratings (red and green traces), and binocular presentations (Fig. 1c) evoking more generally positive responses than monocular presentations (Fig. 1a and b). The interocular conflict conditions (Fig. 1d) produced more generally negative responses than other conditions from around 150ms onwards.

The ERP waveforms for various combinations of conditions were averaged and compared statistically using cluster corrected paired  $t$ -tests. Comparing ERPs for stimuli (both gratings and plaids) presented to the left and right eyes (Fig. 2a) revealed a very brief significant

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