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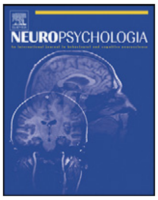

# Pre-stimulus pattern of activity in the fusiform face area predicts face percepts during binocular rivalry

P.-J. Hsieh[a,b,*], J.T. Colas[b], N.G. Kanwisher[b]

[a] *Program in Neuroscience and Behavioral Disorders, Duke-NUS Graduate Medical School Singapore, Singapore*
[b] *Department of Brain and Cognitive Sciences, McGovern Institute, Massachusetts Institute of Technology, United States*

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ABSTRACT

Visual input is ambiguous, yet conscious experience is unambiguous. In binocular rivalry the two eyes receive conflicting images, but only one of them is consciously perceived at a time. Here we search for the neural sites of the competitive interactions underlying this phenomenon by testing whether neural pattern activity occurring before stimulus presentation can predict the initial dominant percept in binocular rivalry and, if so, where in the brain such predictive activity is found. Subjects were scanned while viewing an image of a face in one eye and an image of a house in the other eye with anaglyph glasses. The rivalrous stimulus was presented briefly for each trial, and the subject indicated which of the two images he or she preferentially perceived. Our results show that BOLD fMRI multivariate pattern activity in the fusiform face area (FFA) *before the stimulus is presented* predicts which of the two images will be dominant, suggesting that higher extrastriate areas, such as the FFA, are not only correlated with, but may also be involved in determining the initial dominant percept in binocular rivalry. Furthermore, by examining pattern activity before and after trial onset, we found that pre-trial activity in the FFA for the rivalrous face trials is no more similar to the post-trial activity for the non-rivalrous face trials than to that for the non-rivalrous house trials, indicating a dissociation between neural pattern information, which predicts a given state of awareness, and mean responses, which reflect the state of awareness ultimately achieved.

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## 1. Introduction

All perceptual stimuli are inherently ambiguous. How then do our brains manage to produce conscious perceptual experiences of the world in which this ambiguity has been resolved? Although several imaging studies have examined the neural correlates of conscious experience when viewing bistable or ambiguous stimuli (Donner, Sagi, Bonneh, & Heeger, 2008; Hsieh & Tse, 2009, 2010; Hsieh, Caplovitz, & Tse, 2006; Hsieh, Vul, & Kanwisher, 2010; Lumer, Friston, & Rees, 1998; Polonsky, Blake, Braun, & Heeger, 2000; Schoth, Waberski, Krings, Gobbele, & Buchner, 2007; Tong & Engel, 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998), the causal relationship between neural activity and conscious experience in these studies remains unclear. Here we attempt to go beyond merely analyzing the neural correlates of consciousness by testing whether and how neural pattern activity occurring before stimulus onset can predict the initial percept in binocular rivalry.

Using functional magnetic resonance imaging (fMRI) and multivariate pattern analysis, we investigated whether and how mean responses and pattern activity in the candidate neural sites before stimulus presentation is correlated with the initial dominant percept. Subjects were scanned while viewing an image of a face presented to one eye and an image of a house to the other eye with anaglyph glasses. A rivalrous stimulus was presented briefly for each trial, and subjects were required to indicate which of the two images they perceived (Fig. 1). We sought to determine what, if any, pre-trial pattern of neural responses is predictive of a particular subsequent percept. According to one intuitive hypothesis, states of awareness are determined in part by a simple amplification of pre-trial sensory biases, and hence pre-trial activity that *resembles* the neural signature of percept A more than that of percept B would bias the subsequent percept toward percept A. For example, an above-average mean response in the fusiform face area (FFA) before trial onset might predict a greater likelihood of a face percept in an upcoming rivalrous trial. Note, however, that this hypothesis need not be true; percepts could be determined by distinct pre-trial activity in the same regions or could be predicted by activity in brain regions other than those associated with a characteristic percept. In this case the relevant predictive pre-trial activity would not resemble that of the subsequent percept

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* Corresponding author.
*E-mail addresses:* pojang.hsieh@duke-nus.edu.sg, hsieh.pj@gmail.com (P.-J. Hsieh).

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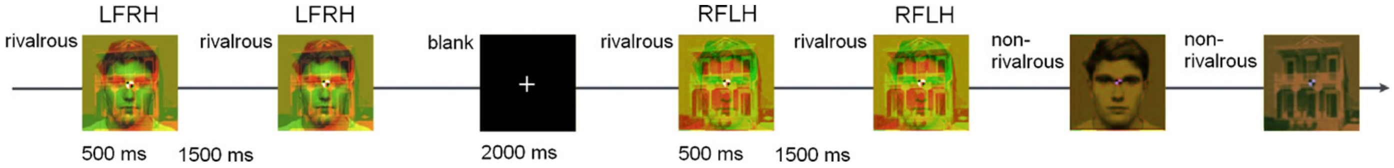

**Fig. 1.** For each trial subjects viewed one of four stimuli through red- and green-filtered anaglyph glasses. There were two kinds of rivalrous stimuli—one consisting of superimposed images of a green face and a red house, and the other consisting of superimposed images of a red face and a green house. The two non-rivalrous stimuli included individual yellow images of the face and the house. Stimuli appeared for 500 ms and were followed by a white fixation cross for at least 1500 ms. All subjects completed a minimum of twelve runs, each with a duration of 240 s. The order of the trials was optimized within each run.

at all. Furthermore, we asked whether any predictive neural activity takes the form of changes in the mean responses of ROIs or in pattern information in those ROIs. A number of prior studies have shown dissociations between mean responses and pattern information, including several cases in which pattern information can discriminate between conditions that cannot be discriminated on the basis of mean responses (Haxby et al., 2001; Kamitani & Tong, 2005) and even cases in which pattern information can discriminate between conditions when no net mean response is observed (Harrison & Tong, 2009; William et al., 2008).

Here we investigate this possibility and show that pre-trial fMRI pattern activity in the FFA predicts which of two rivaling percepts will dominate. Furthermore, we found that pre-trial pattern activity in the FFA for the rivalrous face trials is no more similar to the post-trial activity for the non-rivalrous face trials than to that for the non-rivalrous house trials, suggesting that the spatial pattern information reflects endogenous neural activity, whereas the ultimate perceptual decision is neurally manifested as mean activation after stimulus onset. These findings show that spatiotemporal information in multivariate patterns of fMRI activity may constrain theories of human information processing by (1) going beyond merely analyzing neural correlates to approach neural causes of perceptual awareness and (2) revealing how neural representations, captured with fMRI as multivariate patterns, evolve before and after stimulus onset.

## 2. Materials and methods

### 2.1. Participants

Twelve subjects between 18 and 30 years old participated in the fMRI study and were paid 60 dollars per session. Seven other young adult volunteers participated in the first psychophysical experiment outside of the scanner, which tested whether a stimulus duration of 500 ms sufficiently induces rivalry, and were paid 5 dollars. Another seven adults participated in the second psychophysical experiment, which tested the feasibility of a slow event-related design, and were paid 15 dollars. All subjects were healthy and right-handed and had normal or corrected-to-normal visual acuity. All subjects gave written consent within a protocol passed by the Massachusetts Institute of Technology Committee on the Use of Humans as Experimental Subjects.

### 2.2. Experimental procedures

Scanning was performed in the McGovern Institute at the Massachusetts Institute of Technology in Cambridge, MA, with the Athinoula A. Martinos Imaging Center's 3T Siemens Trio scanner. Functional MRI runs were acquired using a gradient-echo, echo-planar sequence (TR = 2 s, TE = 40 ms, 3.1 × 3.1 × 3.1 mm + 10% spacing). Note that for the time point of "0 s," for example, fMRI data were actually acquired between 0 and 2 s. 32 slices were collected with a 12-channel head coil. Slices were oriented roughly perpendicular to the calcarine sulcus and covered the whole brain.

For each trial subjects viewed one of four stimuli through red- and green-filtered anaglyph glasses. There were two kinds of rivalrous stimuli—one consisting of superimposed images of a green face and a red house, and the other consisting of superimposed images of a red face and a green house. The two non-rivalrous stimuli included individual yellow images of the face and the house, which were generated by combining the original red and green images. Each of the four stimuli appeared in 25% of the trials. All stimuli were presented against a black background, centered on the fixation point, and subtended $1.75^\circ \times 1.75^\circ$ of visual angle. Stimuli were presented for 500 ms, a duration that induces a behavioral state previously classified as predominantly rivalrous (Fox & Check, 1972; Williams, Morris, McGlone, Abbott, & Mattingley, 2004; Wolfe, 1983) but is brief enough to prevent within-trial perceptual switching from occurring (see Fig. 5 for psychophysical results). Stimuli appeared at the beginning of a 2-s scanning repetition (TR) and were followed (for at least 1500 ms) by a white fixation cross subtending $0.35^\circ \times 0.35^\circ$. Note that our rivalrous stimuli were presented only for 500 ms in each trial, as opposed to being continuously on the screen as in Tong et al. (1998). As a result, the rivalrous percept is naturally shorter and less stable than what had previously been reported.

While being scanned, all subjects completed a minimum of twelve runs, each with a duration of 240 s. Prior to the functional scanning, subjects completed dynamic psychophysical testing with a staircase procedure to determine the luminance values of the red and green channels for which the rivalrous stimulus could be perceived as a face or a house with equal frequency (i.e. approximately half of the trials perceived as a face). The order of the trials was optimized within each run using the optimal sequencing program *Optseq2* (NMR Center, Massachusetts General Hospital, MA, USA). One third of the total scanning time consisted of null events with variable duration (2–6 s) that were randomly inserted between trials. For each stimulus presentation, subjects were required to press one of two buttons on a response box (two-alternative forced choice; 2AFC) to indicate which of the two images (face or house) he or she perceived preferentially.

### 2.3. ROI identification

Functional localization of two of the regions of interest (ROIs) was based on three independent runs of 20-s blocks with grayscale images of faces, scenes, common objects and scrambled objects (four blocks per category per run). The fusiform face area (FFA; Kanwisher, McDermott, & Chun, 1997) was defined as the region of the fusiform gyrus that responded more strongly to images of faces than to images of intact objects ($p < 10^{-4}$). The parahippocampal place area (PPA; Epstein & Kanwisher, 1998) was defined as the region of the parahippocampal gyrus that responded more strongly to images of scenes than to images of intact objects ($p < 10^{-4}$).

The foveal confluence (FC; Dougherty et al., 2003) was identified as an ROI from two runs of a retinotopic localizer scan. It was defined as the small region at the posterior end of the calcarine sulcus that responded more strongly to flickering checkerboards presented in the center of the visual field than to those presented in the periphery of the visual field ($p < 10^{-4}$).

### 2.4. Data analysis

Data analysis was conducted using the fMRI software package *FreeSurfer* (http://surfer.nmr.mgh.harvard.edu/) and MATLAB (MathWorks). The processing steps for both the localizer and experimental runs included motion correction and intensity normalization. Processing for the localizer runs also included spatial smoothing with a 6 mm kernel. A gamma function with *delta* = 2.25 and *tau* = 1.25 was used to estimate the hemodynamic response for the localizer runs. For the experimental runs, the time courses were obtained using a finite impulse response (FIR) model without assuming a particular hemodynamic response function, which is optimal for identifying uncontaminated pre-trial signals. Trials in excess of the minimum number of trials between the two conditions ("face" and "house" when grouping by category or "left" and "right" when grouping by eye) were excluded from analysis to ensure that each condition contained an equal amount of data.

To avoid contamination of the pre-trial blood oxygen level-dependent (BOLD) signal by the response to a previous trial (Leopold, Wilke, & Maier, Logothetis, 2002; Pearson & Brascamp, 2008), we eliminated trials as needed to balance the trial histories for each condition post hoc, going back one trial in each case. For example, when we examined whether pre-trial activity differs between rivalrous face and house trials, we grouped the rivalrous stimuli by perceived category such that the two compared conditions were equally preceded by all six possible percepts/stimuli—namely, rivalrous face to the left eye, rivalrous face to the right eye, rivalrous house to the left eye, rivalrous house to the right eye, non-rivalrous face, and non-rivalrous house. If a trial was preceded by fixation, it would instead be categorized according to the percept/stimuli of the trial preceding prior fixation. Note that such equating ensures that the activity of the current trial is not dependent upon the activity of the previous trial.

To test whether the percept/stimulus of the second trial back ($T_{-2}$) can influence the percept of the current trial ($T_0$), we compared the following two likelihoods: (1)

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