

# Traveling waves of activity in primary visual cortex during binocular rivalry

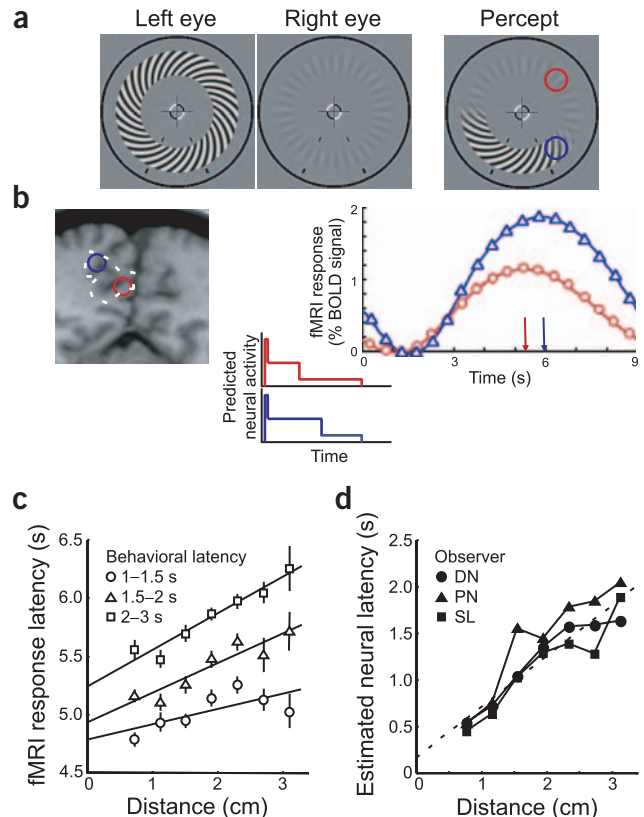
Sang-Hun Lee<sup>1,3</sup>, Randolph Blake<sup>2</sup> & David J Heeger<sup>1</sup>

**When the two eyes view large, dissimilar patterns that induce binocular rivalry, alternating waves of visibility are experienced as one pattern sweeps the other out of conscious awareness. Here we combine psychophysics with functional magnetic resonance imaging to show tight linkage between dynamics of perceptual waves during rivalry and neural events in human primary visual cortex (V1).**

The cortex is an excitable medium through which waves of neural activity can propagate<sup>1,2</sup>. Binocular rivalry, the perceptual alternations induced when incompatible patterns are presented to the two eyes, provides a rare opportunity to observe the perceptual concomitants of neural wave propagation<sup>3</sup>. During an alternation, one sees a traveling wave in which the dominance of one pattern emerges locally and expands progressively as it renders the other pattern invisible<sup>4</sup>. Several converging lines of evidence have suggested that primary visual cortex (V1) may be involved in the spatiotemporal dynamics of these perceptual traveling waves, but that involvement had not, so far, been demonstrated. Here we use functional magnetic resonance imaging (fMRI) to measure and characterize traveling waves of cortical activity during binocular rivalry.

Human observers viewed a dichoptic display designed to induce perceptual waves (Fig. 1a). Experiments were carried out with the written

consent of each observer, and in compliance with the safety guidelines for MRI research, as approved by the Stanford University Panel on Human Subjects in Medical Research. The rival images were a low-contrast radial grating (viewed by one eye) and a high-contrast spiral grating (viewed by the other eye), each restricted to an annular region of the visual field centered on the point of fixation. Exploiting the susceptibility of binocular rivalry to transient stimulation<sup>5</sup>, we triggered shifts in perceptual dominance through a brief, abrupt increase in contrast in a small region of the low-contrast grating at the top of the annulus (see **Supplementary Methods** and **Supplementary Fig. 1** online). This contrast pulse typically evoked a perceptual traveling wave, so that observers perceived the local dominance of the low-contrast image as spreading around the annular region, starting at the top of the annulus and progressively erasing the high-contrast image from visual awareness<sup>4</sup> (**Supplementary Video 1** online). Observers pressed a key when a perceptual wave reached a target area (marked by nonius lines) at the bottom of the annulus. This key press triggered the disappearance of the two monocular gratings until the beginning of the next trial.



**Figure 1** Traveling waves of cortical activity in human V1. **(a)** Left two panels, stimuli were rival gratings viewed dichoptically. Right panel (Percept), snapshot of the perceptual traveling wave in which the low-contrast pattern was seen to spread around the annulus, starting at the top. **(b)** Left, anatomical image passing through the posterior occipital lobe, roughly perpendicular to the calcarine sulcus. Red outline, subregion of V1 corresponding retinotopically to the upper-right quadrant of the stimulus annulus. Blue outline, subregion of V1 corresponding to the lower-right quadrant of the stimulus. Middle, time series of the predicted neural activity according to a simplified model (see **Supplementary Methods** online). Right, time series of the measured fMRI responses corresponding to the two outlined subregions, averaged across ~1,000 trials for one observer. Red and blue arrows, times at which corresponding curves peak. **(c)** Temporal delay in the fMRI responses as a function of cortical distance from the V1 representation of the top of the annulus, categorized by behavioral latency and averaged across observers. Steeper slope corresponds to slower speed. Larger  $y$ -intercept corresponds to longer initial delay. Error bars, s.e.m. **(d)** Estimated propagation speed of the underlying neural activity, averaged across behavioral latencies. Dashed line, best fit to the mean across observers.

<sup>1</sup>Department of Psychology and Center for Neural Science, New York University, 6 Washington Place, 8th floor, New York, New York 10003, USA. <sup>2</sup>Department of Psychology, Vanderbilt University, 512 Wilson Hall, Nashville, Tennessee 37203, USA. <sup>3</sup>Present address: Department of Psychology, Seoul National University, Seoul, South Korea. Correspondence should be addressed to D.J.H. (david.heeger@nyu.edu).

If activity in the visual cortex reflects the spatiotemporal dynamics of rivalry, then there should be a wave of cortical activity coincident with the perceptual wave (Fig. 1b). Specifically, the peak of the fMRI responses at locations along the path of the cortical wave should be increasingly delayed with increasing distance from the cortical representation of the top of the annulus. This is because (i) locations further from the point of origin of the traveling wave will respond to the high contrast for longer durations, and (ii) fMRI responses in V1 increase monotonically with stimulus contrast<sup>6</sup>. It is important to keep in mind, however, that the physical contrasts of both rival gratings remained unchanged—only the perceptual transitions associated with rivalry provided the potential conditions for traveling waves of cortical activity.

V1 did indeed show traveling waves of activity while observers experienced perceptual traveling waves (Fig. 1c and Supplementary Video 2 online). Gray matter corresponding to the V1 representation of the stimulus annulus was identified using conventional retinotopic mapping procedures<sup>7</sup>. For each voxel within this subregion of V1 gray matter, we calculated the temporal delay of the fMRI responses averaged across trials (see Supplementary Methods online). The resulting temporal delays increased with distance from the V1 representation of the top of the stimulus annulus. The correlation between temporal delay and cortical distance was statistically significant in each individual observer ( $P < 0.05$ , Pearson  $\chi^2$  test). This occurred despite the absence of wave-like changes in the stimulus itself.

The dynamics of these cortical waves of V1 activity correlated with the latency of the perceptual waves (Fig. 1c). We segregated the trials into three categories based on the latency of the observers' key-press responses and averaged the fMRI data across trials separately for each of the three ranges of behavioral latencies. Both the speed (slope of the line of best fit) and the initial delay ( $y$ -intercept) of the cortical waves increased with behavioral latency ( $P < 0.0001$ , bootstrap statistical test; see Supplementary Methods online for details).

To compare more directly the fMRI data with the perceptual phenomena during rivalry, we estimated the speed of propagation of the underlying cortical activity from the measured fMRI responses (Fig. 1d). This was done using a model of the underlying neural activity (Fig. 1b) along with a model for how an fMRI signal depends on underlying neural activity (see Supplementary Methods online for details). In addition to the unknown neural response latencies, the model had five free parameters: one parameter corresponded to the ratio of the amplitudes of the tonic neural activity for each of the two stimulus contrasts, another characterized the amplitude of transient neural responses evoked by abrupt stimulus onset at the beginning of each trial, and three were used to characterize the hemodynamic impulse response. Values for these five parameters were determined separately for each observer by fitting the model to the fMRI responses evoked by physical traveling waves. In a separate 'replay' experiment, sequences of monocular images were shown to observers, mimicking perceptual waves under nonrivalry conditions. We had complete information about the timing of neural events during this replay experiment; the neural-response amplitudes and the hemodynamic

impulse response were the only parameters that had to be determined, which was done by fitting the fMRI responses to the physical traveling waves. With those five parameters fixed, we then fit the model to the fMRI responses measured during rivalry, which resulted in separate estimates for the latencies of the underlying neural activity for each voxel of V1 gray matter. A linear fit of the neural latencies revealed wave propagation speeds across the three observers of 1.6–2 cm/s; these propagation speeds compare favorably to the speed value of 2.2 cm/s estimated from psychophysical measurements using essentially the same stimulus<sup>4</sup>.

In summary, the time course of cortical activity varied systematically across the retinotopic map in V1, in correspondence with the subjective perception of traveling waves during binocular rivalry. These results go beyond those from previous single-unit electrophysiology<sup>8–10</sup> and neuroimaging<sup>11–15</sup> studies by demonstrating that V1 activity reflects the spatiotemporal dynamics of perception during rivalry. Furthermore, the data show that fMRI is capable of resolving timing differences of ~115 ms over a distance of ~3.5 mm (Fig. 1c). It remains to be seen whether these cortical waves originate in V1 via long-range intracortical connections or whether they are evoked by feedback from higher-order visual cortical areas.

Note: Supplementary information is available on the Nature Neuroscience website.

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#### COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

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