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Travelling waves of activity in primary visual cortex during binocular rivalry

Sang-Hun Lee¹, Randolph Blake², and David J. Heeger¹

¹Department of Psychology and Center for Neural Science, New York University, 6 Washington Place, 8th floor, New York NY, 10003

²Department of Psychology, Vanderbilt University, 512 Wilson Hall, Nashville, TN 37203

Abstract

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 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^{1,2}. A rare opportunity to observe the perceptual concomitants of wave propagation is conferred by binocular rivalry, the perceptual alternations induced when incompatible patterns are presented to the two eyes³. During an alternation, one sees a travelling wave in which the dominance of one pattern emerges locally and expands progressively as it renders the other pattern invisible⁴. Several converging lines of evidence suggest that primary visual cortex (V1) may be involved in the spatiotemporal dynamics of these perceptual travelling waves, but that involvement remained to be demonstrated. Toward that end, we used functional magnetic resonance imaging (fMRI) to measure and characterize travelling waves of cortical activity during rivalry.

Human observers viewed a dichoptic display designed to induce perceptual waves (Fig. 1a). 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 rivalry's susceptibility to transient stimulation⁵, we triggered shifts in perceptual dominance by a brief and abrupt increase in the 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 travelling wave such that observers perceived the local dominance of the low-contrast image to spread around the annular region, starting at the top of the annulus and progressively erasing the high-contrast image from visual awareness⁴ (**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. Upon this key press, the two monocular gratings disappeared until the beginning of the next trial.

If activity in 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

Correspondence and requests for materials should be addressed to D.J.H. (e-mail: david.heeger@nyu.edu). (S.H.L. is now at Department of Psychology, Seoul National University, Seoul South Korea)

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annulus, because: 1) locations further from the point of origin of the travelling wave will respond to the high contrast for longer durations, and 2) fMRI responses in V1 increase monotonically with stimulus contrast⁶. 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 travelling waves of cortical activity.

Primary visual cortex (V1) did indeed exhibit travelling waves of activity while observers experienced perceptual travelling 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 procedures⁷. 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 χ^2 test). This occurred despite there being no 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 range of behavioral latencies. Both the speed (slope of the best-fit line) 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 more directly compare 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 along with a model for how the fMRI signal depended on the 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, one parameter characterized the amplitude of transient neural responses evoked by abrupt stimulus onset at the beginning of each trial, and three free parameters 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 travelling waves. In a separate "replay" experiment, sequences of monocular images were shown to observers, mimicking perceptual waves under nonrivalry conditions. Note that we had complete information about the timing of neural events during this replay experiment; only the neural response amplitudes and the hemodynamic parameters were determined by fitting the fMRI responses to the physical travelling waves. Then, with those five parameters fixed, we fitted the model to the fMRI responses measured during rivalry, resulting in estimates for the latencies of the underlying neural activity, separately 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 stimulus⁴.

In summary, the time course of cortical activity varied systematically across the retinotopic map in V1, in correspondence with the subjective perception of travelling waves during binocular rivalry. These results go well beyond those from previous single-unit electrophysiology^{8–10} and neuroimaging studies^{11–15} by demonstrating that V1 activity reflects the spatiotemporal dynamics of perception during rivalry. Furthermore, the data in Figure 1c demonstrate the capability of fMRI to resolve timing differences of ~115 ms over a distance of ~3.5 mm. It remains to be seen if these cortical waves originate in V1 via long-

range intracortical connections, or if they are evoked by feedback from higher-order visual cortical areas.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.

Travelling waves of cortical activity in human V1. **(a)** Stimuli, rival gratings viewed dichoptically. Percept, snap shot of travelling wave in which the low contrast pattern was seen to spread around the annulus, starting at the top. **(b)** Gray scale, 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. Green outline, subregion of V1 corresponding to the lower-right quadrant. Inset, time series of the predicted neural activity according to a simplified model (see Supplementary Methods online). Red and green curves, time series of the measured fMRI responses corresponding to the two outlined subregions, averaged across ~1000 trials for one observer. Red and green arrows, locations in time where these 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, SEM. **(d)** Estimated propagation speed of the underlying neural activity, averaged across behavioral latencies. Dashed line, best-fit to the mean across observers.