**Travelling waves of activity in primary visual cortex during binocular rivalry**

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# Supplementary Methods

Data were acquired from three male observers, 25-34 years old, all with normal or corrected-to-normal vision, on a GE 3 Tesla scanner with a custom dual surface coil (NMSC-002-TR-3GE transmit-receive coil, Nova Medical, Wakefield, MA). Experiments were carried out with the written consent of each observer, and in compliance with the safety guidelines for MR research, as approved by the Stanford University Panel on Human Subjects in Medical Research. Each observer participated in multiple scanning sessions: one session to obtain a high-resolution anatomical volume, one session to define the early retinotopic visual areas including V1, one session to locate the subregion of each visual area that corresponded to the annulus region in which stimuli were presented, and several fMRI scanning sessions to measure fMRI responses under the various experimental conditions.

Each MR scanning session began by acquiring a set of anatomical images using a T1-weighted SPGR pulse sequence (TR = 10 ms, minimum TE, FA = 15°, 6 NEX, FOV = 220 mm, 3-mm slice thickness) in the same slices as the functional images. The eight oblique slices, roughly perpendicular to the calcarine sulcus, were arranged carefully to encompass the subregion of V1, and other visual areas if possible, that corresponded to the stimulus annulus, which was defined in a separate scanning session (see below). These inplane anatomical images were aligned to a high-resolution anatomical volume of each observer's brain using custom software[1], so that the functional data across multiple scanning sessions from a given observer were coregistered to an accuracy of ~ 1 mm.

Each fMRI scanning session included 8-13 functional scans. During each scan, a time series of fMRI volumes was acquired using a single-shot, T2*-sensitive, spiral-trajectory, gradient-recalled-echo pulse sequence[2] (TE = 30 ms, TR = 500 ms, FA = 46, FOV = 220 mm, effective inplane pixel size = 3 x 3 mm, 3-mm slice thickness). To minimize head movements, observers were stabilized on a bite bar.

Rival stimuli were a radial grating and a spiral grating, each restricted to an annulus around fixation (spatial frequency = 2.5 cyc/°, radius of annulus center = 4°, width of spiral grating annulus = .8°, Gaussian half-width of radial grating annulus = .4°). The two monocular images were presented on the two halves of a flat-panel display (Multisync LCD 2000, NEC-Mitsubishi, Japan) positioned at the foot of the scanner bed. The display was viewed through binoculars. A pair of angled mirrors, attached to the binoculars, enabled the observer to see the two monocular images. A septum was placed near the observer's knees, and the mirrors were adjusted so that the observer could see only one image in each eye.

Each trial lasted 9 s and consisted of several phases (**Supplementary Fig. 1** online). First, the low-contrast grating was presented to one eye, followed 30 ms later by the high-contrast grating to the other eye. This sequence of events promoted complete perceptual dominance of the high-contrast grating. Shortly (450 ms) thereafter, the contrast in a small region of the low-contrast grating at the top of the annulus was increased briefly (75 ms) and abruptly, then returned to its original low-contrast value. This contrast pulse typically triggered a perceptual travelling wave (**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.

On a minority of trials (38%), the contrast pulse either failed to evoke a perceptual travelling wave or the travelling wave dissipated somewhere along both paths before reaching the target area. Observers pressed a different key to indicate these failure trials. At all times during the trials, observers maintained strict fixation on the small checkerboard located in the center of the stimulus annulus.

The contrast of the spiral grating was always 100% whereas the contrast of the radial grating was adjusted to achieve two goals simultaneously: i) to maximize the number of trials in which perceptual travelling waves were experienced and ii) to maximize the difference in contrast between the spiral and the radial grating. To do this, the contrast level of the radial grating was adjusted throughout each scanning session. At the beginning of each session, we chose the initial contrast level based on a psychophysical test, which determined the contrast level at which the observer perceived travelling waves most frequently. During the first scan, the contrast of the radial grating slightly varied around the initial contrast level. In the following scan, the contrast varied around a new level, at which waves were experienced most frequently in the previous scan. This contrast adjustment was repeated throughout each session.

The fMRI data were analyzed as follows. First, we discarded the first 9 seconds of data from each scan to minimize the effects of transient magnetic saturation. Second, any residual head movements within each scan and across scans were corrected using custom software[1]. Third, the time series from each slice was interpolated (linear interpolation) and shifted in time to compensate for the differential slice acquisition times. Fourth, the time series at each voxel was high-pass filtered to compensate for the slow signal drift in the fMRI signals. Fifth, the time series at each voxel was divided by its mean intensity to convert the data from arbitrary image intensity units to percent

signal modulation and to compensate for the decrease in mean image intensity with distance from the receive coil.

The resulting time series were analyzed for gray matter voxels in each visual area that corresponded retinotopically to the stimulus annulus. These voxels were identified separately for each observer in four steps. First, the retinotopically organized visual areas were identified, following well-established methods, by measuring polar angle and eccentricity components of the cortical retinotopy map[3-6]. Second, a subset of voxels in these visual areas that corresponded to the cortical representation of the stimulus annulus was selected based on a separate series of reference scans. During these reference scans, observers held fixation while the display alternated every 9.4 s between a high-contrast checkerboard within the stimulus annulus and its geometric complement, a checkerboard pattern everywhere except the annulus. Data were averaged across six to ten repeated scans, each with eleven cycles of alternations. Voxels were included in the analysis only if they were strongly correlated ($r > .6$ and 0-6 time lag) with the stimulus alternations. Third, the selected voxels were further restricted according to two localizer scans, one at the start and the other at the end of each scanning session. During these localizer scans, the display alternated between a high-contrast checkerboard within the stimulus annulus and a uniform gray field of the same mean luminance. We chose the subset of voxels that were correlated ($r > .7$) with the stimulus alternations in both of the reference scans. This was done because a portion of the session-to-session variability in fMRI responses derives from small differences in slice orientation and position such that voxels which were mostly gray matter in one session are only partially gray matter in a subsequent session. We have found that a within-session localizer can effectively compensate for this source of variability,

leading to noticeable improvement in the session-to-session reliability of the measurements. Fourth, for each voxel, we estimated the distance on the flattened cortical surface from the cortical representation of the top of the annulus based on its polar angle measurement from the retinotopy session. Cortical distances were measured in the 3D cortical manifold (the boundary between white matter and gray matter) using custom software[7]. We discarded voxels that represented the visual field within 30° on either side of the upper vertical meridian, where the trigger was presented, because fMRI responses at those voxels were likely to be contaminated by the physical contrast increment.

FMRI response amplitudes and temporal delays were computed as follows. The measured time series for each of the identified gray matter voxels was averaged across trials. This averaged time series was then fitted using a sinusoidal function. The best-fit sinusoid provided a continuous description of the time series. The temporal delay (time-to-peak) and response amplitude of the fMRI responses were estimated as the phase and amplitude, respectively, of the best-fit sinusoid. Correlations between temporal delay and distance (Fig. 1c) were computed using linear regression. The Pearson $\chi^2$ test was used to determine whether correlation values were significantly different from zero. Previous measurements in our lab have indicated modest spatial correlations in the noise in our fMRI measurements such that the data are over-sampled by a factor of ~4, i.e., by a factor of 2 in each of the 2 image dimensions (unpublished observations). In performing the chi-square test, therefore, the number of degrees of freedom was reduced by a factor of 4 to compensate for the existence of correlated noise in adjacent voxels.

Error estimates for the statistical test of slopes and y-intercepts in Fig 1c were obtained with a bootstrap method[8] in which random picks (with replacement) were

repeatedly taken from the experimentally obtained data sets, separately for each speed condition (slow, medium, fast). The means and standard errors of slopes and y-intercepts were then computed from 1000 samples of these synthetic data, thus generating bootstrap estimates of the sampling distributions.

The latencies of the underlying neural activity at each voxel (Fig. 1d) were estimated from the fMRI responses by adopting a model of the neural activity and a model of the hemodynamics:

$$r(t) = h(t) * n(t)$$

where $r(t)$ is the fMRI response, $h(t)$ is the hemodynamic impulse response, $n(t)$ is the neural activity, and * represents convolution[10]. The underlying neuronal activity at each voxel, n(t), was assumed to go through four states during each trial: a transient response to the onset of stimulus (assumed to last for 200 ms), a sustained response to the higher contrast, a sustained response to the lower stimulus contrasts, and no response while the display was blank (uniform gray) during the inter-trial interval. These four states were characterized by two parameters: the amplitude of the transient response ($R_t$), and the ratio of the responses to the high and low contrasts ($R_c$). The hemodynamic impulse response was modeled as:

$$h(t) = \exp(-t/\tau_1) \sin(2\neq f_1 t) - a \exp(-t/\tau_2) \sin(2\neq f_2 t).$$

We have found in previous work[9] (D. Ress, B.T. Backus & D.J. Heeger, *Soc. Neurosci. Abstr.*, 2000) that this functional form is a better fit to the hemodynamics than the commonly used Gamma function[10]. The parameters $\tau_2$ and $f_2$ were set to 7.4 s and 0.12 Hz, respectively, based on previous measurements in our lab[9] (D. Ress, B.T. Backus & D.J. Heeger, *Soc. Neurosci. Abstr.*, 2000). The remaining parameters ($R_t$, $R_c$, $\tau_1$, $f_1$, $a$)

were determined separately for each observer by fitting the data from the replay/physical wave experiment. Specifically, the model was chosen to fit simultaneously the measured fMRI responses from four subregions of V1 gray matter (each corresponding to a 30° segment of the stimulus annulus from a quadrant of the visual field). Note that we had complete information about the timing of neural events during replay; only the neural response amplitudes and hemodynamic parameters were determined by fitting the model. The model accounted for 94% of the variance in the measured fMRI responses in V1 during replay, for each of the 3 observers. The best-fit parameters were comparable across the 3 observers ($R_t$=0.5-0.75; $R_c$=5.5-8.0; $\tau_1$=6.5-7.0; $f_1$=0.35-0.65; $a$=0.08-0.1).

The model was then used, with the model parameters fixed, to estimate the latencies of the underlying neural activity during rivalry. This was complicated by the fact that the contrast pulse failed to evoke complete perceptual travelling waves on some trials (see above). Because we did not know exactly what happened on each such failure trial, and because the failure trials were interleaved with the valid trials, we could not perform a straightforward least-squares fit to the measured time series. Instead, we used the model to generate simulated fMRI responses (response amplitudes and temporal delays) which were used as lookup tables to determine the neural latencies. Specifically, we simulated 100 scans for each observer, resulting in about 1000 ~ 1500 complete travelling waves (assumed to propagate at constant velocity) interleaved with a number of failure trials (matching the proportion of failures reported by each observer). The model response amplitudes and temporal delays were extracted from these simulations, following the steps that were used to analyze the real fMRI data. This resulted in a lookup table for each observer which associated the temporal latency of the

underlying neural activity with a corresponding fMRI response amplitude and temporal delay. Finally, we used the lookup tables to determine the neural latencies associated with simulated response amplitudes and delays that best matched the measured response amplitudes and delays.

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