

Hierarchy of cortical responses underlying binocular rivalry

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During binocular rivalry, physical stimulation is dissociated from conscious visual awareness. Human brain imaging reveals a tight linkage between the neural events in human primary visual cortex (V1) and the dynamics of perceptual waves during transitions in dominance during binocular rivalry. Here, we report results from experiments in which observers' attention was diverted from the rival stimuli, implying that: competition between two rival stimuli involves neural circuits in V1, and attention is crucial for the consequences of this neural competition to advance to higher visual areas and promote perceptual waves.

When your eyes view dissimilar patterns, you experience a perceptual illusion called binocular rivalry. Rather than melding into a stable, single image, the two patterns compete for visibility, with one temporarily dominating perception for several seconds, only to be replaced in awareness by the other. What makes this phenomenon remarkable is the dissociation between constant physical stimulation and fluctuating perceptual experience. Because of this dissociation, binocular rivalry provides a compelling means for studying visual awareness. Despite an impressive volume of work on rivalry, however, central questions remain unanswered concerning the neural processing underlying this beguiling phenomenon. Particularly controversial are the roles of primary visual cortex (V1) in rivalry^{1–6} and, consequently, in awareness^{7–9}.

To address this controversy, we have capitalized on a compelling aspect of rivalry: during transitions in perceptual state, one typically sees a traveling wave in which the perceptual dominance of one pattern emerges locally and expands progressively as it renders the other pattern invisible. Previous psychophysical experiments provided indirect evidence for the involvement of V1 in the propagation of these traveling waves¹⁰, and functional magnetic resonance imaging (fMRI) experiments established a tight linkage between the dynamics of perceptual waves during rivalry and the spatiotemporal dynamics of V1 activity¹¹. Specifically, traveling waves of cortical activity propagate over subregions of V1 that correspond topographically to perceptual waves, and the spatiotemporal dynamics of cortical waves co-vary with the propagation speed of those perceptual waves. But are these cortical waves also seen in other, extrastriate visual areas, and if so, how does that activity relate to that measured in V1?

Here, we carried out experiments that used attention as a tool to dissociate the conscious perception of traveling waves during rivalry from the automatic neural processing underlying the initiation and propagation of these waves. We measured activity in human visual cortex with fMRI while observers viewed rival stimuli. When attention

was diverted from the spatial location of the perceptual waves, the spatiotemporal dynamics of neural activity differed across the hierarchy of visual cortical areas; waves of cortical activity were preserved in primary visual cortex (V1), whereas they were eliminated in visual area V2 and even reversed in V3.

RESULTS

Human observers viewed a dichoptic display that was designed to induce perceptual waves (Fig. 1). The rival images comprised a low-contrast carrier grating (viewed by one eye) and a high-contrast mask grating (viewed by the other eye). Each was restricted to an annular region of the visual field, centered on the point of fixation. Exploiting the susceptibility of binocular rivalry to transient stimulation¹², we triggered a switch in perceptual dominance through a brief and abrupt increase in contrast in a small region (either at the top or the bottom of the annulus) of the otherwise low-contrast carrier grating. When presented while the carrier grating was suppressed from vision, this contrast pulse typically ignited a perceptual traveling wave; observers perceived the carrier emerging from suppression, with its visibility first arising at the location of the triggering pulse and progressively erasing the high-contrast mask grating from visual awareness^{10,11}.

During each fMRI scanning session, observers were instructed to maintain fixation at the center of the display while carrying out either a perceptual latency task or a diverted attention task. Each observer performed a large number of repeated trials (384–576) for each task. In the perceptual latency task (Fig. 1a), observers directed attention (without moving their eyes) to the rival gratings in the near-periphery of the visual field. When a perceptual wave reached a target area (marked by nonius lines), observers pressed a key, thereby providing a measure of the arrival time of the perceptual wave. The two monocular rival gratings disappeared when the key was pressed.

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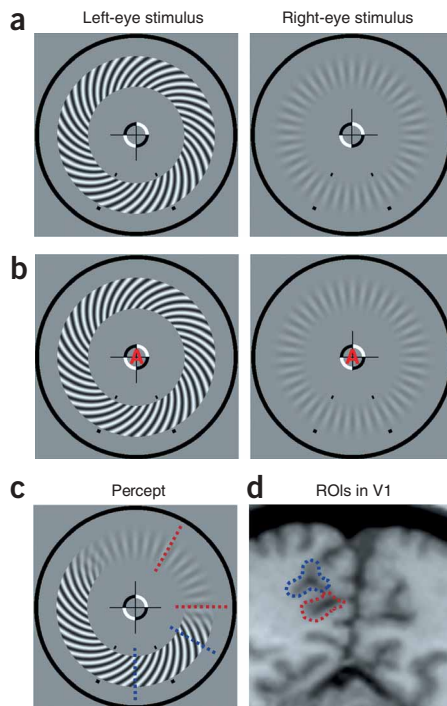


Figure 1 Rival stimuli, percepts and corresponding regions of primary visual cortex (V1). **(a)** Visual stimuli presented during the rivalry experiment. Each trial lasted 9 s and consisted of several phases. First, the low-contrast grating was presented to one eye, followed 30 ms later by the high-contrast grating being presented to the other eye. This sequence of events typically promoted the 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 traveling wave. **(b)** Visual stimuli presented during the diverted attention task were identical, except that a rapid series of small (<0.5 deg), colored letters and numbers appeared at fixation continuously while the rival gratings were presented (7–15 characters per trial, each presented for 195 ms). **(c)** Example of an observer's perceptual experience. This example depicts a case in which a perceptual wave propagated more rapidly in the right hemifield than in the left hemifield. Note that perceptual traveling waves occurred during the rivalry condition even though there were no wave-like changes in the stimulus itself. Red and blue dotted lines denote subregions of the visual field that showed different spatiotemporal dynamics. The regions marked by the blue lines appeared high contrast for a longer period of time than did those marked by the red lines. **(d)** V1 regions of interest (ROIs) from one example observer. Gray scale, anatomical image passing through the posterior occipital lobe, roughly perpendicular to the calcarine sulcus. Blue and red dotted outlines show subregions of V1 corresponding to the upper and lower visual-field subregions marked in **c**.

In the diverted attention task (Fig. 1b), the dichoptic rival gratings and the sequence of events were identical to those in the perceptual latency task, except that a rapid series (one every 190 ms) of small, colored letters and numbers appeared at fixation. The onset of the letters was simultaneous with the onset of the carrier grating, and the offset of the rival gratings and letters was determined by randomly sampling from the distribution of trial durations during rivalry. During each trial, one of the colored characters was repeated, and after each trial the observers reported whether the repeated item was a letter or a number. The repeated character always occurred near the end of the trial, forcing observers to maintain attention to the stream of characters, to bind the color and identity of each character, and to remember the full sequence of characters presented during each trial. Observers were not required to monitor the rival gratings while carrying out this task, which was sufficiently demanding (65–85% correct) that the observers reported perceiving only the transient onset of the rival gratings at the beginning of each trial; they were completely unaware of the dynamics of the traveling waves (as confirmed in an ancillary experiment, see Methods). At the beginning of each fMRI scan, stimulus contrast was optimized such that observers experienced perceptual waves without carrying out the letter-versus-number identification task.

Replicating and extending our previously published results¹¹, we found that activity in early visual cortex reflected the spatiotemporal dynamics of rivalry while observers attended the rival gratings and carried out the perceptual latency task (Fig. 2a–c, example data from a typical observer; Fig. 3, black bars, average across observers; Fig. 4a–c, gray circles, average across observers). We carried out two separate, complementary analyses on the fMRI data, averaged across trials. In one analysis, we averaged fMRI responses throughout gray matter voxels corresponding retinotopically to the upper and lower visual-field quadrants (Figs. 2 and 3). In a second analysis, we averaged fMRI responses at cortical locations that corresponded to five retinotopically

defined locations along the path of the cortical representation of the stimulus annulus in each visual hemifield (Fig. 4). Both analyses supported the same conclusions.

The peak of the fMRI responses was increasingly delayed with increasing distance from the cortical representation of the triggering pulse (that is, waves of cortical activity). We previously reported that the latency and propagation speed of cortical waves in V1 and perceptual waves were correlated with one another¹¹. Here, we report that similar results were observed in each of the three visual cortical areas studied (V1, V2 and V3). These differences in the timing of the fMRI responses were predicted because: (i) the amount of time that the high-contrast grating was perceived increased with distance from the location of wave originated, (ii) responses in visual cortex increase monotonically with stimulus contrast¹³, and (iii) the hemodynamic response can be modeled as a leaky integrator (a low-pass temporal filter)¹⁴ such that the peak latency of the response increases with the persistence (or sustained duration) of elevated neural activity. The cortical waves also reflected neural activity evoked by observers' attention to the perceptual waves (see below). In addition, the cortical waves may have reflected neural responses to the (second-order) motion of the perceived contrast boundary¹⁵. Note, 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.

Waves of activity were preserved in V1 during the diverted attention experiment (Fig. 2g; Fig. 3, leftmost light gray bar; Fig. 4a, gray squares), even though disengaging attention from the spatial location of the rival gratings abolished awareness (see Methods) of the waves. When attention was diverted, the response latencies were shorter and the response amplitudes were weaker than those latencies and amplitudes measured when observers perceived the waves (Table 1). Although it may be counter-intuitive that diverting attention shortened response latencies, both changes in response latency and response amplitude might be explained by assuming that a component of the cortical waves reflected neural activity that was evoked by observers' attentional tracking of the perceptual wave fronts. The percent difference in response latencies between upper and lower visual-field

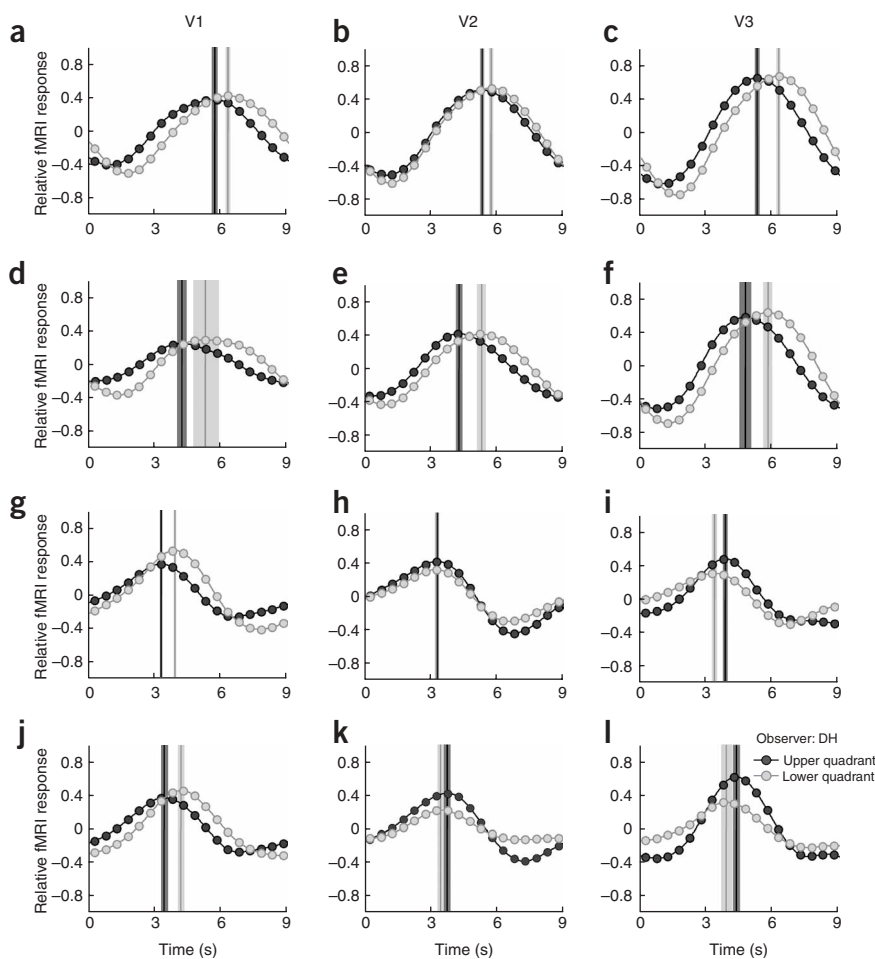


Figure 2 Temporal sequences of fMRI responses, averaged across trials for one observer in each experimental condition and each visual area. Black and gray curves correspond, respectively, to the two outlined subregions in **Figure 1d**. Note that the curves are periodic because each trial began 9 s after the preceding trial; hence, a shift in the underlying neural response latency resulted in a periodic phase shift of these curves. Black and gray vertical lines represent peak latency in the fMRI responses (times when the curves peak). Shaded regions represent 95% confidence intervals for peak latencies. Left column, V1. Middle column, V2. Right column, V3. **(a–c)** Rival stimuli with perceptual latency task. **(d–f)** Replay (physical wave) stimuli with perceptual latency task. **(g–i)** Rival stimuli with diverted attention task. **(j–l)** Replay (physical wave) stimuli with diverted attention task.

activity in V1 suppressed the activity at retinotopically corresponding locations in V3, thereby evoking a wave of suppression in V3 that was coincident with the waves of enhanced activity that were preserved in V1. The response amplitudes were weaker in V2 and V3, as in V1, when attention was diverted (**Table 1**). Note, however, that the physical presentation of the stimuli still evoked strong responses in V2 and V3 (**Table 1**). Hence, diverting attention markedly altered the spatiotemporal dynamics of the responses (the response latency differences were eliminated or reversed), but had only a modest effect on the amplitudes of the stimulus-evoked responses.

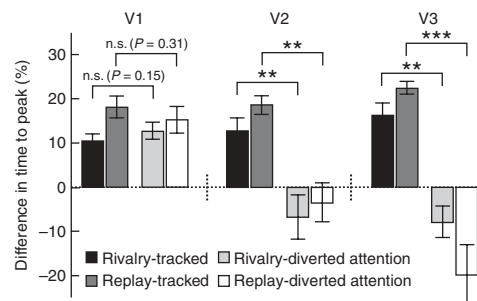
Spatiotemporal patterns of cortical activity

quadrants was, however, indistinguishable with and without attention and perception (**Fig. 3**; see also **Supplementary Tables 1** and **2** for results from individual observers).

In V2 and V3, and unlike in V1, cortical waves were profoundly affected by diverting attention (**Figs. 2h,i**, **Fig. 3** and **Fig. 4b,c**). Recall that when observers experienced rivalry, the temporal delay of the fMRI responses in V2 and V3 increased with distance from the cortical representation of the trigger, as did responses in V1. However, when observers carried out the letter identification task, and thereby diverted attention from the stimulus annulus, the differences in response timing were abolished in V2 and even reversed in V3 (**Figs. 3** and **4**, **Table 1**, and **Supplementary Tables 1** and **2**). Why did the waves reverse direction in V3 when attention was diverted? This was an unexpected result for which we have no ready interpretation; it could mean that

during rivalry were compared with those evoked by a replay condition, where sequences of monocular images mimicking perceptual waves were presented to observers under nonrivalry conditions. During each replay trial, physical waves were created by progressively replacing the high-contrast mask grating with the low-contrast carrier grating. The propagation times of physical waves were determined by randomly sampling from the distribution of propagation times measured during rivalry, with the speed of propagation constant within each trial, but varying across trials (median propagation time, 1.68 s; median angular speed, 90.10 deg s⁻¹). In separate experiments, observers carried out the same two tasks as before. When these physical waves were attended, observers perceived them to be similar to perceptual waves during rivalry. When attention was diverted, observers reported that they perceived only the

Figure 3 fMRI response latency differences averaged across observers. For comparison across observers, differences in response latencies between the upper and lower visual quadrants were divided by their average to convert them to percent differences. Black, rival stimuli with perceptual latency task. Dark gray, replay (physical wave) stimuli with perceptual latency task. Light gray, rival stimuli with diverted attention task. White, replay stimuli with perceptual latency task. Error bars represent s.e.m. latency differences across observers. Statistical significance (n.s., not statistically significant; * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$) was determined by paired t -tests assuming the null hypothesis that differences in response latencies between upper and lower visual field quadrants were unaffected by diverting attention. $n = 7$ observers for rivalry, $n = 4$ for replay.



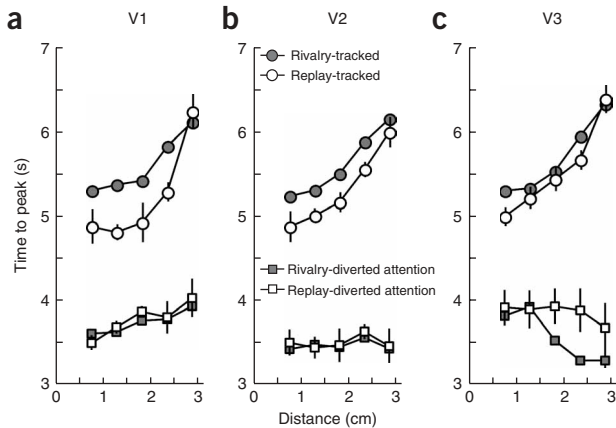


Figure 4 Traveling waves of cortical activity, averaged across four observers, in each visual area. (a) V1, (b) V2 and (c) V3. Gray circles, rival stimuli with perceptual latency task. White circles, replay (physical wave) stimuli with perceptual latency task. Gray squares, rival stimuli with diverted attention task. White squares, replay (physical wave) stimuli with diverted attention task. Error bars represent s.e.m. across observers, estimated with a bootstrap procedure (see **Methods**).

transient onset of the gratings at the beginning of each trial, and not the wave itself.

The patterns of cortical activity elicited by physical waves were qualitatively similar to those observed during rivalry (**Figs. 2–4**, **Table 1**, and **Supplementary Tables 1** and **2**). Cortical waves were evident in all three visual cortical areas when observers attended to the physical wave stimuli. When attention was diverted, waves were preserved in V1, but eliminated in V2 and reversed in V3. Response latencies were shorter and response amplitudes were smaller in all three visual areas when attention was diverted (**Table 1**). Only in V1, however, were the percent differences in response latencies between the upper and lower visual-field quadrants unaffected by diverting attention (**Fig. 3** and **Supplementary Tables 1** and **2**).

As a control for possible inherent differences in response latencies between upper and lower visual-field quadrants, we took measurements in a subset of the observers with the triggering pulse at the top of the stimulus annulus on some trials, and at the bottom of the stimulus annulus on other trials. The measured fMRI response latency differences were reversed, which is consistent with the waves traveling in the opposite direction (**Fig. 5**). To rule out the possibility that the triggering contrast pulse evoked artifactual responses that were misinterpreted as traveling waves, we carried out two additional controls. First, the triggering contrast pulse was presented by itself in the absence of the rival stimuli. Second, it was presented to one eye with the mask grating in the other eye, but in the absence of the carrier grating. Neither of these stimulus conditions evoked a traveling wave percept, and in neither case did we observe traveling waves of cortical activity (**Fig. 5b,c**; **Fig. 5d**, open bars). We carried out a final control experiment to rule out the possibility that the mere presence of the rapid sequence of characters at fixation was sufficient to disrupt the traveling waves in V2 and V3. Waves were preserved in all three visual areas as long as the observers carried out the perceptual latency task, attending to the rival stimuli and ignoring the characters (**Supplementary Fig. 1**). Waves were eliminated or reversed only when the observers performed the diverted attention task (**Figs. 2–4**).

Table 1 Effects of attention on fMRI response amplitudes and latencies

Relative response amplitudes (% change image intensity)	Tracked	Div. Att.	(Tracked > Div. Att.)
Rivalry			
V1			
UQ	0.33	0.20	**
LQ	0.36	0.24	*
(LQ > UQ)	($P = 0.07$)	($P = 0.08$)	
V2			
UQ	0.39	0.16	***
LQ	0.41	0.18	**
(LQ > UQ)	n.s. ($P = 0.40$)	n.s. ($P = 0.18$)	
V3			
UQ	0.39	0.25	**
LQ	0.42	0.18	**
(LQ > UQ)	n.s. ($P = 0.18$)	n.s. ($P > 0.99$)	
Replay			
V1			
UQ	0.30	0.27	n.s.
LQ	0.39	0.33	n.s.
(LQ > UQ)	n.s. ($P = 0.14$)	n.s. ($P = 0.10$)	
V2			
UQ	0.37	0.24	**
LQ	0.44	0.23	**
(LQ > UQ)	n.s. ($P = 0.16$)	n.s. ($P = 0.58$)	
V3			
UQ	0.33	0.26	*
LQ	0.38	0.21	*
(LQ > UQ)	n.s. ($P = 0.10$)	n.s. ($P = 0.89$)	
Response latencies (s)	Tracked	Div. att.	(Tracked > div. att.)
Rivalry			
V1			
UQ	5.33	3.82	**
LQ	5.91	4.34	**
(LQ > UQ)	***	***	
V2			
UQ	5.15	4.01	**
LQ	5.80	3.70	***
(LQ > UQ)	**	n.s. ($P = 0.90$)	
V3			
UQ	5.11	3.72	***
LQ	6.03	3.44	***
(LQ > UQ)	***	n.s. ($P > 0.95$)	
Replay			
V1			
UQ	4.88	3.51	**
LQ	5.81	4.10	**
(LQ > UQ)	**	*	
V2			
UQ	4.67	3.63	**
LQ	5.62	3.50	***
(LQ > UQ)	**	n.s. ($P = 0.75$)	
V3			
UQ	4.72	4.00	*
LQ	5.90	3.27	**
(LQ > UQ)	***	n.s. ($P > 0.95$)	

n.s., not statistically significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Tracked, relative response amplitudes and latencies when observers carried out the perceptual latency task (attending to the rival gratings). Div. att., response amplitudes and latencies when observers carried out the diverted attention task; LQ, lower visual quadrant; UQ, upper visual quadrant. LQ > UQ, statistical significance (paired t -tests) of response differences between upper and lower visual-field quadrants. Tracked > Div. att., statistical significance (paired t -tests) of response amplitude and latency differences between the perceptual latency and diverted attention tasks. $n = 7$ observers for rivalry, $n = 4$ for replay.

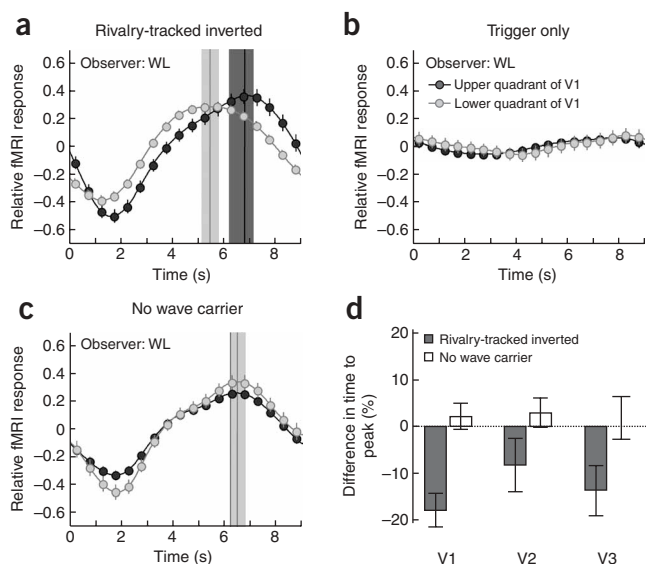


Figure 5 Control experiments. (a–c) fMRI responses in V1 from a typical observer (same format as Fig. 2). Perceptual waves propagated in the opposite direction (triggered at the bottom instead of the top, a). The triggering contrast pulse was presented by itself in the absence of the rival gratings (b). The triggering contrast pulse was presented to one eye with the mask grating in the other eye, but in the absence of the carrier grating (c). (d) fMRI response latency differences in all three visual areas, averaged across observers (same format as Fig. 3).

attention diverted. Nor can we rule out the possibility that traveling waves of neural activity originate in visual areas beyond V2 or V3 (for example, V4 or inferotemporal cortex), with the wave behavior in V1 being triggered by feedback from those higher areas. According to this argument, those feedback signals would be affecting V1 without having a measurable impact on V2 or V3. Moreover, those feedback signals from high-level areas would have to possess sufficient retinotopic specificity to orchestrate the orderly spatiotemporal propagation that characterized the traveling waves in V1. Future investigation using complementary physiological techniques will hopefully elucidate the relative contributions of intrinsic interactions in V1 and potential feedback effects propagating from higher areas to early areas.

Regardless of the source of these V1 cortical waves, our results are consistent with the assertion that processing in V1 is necessary, but not sufficient, for awareness⁷, at least under our stimulus conditions. Waves of activity in V1 (but not in V2 or V3) accompanied the viewing of rival patterns regardless of their perceptual consequences. This implies that V1 is not sufficient for awareness because observers were unaware of the traveling waves in V1 and were unable to make accurate behavioral responses concerning those waves (see **Methods**), unless the waves were also present in higher cortical areas. Activity in V3, likewise, was dissociated from awareness because it showed reversed-direction waves of which observers were unaware when attention was diverted.

Our data support recent computational models that posit a hierarchy of processing stages in binocular rivalry^{28,29}. According to those models, different areas in the hierarchy might be involved, depending on the type of stimuli used or the manner in which they are presented. Some stimuli (for example, dichoptic, oriented grating patterns like those used in the current study) are tailor-made to evoke cooperative and competitive interactions among subpopulations of neurons in V1, because V1 shows a functional organization for these stimulus features (orientation columns, ocular dominance columns, precise retinotopic map). Other stimuli, because of their spatial configuration³⁰ or their temporal properties^{31,32}, may evoke stronger competitive and cooperative interactions in later visual areas²⁸. In addition, feedback projections from later visual areas might modulate V1 activity during binocular rivalry to stabilize the neuronal representations that correspond to coherent percepts during rivalry³³ or other bistable phenomena. In the absence of the contrast pulse that we used to exogenously trigger the perceptual transitions and cortical waves, activity in higher cortical areas (for example, prefrontal cortex) may act, as the contrast pulse did, to trigger spontaneous alternations during binocular rivalry and other bistable perceptual phenomena^{34,35}.

Our results also reveal properties of the functional organization and neural circuitry in V1. The cortical wave propagation speed that we observed was remarkably slow, $\sim 2 \text{ cm s}^{-1}$ (ref. 11), relative to the latency of action potential propagation and synaptic transmission. Hence, wave propagation is unlikely to be mediated simply by direct, long-range horizontal connections in V1^{36–39}; there must be an additional processing delay of approximately 100 ms per hypercolumn (2 mm), consistent with the hypothesis that perception is discrete in time with a discrete perceptual ‘frame’ of $\sim 100 \text{ ms}$ in which stimuli are grouped and subjectively interpreted⁴⁰.

DISCUSSION

We found that the time course of cortical activity varied systematically across the retinotopic maps in early visual cortex, in correspondence with the subjective perception of traveling waves during binocular rivalry. We also found differential effects of attention on wave propagation in those different retinotopic maps; in V2 and V3, but not in V1, the fMRI responses signifying cortical waves were eliminated (or reversed direction in V3) when attention was diverted from the rival stimuli.

It is well known that attention strongly influences neural activity throughout visual cortex¹⁶. In our study, the amplitudes of cortical responses to the rival stimuli were reduced in V1, V2 and V3 when observers were engaged in a demanding task whose difficulty was verified in an ancillary experiment (see **Methods**). These wholesale amplitude reductions imply that attention was effectively diverted from the rival stimuli. Nonetheless, cortical waves were still evident in V1 despite diverted attention; in contrast, waves were evident in V2 and V3 only when observers attended and tracked perceptual transitions during rivalry. Previous studies have noted analogous dissociations between response amplitudes in V1 and later visual cortical areas^{17–19} by diverting attention, but such a marked dissociation in response timing between V1 and later visual cortical areas, caused by redirecting attention, has not been previously described.

One plausible interpretation of our results is that traveling waves arise from processing that is intrinsic to V1 (ref. 3) with, perhaps, contributions from the lateral geniculate nucleus^{20,21}. It is well known that activity in a given visual area can be modulated by feedback from a number of widely separated cortical areas^{22–24}, and that the specific role of attention could be to promote these long-range interactions^{25–27}. But in addition to modulating wave-related activity, is feedback from higher visual areas responsible for generating cortical waves in V1? It seems unlikely that V1 cortical waves arise from feedback originating in V2 or V3, as waves in those extrastriate areas were not observed (or were reversed in direction), whereas the waves in V1 were intact under diverted attention. We cannot rule out the possibility that the failure to observe waves in V2 with attention diverted occurred because the level of activity that is associated with those waves was too weak to measure using fMRI; however, physical presentation of wave stimuli evoked strong responses in V2 even during diverted attention and responses in V3 were sufficiently strong to reveal reverse-direction waves with

METHODS

Data were acquired from six observers (two female, 23–43 years old), all with normal or corrected-to-normal vision. 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 Human Subjects Internal Review Boards at Stanford University and New York University (NYU). Two observers participated in experiments at Stanford, three at NYU, and one observer participated in both sets of experiments (which we treat as independent observations). 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 responses under the various experimental conditions.

Each fMRI scanning session included 8–13 functional scans. MRI data were acquired at NYU on a Siemens 3T Allegra scanner equipped with a transmit head-coil (NM-011 Nova Medical) and a four-channel phased array receive coil (NMSC-021 Nova Medical). Echoplanar imaging was used to measure blood oxygenation level-dependent changes in image intensity. The pulse sequence parameters were: eight slices (roughly perpendicular to the calcarine sulcus), repetition time = 500 ms, echo time = 30 ms, flip angle = 55 deg, 64×64 matrix size, voxel size = $3 \times 3 \times 3$ mm. Data were acquired at Stanford on a General Electric 3 Tesla scanner with a custom-designed dual surface coil using a single-shot, T2*-sensitive, spiral-trajectory, gradient-recalled-echo pulse sequence⁴¹. The pulse sequence parameters were: repetition time = 500 ms, echo time = 30 ms, flip angle = 46 deg, effective voxel size = $3 \times 3 \times 3$ mm.

Data from each scanning session were coregistered. At the beginning of each session we acquired a T1-weighted anatomical volume in the same slices that were used for the functional scans, but with twice the in-plane resolution (voxel size $1.5 \times 1.5 \times 3$ mm). This anatomical volume was aligned with the observer's high-resolution anatomical scan (used for cortical surface extraction) by an automated robust image registration algorithm⁴².

The two rival figures, an annular-shaped radial grating and an annular-shaped spiral grating, were presented on the two halves of a display. At NYU, stimuli were projected on the two halves of a rear-projection screen located in the scanner bore, with an EIKI LC-XG100 projector and a custom-made zoom lens. The two grating annuli (inner radius = 1.6 deg, outer radius = 2.66 deg), were viewed through a mirror haploscope, custom-made to fit in the bore of the magnet. At Stanford, stimuli were presented on the two halves of a flat-panel display (Multisync LCD 2000, NEC-Mitsubishi) positioned at the foot of the scanner bed. Observers viewed the gratings (inner radius = 3.6 deg, outer radius = 4.4 deg), through binoculars. A pair of angled mirrors, attached to the binoculars, enabled the observers to see the two monocular images. The only substantial difference between the two different displays at the two sites was that the gratings were imaged closer to the fovea at NYU because of the limited field of view that was afforded by the smaller bore. Head movements were minimized by having observers bite a dental impression bar. Eye position was not measured, but observers were instructed to hold their gaze on a central fixation point marked by nonius lines, which enabled them to monitor their vergence eye movements.

The contrast of the mask grating ranged from 90–100%, whereas the contrast of the low-contrast carrier grating was adjusted to maximize the number of trials in which perceptual traveling waves were experienced and the difference in contrast between the mask and the carrier gratings. The resulting carrier contrasts ranged from 5.8–16.6%. On a minority (37.5%) of trials during the perceptual latency task (when observers attended the rival gratings), the contrast pulse either failed to evoke a perceptual traveling wave, or the traveling wave dissipated somewhere along both paths before reaching the target area. The data were averaged across all trials, including these failure trials, because there were no means for identifying failures during the diverted attention task.

In the diverted attention experiment, observers reported that they were completely unaware of the dynamics of the traveling waves. This subjective impression was confirmed objectively by a separate psychophysical experiment carried out outside of the scanner using the replay (physical wave) condition. In this experiment, five of the same observers were required to perform two tasks simultaneously⁴³: to identify whether the repeated item at fixation was a letter

or a number and to determine whether the physical wave that reached the bottom of the annulus was in the left or right hemifield. The physical wave front only reached the bottom on one side of the annulus; the wave in the other side of the annulus stopped at the horizontal meridian. Over trials, the physical wave reaching the bottom of the annulus appeared randomly in either the left or right hemifield. When instructed to attend to the letters and numbers at fixation, observers performed at chance levels on the traveling-wave task (45–54%). When instructed to attend to the physical traveling waves, observers were highly accurate on the traveling-wave task (95–100%), but performed at chance levels on the letter-versus-number identification task (44–54%).

To analyze the fMRI data, we first discarded the first 9 s of data from each scan to minimize the effects of transient magnetic saturation. Second, we corrected any residual head movements within each scan and across scans using custom software⁴². Third, we interpolated (linear interpolation) and shifted in time the time series from each slice to compensate for the differential slice acquisition times. Fourth, we high-pass filtered the time series at each voxel to compensate for the slow signal drift in the fMRI signals. Fifth, we divided the time series at each voxel 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. The retinotopically organized visual areas were identified, following well-established methods, by measuring the polar angle and eccentricity components of the cortical retinotopy map^{44,45}. A subset of voxels in these visual areas that corresponded to the cortical representation of the stimulus annulus were selected on the basis of a separate series of reference scans, using methods described in detail elsewhere (see **Supplementary Methods** of ref. 11). Finally, we discarded voxels that represented the visual field in 30 angular degrees on either side of the upper (or lower) vertical meridian, where the trigger was presented, because fMRI responses at those voxels were likely to be contaminated by the physical contrast increment.

The response latencies and response amplitudes during rivalry and replay, with and without attention diverted (**Figs. 2–4**) were computed as follows. Time series of fMRI responses were obtained from the two subregions in each visual area that represented the 30–90 degree and 120–180 degree portions of the annulus (**Figs. 2 and 3**). fMRI responses were also sampled from five locations along the path of the cortical representation of the annular stimuli in each visual hemifield (**Fig. 4**). To compare across different subregions in different visual areas, we computed relative response amplitudes, dividing the response amplitudes from the experimental scans by those from the reference scans (in which full-contrast visual stimuli were presented to both eyes in the same annulus). This calculation was carried out separately for each voxel, visual area and observer. The resulting time series were averaged across trials, scans and sessions for each viewing condition. Smooth curves were fit to the averaged time series using cubic spline functions (**Figs. 2 and 5**). Peak response amplitudes and latencies were estimated by finding the maximum of the best-fitting curve. Paired *t*-tests were used to assess the statistical significance of differences in response amplitudes and latencies, across observers. Confidence intervals for response amplitudes and latencies from individual observers (**Figs. 2 and 4**, and **Supplementary Tables 1 and 2**) were obtained with a bootstrap method⁴⁶, in which random picks of trials (with replacement) were repeatedly taken from the experimentally obtained datasets, and fit as described above. This procedure was repeated 1,000 times, thereby generating bootstrap estimates of the amplitude and latency distributions.

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

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COMPETING INTERESTS STATEMENT

The authors declare no competing financial interests.

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