Periodic perturbations producing phase-locked fluctuations in visual perception

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This paper describes a novel psychophysical and analytical technique, called periodic perturbation, for creating and characterizing perceptual waves associated with transitions in visibility of a stimulus during binocular rivalry and during binocular fusion. Observers tracked rivalry within a small, central region of spatially extended rival targets while small, brief increments in contrast ("triggers") were presented repetitively in antiphase within different regions of the two rival targets. Appropriately timed triggers produced entrainment of rivalry alternations within the central region, with the optimal timing dependent on an observer's native alternation rate. The latency between trigger and state switch increased with the distance between the location of the trigger and the central region being monitored, providing evidence for traveling waves of dominance. Traveling waves produced by periodic perturbation exhibited the same characteristics as those generated using a less efficient, more demanding discrete trial technique. We used periodic perturbation to reveal a novel relation between the dynamics associated with the spontaneous perceptual alternations and the speed of traveling waves across observers. In addition, we found evidence for traveling waves even when the events triggering them were initiated within regions of the visual field where binocular vision was stable, in the absence of binocular rivalry, implying that perceptual organization generally depends on spatio-temporal context.

Keywords: binocular vision, perceptual organization, visual cortex, perceptual waves, binocular rivalry

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Introduction

Visual perception arises from an amalgam of neural events distributed over space and time, and the interplay of these dynamic events promotes contextual effects that are evident in perception. Thus, for example, the visual appearance of a figure at a given spatial location can be markedly influenced by prior stimulation at that same location (Breitmeyer, 1984; Clifford & Rhodes, 2005) or by the simultaneous presence of other objects at nearby locations (Eriksen & Eriksen, 1974; Intriligator & Cavanagh, 2001). These contextual effects have long been recognized, and the Gestalt Psychologists thought they arose from dynamic electrical fields distributed over space and time within the brain (Köhler, 1940). While specifics of the Gestalt theory were subsequently disproven (Sperry, Miner, & Myers, 1955), the general notion of isomorphism between neural dynamics and perceptual dynamics has been retained in modern neuroscience (Churchland & Churchland, 2002; Teller, 1984).

Phenomena that compellingly underscore the dynamic nature of perception are those in which transitions in visual appearance spread over space and time. Examples of this wave-like propagation of perception include perceptual filling-in (De Weerd, Desimone, & Ungerleider, 1998), migraine aura (Hadjikhani et al., 2001), depth propagation (Nishina, Okada, & Kawato, 2003), neon color spreading (Bressan, Mingolla, Spillmann, & Watanabe, 1997), the line-motion illusion (Hikosaka, Miyauchi, & Shimojo, 1993; Jancke, Chavane, Naaman, & Grinvald, 2004), and expansion of illusory contours (Gold & Shubel, 2006). Here, we focus on perceptual dynamics as revealed by the wave-like propagation of perceptual dominance during binocular rivalry (Lee, Blake, & Heeger, 2005, 2007; Wilson, Blake, & Lee, 2001). The procedures used in our initial work to induce and measure perceptual waves, however, proved somewhat inefficient and required considerable practice before formal data collection with naive observers. With the original procedure, observers had to initiate contrast increments on discrete trials dependent on the subjective perceptual state being experienced, and at the end of each trial, they had to indicate whether or not wave propagation was successful; unsuccessful trials were discarded because of spontaneous perceptual switches or because the triggers

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were ineffective. Moreover, that discrete trial procedure required observers to distribute their attention over different regions of the visual field when initiating triggers and, then, when monitoring rivalry, all the while maintaining strict fixation at a given location outside the region of rivalry.

To circumvent the above-mentioned inefficiencies and challenging task demands, we have developed novel psychophysical and analytical techniques for creating and characterizing perceptual waves associated with transitions in rivalry dominance. By way of preview, our technique—termed periodic perturbation—entails remotely triggering switches in perceptual dominance and indexing the spatio-temporal properties of those switches based on simple, binary categorizations performed by observers viewing binocular rivalry between two dissimilar monocular patterns. The technique exploits the potency of a localized increment in contrast to promote local dominance of a small part of a previously suppressed pattern and, moreover, for that local region of dominance to spread over neighboring areas of the visual field (Wilson et al., 2001).

Our novel technique is illustrated in Figure 1 (see also Quicktime© movie). The observer views two rival patterns, one presented to each eye via a mirror stereoscope, and simply indicates by key presses which one of the two patterns is currently dominant within a restricted, central region of the display (the "monitoring region"). Because this region is small, the state of rivalry tends to be unitary and unambiguous during the entire viewing period. Within two small regions of the rival patterns, one above and the other below the monitoring region, local contrast increments are periodically presented in antiphase (i.e., one increment delivered to the top of one eye's pattern and then, some time later, the other increment delivered to the bottom of the other eye's pattern, and so on). With appropriately timed triggers, the dominance state within monitoring region switches repetitively between the two rival patterns, with these switches delayed but time-locked to the triggers.

Using periodic perturbation, we performed several experiments, the results of which verify that our technique is measuring the same properties of traveling waves as those characterized by the previous technique. Results from these experiments also reveal novel properties of traveling waves that have implications for models of binocular rivalry. In addition, we have found evidence for traveling waves even when the events triggering them were initiated within regions of the visual field where binocular vision is stable.

Perceptual waves during binocular rivalry

Methods for Experiments 1–4

Stimuli and trial-related events were controlled by a Macintosh G4 computer (Apple, CA) running Matlab (Mathworks, MA) in conjunction with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on the screen of a Sony E540 21-inch monitor (1024 H × 768 V resolution; 120-Hz frame rate; 21.67 cd/m^2 mean luminance) in a dimly illuminated room. In this and the following experiments, stimuli were

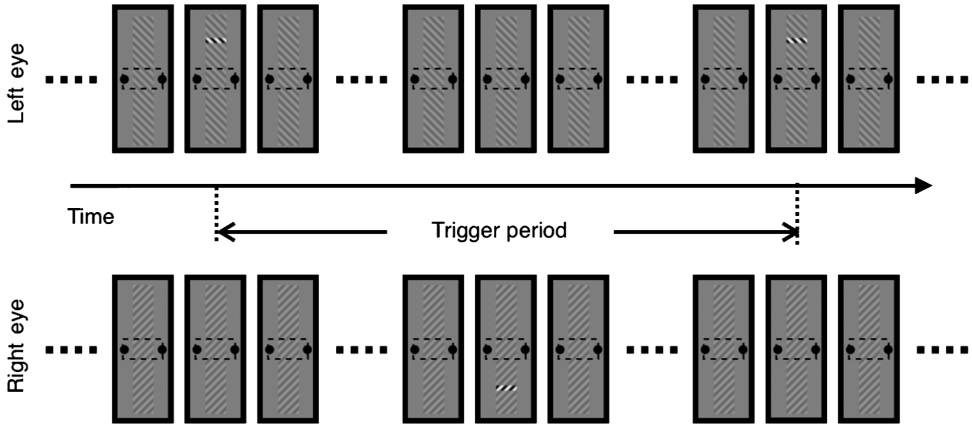

Figure 1. Schematic diagram illustrating the periodic perturbation technique. Triggers are presented periodically in antiphase within the upper region of one pattern and within the lower region of the other rival pattern, with this sequence lasting throughout an extended period of binocular rivalry; a trigger constitutes a brief increment in contrast within a horizontally elongated, sharp-edged region of one part of the rival target. (The dots denote extended periods during which the rival targets are presented without triggers.) Trigger period is defined as the interval of time elapsing between two successive trigger presentations to the same eye. The observer simply reports perceptual alternations in rival dominance within the central region of rival stimulation, called the monitoring region and indicated here by a dashed box (which was not presented during the experiment). Also shown in this figure are the markers that were present on either side of the central monitoring regions.

viewed against a gray background (21.67 cd/m^2) through a mirror stereoscope placed 90 cm from the monitor.

Vertically elongated rival stimuli (0.8° × 5° visual angle) were presented to the left and right eyes, and to promote stable binocular alignment each rival stimulus was bordered with a black rectangular frame (3.6° × 8°), the width of which was 0.25°. Observers adjusted the mirrors of the stereoscope until the two half-images were accurately aligned. The rival stimuli comprised left- and right-tilted sinusoidal gratings of spatial frequency 4.5 cyc/deg. The contrast of the two rival stimuli was identical. For Experiment 1, contrast was either 22.5% or 40.0%, for Experiment 2 only one contrast level, 22.5%, was used, and for Experiments 3 and 4 a single contrast level was selected for each observer (range was 20%–30%) to produce approximately equivalent dominance durations across observers. A small region at the center of each rival stimulus was demarcated by the presence of dotted markers located to the left and the right of this central monitoring region. These markers served as indicators of monitoring region during the tracking period. At locations symmetrically spaced above or below this monitoring region could appear brief (200 msec), localized (~0.8° × 0.2°) contrast increments to each of the rival gratings. For any given observation period, these increments occurred in the upper part of one eye's rival grating and in the lower part of the other eye's rival grating.

Observers were instructed to fixate the center of the monitoring region and to track fluctuations in perceptual dominance within that region by pressing and holding either of two keys associated with left/right-titled gratings. Unless specified otherwise, observers declared dominance only when one or the other of the rival gratings within the monitoring region was exclusively dominant, with neither key being pressed when mixtures were experienced. Each tracking episode lasted 80 sec (Experiments 1 and 2) or 60 sec (Experiments 3 and 4). All test conditions in each experiment were repeated four times with the order of conditions randomized within a block of trials. Enforced rest periods were interleaved between trials.

Trigger period is defined as the time elapsing between successive trigger presentations within the same eye (Figure 1). Our initial pilot observations suggested that the optimal trigger period for a given observer was dependent on that observer's average rate of rivalry alternations (a point verified in our main Experiments). Thus in Experiment 1, the effect of periodic triggers on rivalry dynamics within the monitoring region was assessed for trigger periods ranging from 2 to 6 sec. We also included conditions in which the contrast of the trigger increment was zero, meaning that the alternations in rivalry at the monitoring region were governed entirely by intrinsic neural events; these data provided for each observer an estimate of the mean and variance of dominance durations associated with the spontaneous perceptual alternations unaffected by external triggers. In Experiments 1, 3, and 4, the trigger distance (center of trigger to center of monitoring region) was always 1.5°, and in Experiment 2, three trigger distances (1.0°, 1.5°, and 2.0°) were used to determine whether perceptual switches at the monitoring region were systematically delayed dependent on trigger distance.

A total of nine observers (8 males, 1 female) including two of the authors participated in Experiment 1; both 22.5% and 40.0% contrast stimuli were examined for four observers, and for the other five observers, one of these two contrast levels was used. Seven of these observers, all male, participated in Experiment 2, and five observers (three observers participated in Experiments 1 and 2 with two new observers who never experienced binocular rivalry prior to this experiment) participated in Experiments 3 and 4. Except for the two authors, all other observers were naive to the purpose of the study. All had normal or corrected-to-normal visual acuity and normal stereopsis; all gave informed consent after thorough explanation of the procedures. All aspects of this study were approved by the Vanderbilt University Institutional Review Board.

Experiment 1: Details of periodic perturbation

The perceptual consequence of appropriately timed, repetitive triggers was obvious to all observers: the dominant pattern switched periodically between the two alternatives, and this periodicity was conspicuous in the observers' tracking records. Rather than comprising a series of unpredictable dominance durations (Fox & Herrmann, 1967), the periodic perturbation technique yielded a highly ordered series of dominance states (Figure 2). This outcome resembles what happens when the rival targets themselves are flickered in antiphase (Kim, Grabowecky, & Suzuki, 2006). The important difference is that here entrainment is being produced by stimulus events occurring elsewhere within the visual field and preceding the perceptual transitions within the monitoring region by many hundreds of milliseconds.

To quantify the salience of periodicity in perceptual switches in the time domain, we created an index termed the (probability) switch function that provides a succinct but comprehensive representation of the trigger's propensity to entrain dominance durations. As illustrated in Figure 2, we derived for each periodic trigger event a record of the rivalry state time-locked to that trigger and extending until the next trigger presented to the other eye. We then averaged all of those records to obtain the switch function for that observer tested on a given stimulus condition. Figure 3 shows representative, averaged switch functions for different trigger periods.

Three key characteristics of rivalry can be deduced from the switch function. First, the index specifies the likelihood of a change in perceptual state at each time following presentation of a trigger. When the timing of the

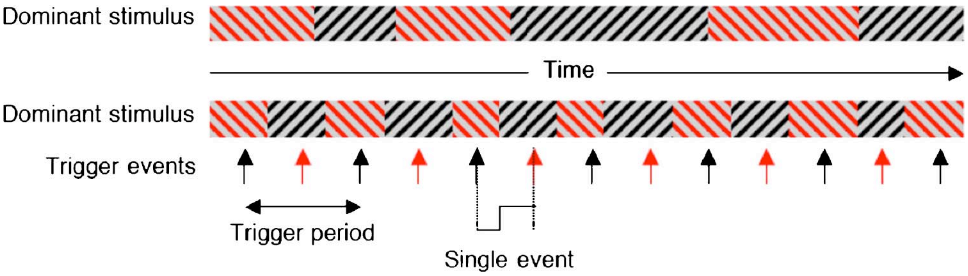

Figure 2. Perceptual alternations for rivalry and periodic perturbation. The upper time series represents perceptual alternations measured without periodic trigger presentations. Excerpt (~40 sec) from an 80-sec time series of fluctuations in rivalry dominance (denoted here with gray and red gratings) within the central, "monitoring" region of a pair of rival targets like those shown in Figure 1. Not shown are the very brief periods of mixed dominance between successive periods of exclusive dominance. The lower time series shows successive durations associated with presentation of periodic triggers at locations above and below the monitoring region. Triggers at these two locations are presented in antiphase, i.e., to one stimulus and then to the other (red arrows indicate triggers delivered to the rival target whose contours are oriented diagonally right; black arrows indicate triggers delivered to the diagonal left grating). Triggers are delivered independently of rival state, but rival states become entrained (with a phase lag) with the triggers for an optimal trigger period. From each extended period of rivalry tracking, the states of rivalry following each trigger (including mixtures) are recorded as a string of binary data (with mixed states equaling 0.5) that spans the period from one trigger to the next. All of those individual records are averaged to produce the switch function for that tracking sequence (see Figure 3).

local contrast increments is grossly out of synchrony with the observer's average rate of spontaneous rivalry alternations, the values defining the switch function fluctuate irregularly around a value of 0.5—switches in perceptual dominance occur irregularly relative to the periodic triggers. In contrast, for trigger periods more closely matching a given observer's alternation rate, the switch function more nearly resembles a step function—switches in perceptual dominance are closely time-locked to the trigger period. Second, the mean perceptual state of the switch function at the onset of trigger reveals the probability that a trigger was delivered during a suppression phase of rivalry, and the difference in amplitude across the perceptual switches reveals the effectiveness of triggers. Third, the switch function reflects the delayed perceptual switches in response to the triggers; an index of this latency can be derived by estimating the delay time where the switch function crosses the mean perceptual state equaling 0.5.

For any given observer, the optimal trigger period is defined as the value yielding a switch function most closely resembling a step function; this property is readily defined by the amplitude between the minima and maxima of the switch function. Large amplitude values mean that most triggers are being delivered during suppression phases of rivalry, with the triggers reliably inducing perceptual switches and with the incidence of spontaneous perceptual alternations being minimal.

Results from these measurements confirm what our pilot observations suggested: the optimal trigger period for a given observer is strongly related to that individual's mean dominance durations obtained from rivalry tracking records without trigger presentations (Figure 4). This is true regardless of the contrast of the rival stimuli, so all

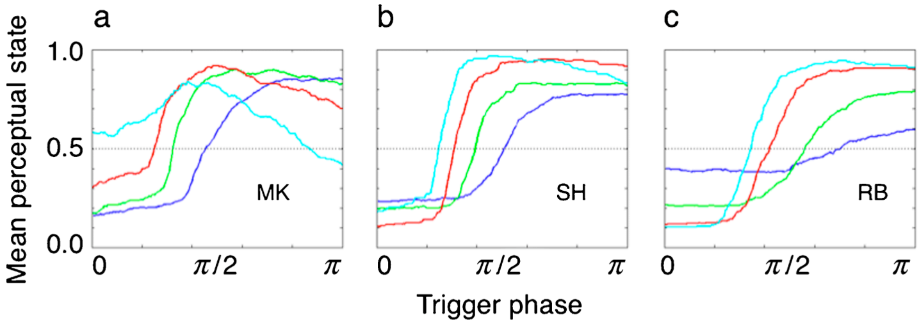

Figure 3. Switch functions for three representative observers (a–c) and for four different trigger periods (blue: 3 sec, green: 4 sec; red: 5 sec; cyan: 6 sec). A switch function expresses the probability (*y*-axis) that a given rival target is dominant at different times relative to trigger presentations (*x*-axis). Each switch function was created by averaging the sequences of tracking records, time-locked to the onsets of the triggers. Optimal trigger periods identified from these switch functions are 4 sec (MK), 5 sec (SH), and 6 sec (RB), respectively. Note that the number of tracking records comprising the single averaged switch function was 160, 128, and 106 for 4-sec, 5-sec, and 6-sec trigger periods, respectively.

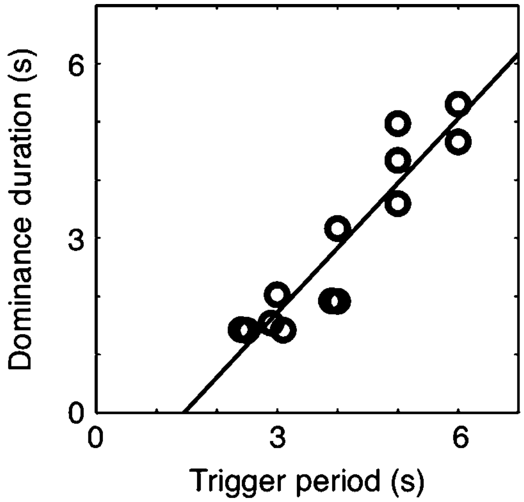

Figure 4. Optimal trigger period depends on mean dominance duration. Plotted are the optimal trigger periods derived from the switch function versus the mean dominance durations obtained when triggers are not presented. Each data point represents an observer. To avoid overlapping data points, three data points (at trigger periods of 2.5, 3, and 4 sec) are jittered horizontally. The regression line is approximately unity slope ($r = 0.92$).

contrast conditions were combined for analysis [$r = 0.92$, $t(11) = 8.33$, $p < 10^{-5}$]. Thus, the optimal trigger period must be specified individually, and our data suggest that a valid estimate for the optimal trigger period is a value approximately 1 sec less than the mean dominance duration for a given observer.

Experiment 2: Estimating traveling wave latency

Using the trigger period optimized for a given observer, we next collected tracking data under conditions where the distance between the triggers and the monitoring region was varied over trials, revealing evidence for traveling waves. Figure 5a shows the averaged switch function from seven observers at three different trigger distances. Notice that switch functions are shifted rightward as the trigger distance increases, as expected if the consequence of the trigger propagates from trigger location to monitoring region—this is the perceptual signature of a traveling wave. Figure 5b, summarizing the latencies at three trigger distances, shows that the latency increases linearly as a function of trigger distance. This pattern of results was seen in the results of each of the seven observers tested, and it was statistically significant as revealed by one-way repeated measure of ANOVA with three levels of trigger distance ($F(2,12) = 14.40$, $p < 0.001$).

One might suspect that it is necessary to use different trigger periods for the different trigger distances; for trigger positions closer to the monitoring region, the current state of the monitoring region will get perturbed a little earlier in time (relative to the time at which the state changed) than it will when the trigger positions are located farther away. But this time difference (Figure 5b, latency differences between the largest and smallest trigger distances are about 0.2–0.5 sec) is an order of magnitude shorter than the trigger period used to evoke perceptual waves (Figure 4, trigger periods are about 3–6 sec) and, therefore, inconsequential to our estimates.

In addition to the rightward shift in switch functions, the mean perceptual state of the switch function becomes closer to 0.5 as the trigger distance increases, implying that repetitive triggers closer to the monitoring region more reliably promote perceptual switches. This second observation is not surprising because several sources of variability are introduced by increasing the trigger distance, including the increased likelihood of spontaneous perceptual switches.

Traveling wave speed covaries with alternation rate

As mentioned earlier, an advantage to the periodic perturbation technique is the capability of comparing the stochastic dynamics of binocular rivalry to the temporal properties of the perceptual waves simply by omitting or presenting periodic perturbations while the observer performs the same task. Using this strategy, we reexamined the data from the previous two experiments to learn whether observers who exhibit relatively slow rivalry alternations experience traveling waves whose

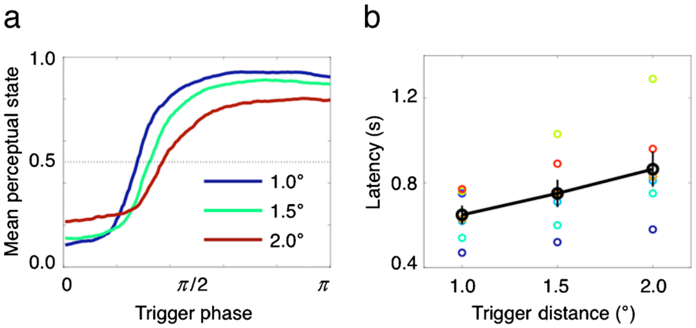

Figure 5. Perceptual switch latencies depend on trigger distance. (a) Averaged switch function from seven observers. The three curves are switch functions obtained from three trigger distances (1°, 1.5°, and 2°). Switch functions are shifted rightward as trigger distance increases. (b) Switch latencies at three trigger distances. Latency is derived from individual switch functions by estimating the time value at which the switch function crosses the 0.5 line. The average latency (black) increases linearly as the trigger distance increases, evidencing perceptual waves during binocular rivalry. Error bars, *SEM* across observers. Small symbols indicate latencies of the individual observers with a different color for each of the 7 observers.

speeds differ from the waves experienced by fast alternators.

We found that the inferred speeds of traveling waves are faster for observers with faster alternation rates. Figure 6a plots for each of seven observers the estimated speed of traveling wave as a function of that individual's alternation rate (reciprocal of mean dominance duration for both eyes). We estimated traveling wave speed by regressing latency as a function of trigger distance using the data set summarized in Figure 5b. The inverse of the slope of that regression provides the traveling wave speed. The values of alternation rate associated with spontaneous perceptual alternations (i.e., tracking periods without perturbations) were obtained from the experiment measuring traveling wave dynamics while varying trigger period for each observer. With increasing alternation rate, the speed of traveling waves tended to increase [$r = 0.78$, $t(5) = 2.22$, $p < 0.05$]. One prediction of this correlation between the speeds of traveling waves and alternation rates is that the latency of the traveling waves should monotonically decrease with increasing alternation rate (i.e., with decreasing dominance duration). As shown in Figure 6b, this prediction is confirmed by plotting the latencies of the traveling waves as a function of alternation rate using the same data set used to create Figure 4 [$r = -0.76$, $t(11) = 3.45$, $p < 0.01$]. These two analyses, then, reveal a heretofore unrealized pattern of dynamics associated with rivalry: slow alternators indeed experience slower traveling waves during binocular rivalry compared to fast alternators.

This correlation between alternation rate and traveling wave speed suggests two reasons why traveling waves should be perceptually more salient for slow alternators. First, the waves, being slower, are simply more conspicuous as a previously suppressed stimulus emerges from dominance and spreads over the extent of the stimulus field. Second, it is more likely that the emerging wave will complete its engulfment of the stimulus field before a spontaneous change in state disrupts the smooth transition. For fast alternators, however, spontaneous perceptual alternations are more frequent, making it more difficult to distinguish unusually fast traveling waves from spontaneous perceptual alternations. This tendency for spontaneous alternations to mask the wave transitions can be minimized to some extent by higher rates of periodic perturbation, but this will not slow the waves experienced in this situation.

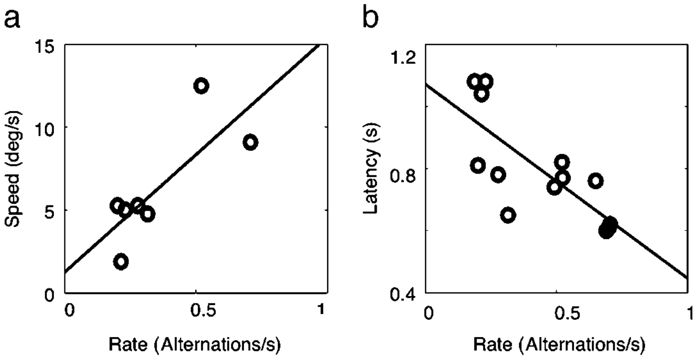

Figure 6. Traveling wave speed covaries with alternation rate. (a) Using the same data for creating Figure 5b, the speed of traveling waves was estimated and plotted as a function of alternation rate (reciprocal of the mean dominance duration). (b) Using the same data for creating Figure 4, the latency was estimated and plotted as a function of alternation rate.

Experiment 3: Contour orientation influences traveling wave speed

In five observers we asked whether perceptual waves inferred using periodic perturbation travel faster over collinear contours than over orthogonal contours. Such a difference in wave speed was observed by Wilson et al. (2001), so we were motivated to learn whether our new technique was sufficiently sensitive to reveal this characteristic.

To pursue this question, we used rival targets just like those shown in Figure 1, with the exception that one of the two eyes' diagonal gratings was replaced with either a vertical grating (collinear condition) or a horizontal grating (orthogonal condition). Each tracking session lasted 60 sec and the tracking records used to create the switch function were limited to those associated with triggers appearing within the vertical or horizontal rival patterns. Otherwise, the monitoring region was the same size and location as before, and the task was the same (i.e., tracking rivalry alternations experienced within the monitoring region).

Using periodic perturbation we replicated the faster speed of perceptual waves traveling over collinear contours. The switch functions for the collinear and orthogonal conditions, shown in Figure 7a, readily show that triggers delivered to the vertical grating produce a switch function shifted to the left relative to the switch function produced by triggers delivered to the horizontal grating; this pattern of results was reliably seen for each of the individual observers. These results, while not unanticipated, verify that the technique is sufficiently sensitive to register this interesting effect of stimulus configuration.

Experiment 4: Traveling waves can jump gaps

Using the discrete trial technique, several laboratories have found that a gap placed in one rival target tends to retard, and sometimes abolish, the traveling wave's arrival at a monitoring point on the other side of the gap relative to the location where that wave was triggered (Kim, Blake, & Lee, 2005; Wilson et al., 2001). Can periodic perturbation reveal this effect of a gap on traveling waves? To find out we placed a gap at the middle of one rival

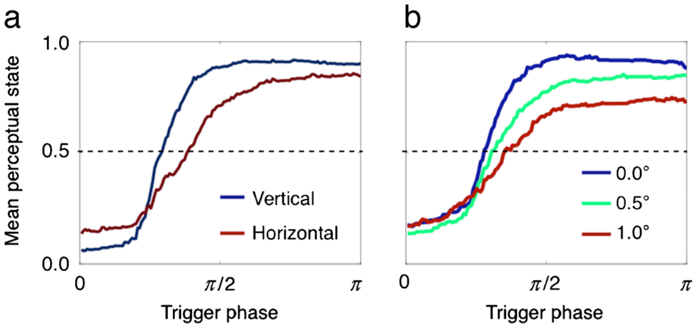

Figure 7. (a) Contour orientation influences traveling wave speed. Blue curve, averaged switch function associated with traveling waves emerging from a vertical grating (collinear with the direction of propagation). Red curve, averaged switch function for horizontal grating (orthogonal to the direction of propagation). The blue curve is shifted leftward, implying that the speed of traveling waves is faster for the collinear grating condition compared to the orthogonal grating. (b) Traveling waves can jump gaps. Averaged switch function associated with the traveling waves emerging from the vertical grating at three gap sizes (blue: 0.0°, green: 0.5°, and red: 1.0°). The modulation in the switch function systematically decreases, with increasing gap size.

target, in the region where the monitoring region is demarcated in Figure 1. The size of the gap was either 0.5° or 1.0°, and for these measurements the observer monitored the region of rivalry located just above/below the gap opposite (below/above) to the location where the periodic trigger occurred for that rival target. The location of monitoring regions was, therefore, displaced from the center of stimuli by 1.0°.

The switch functions become shallower with gap size (Figure 7b), indicative of the decreased probability of synchronized state changes in the monitoring region associated with the trigger periodically presented on the other side of the gap. The incidence of perceptual waves, in other words, is inversely related to the size of the gap in the rival stimulus within which the wave was triggered. There is also some indication that latencies may increase with gap size, as if wave must pay a time penalty when jumping a gap. This interpretation is tentative, however, since latency is more difficult to estimate for the larger gap sizes because of the reduced incidence of wave.

Evidence for perceptual waves during binocular fusion

Periodic perturbation clearly triggers perceptual waves that culminate in transitions in dominance under conditions for which the two eyes receive dissimilar visual stimulation throughout the visual display—the perceptual waves associated with transitions in dominance are visibly evident. Can periodic perturbation reveal the existence of traveling waves originating within regions of the visual field in which the two eyes receive concordant, not rival, binocular stimulation?

To answer this question, we created stimulus arrays in which rivalry within the middle of the display was flanked by stimuli that promoted stable binocular single vision (Figure 8a). The contrast increments constituting the triggers were presented within these regions of binocular fusion, with the trigger presented to one eye in the top-half of the array and the trigger presented to the other eye in the bottom half of the array. For each observer the trigger period was based on the mean dominance duration for that observer estimated from tracking data obtained without trigger presentations.

Experiment 5: Waves generated within regions of binocular fusion

Five male observers including two of the authors participated in this experiment. Two vertically elongated patterns (0.8° × 5°) were presented separately to the two eyes (Figure 8a). Located in the center of these patterns were the rival stimuli, orthogonally oriented, diagonal sinusoidal gratings whose angular dimensions were 0.8° × 0.8°. The upper and lower regions of the rest of the patterns were identical in left- and right-eye views. The contrast of all parts of both patterns was 22.5% and the triggers (small regions of contrast increment) were presented 1.0° from the center of the rivalry region. Other aspects of stimuli and procedure were the same as those used in Experiment 2.

There is clear evidence for entrainment of dominance switches driven by triggers delivered to regions of the

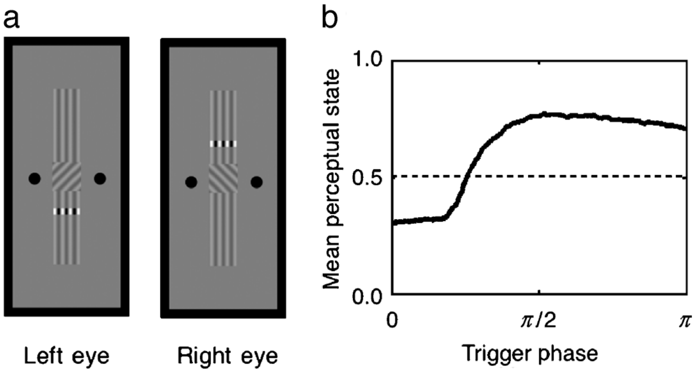

Figure 8. Perceptual waves during binocular fusion. (a) Stimuli used for Experiment 5. Central region of binocular rivalry (0.8° × 0.8°) is flanked above and below with binocularly matched pattern (vertically oriented grating). (b) Averaged switch function from four observers; rivalry dominance is modulated in phase-lagged synchrony to the triggers presented within regions receiving non-rival, binocularly matched stimuli.

stimulus display where patent rivalry was not occurring. Figure 8b shows the averaged switch functions from five observers. The amplitude of modulation of the switch function is statistically significant [$t(4) = 10.15$, $p < 0.01$]. This result suggests that triggers can generate traveling waves of neural activity that spread from areas of binocular fusion to areas of binocular rivalry. It remains for future work to determine whether the characteristics of this spread (likelihood and latency) are equivalent to those measured under conditions of patent rivalry, and whether the spread depends on the similarity between spatial features defining the rival targets and the regions of fusion.

Experiment 6: Does rivalry occur within the region of fusion?

One could argue that the region of matched binocular stimuli within which the triggers occur are, in fact, undergoing unobservable rivalry that has spread from the central region containing rival stimulation (e.g., Kaufman, 1963). We find that unlikely in the case of our stimuli, because other work shows that fusion takes precedence over rivalry (Blake & Boothroyd, 1985). Still, we felt it worthwhile to determine whether suppression might be spreading to the region of identical binocular stimulation under the conditions tested here. To test for spread of suppression, we employed a test-probe technique that is highly sensitive to the perceptual state of a given region of the visual field (Blake & Camisa, 1978; Fox & Check, 1968; O'Shea, 1987). Specifically, we measured contrast increment detection thresholds of a trigger delivered within a region of binocular fusion contingent on the state of rivalry within the central monitoring where rivalry was evident. Elevated contrast thresholds for trials when the central region's stimulus was suppressed, relative to when that region was dominant, would constitute evidence for spread of suppression from that region of rivalry into the region of binocular fusion.

In this experiment, all aspects of the stimuli were the same with those in Experiment 5, i.e., the stimulus patterns at the regions of binocular fusion were identical for both upper and lower regions of the arrays, with rival stimulation confined to the small, central region. Observers waited until a designated rival pattern achieved dominance before initiating a brief (200 msec), abrupt contrast increment presented to one eye either 1.0° above or 1.0° below the center of the region of rival stimulation, i.e., the same location as the triggers used in the rivalry

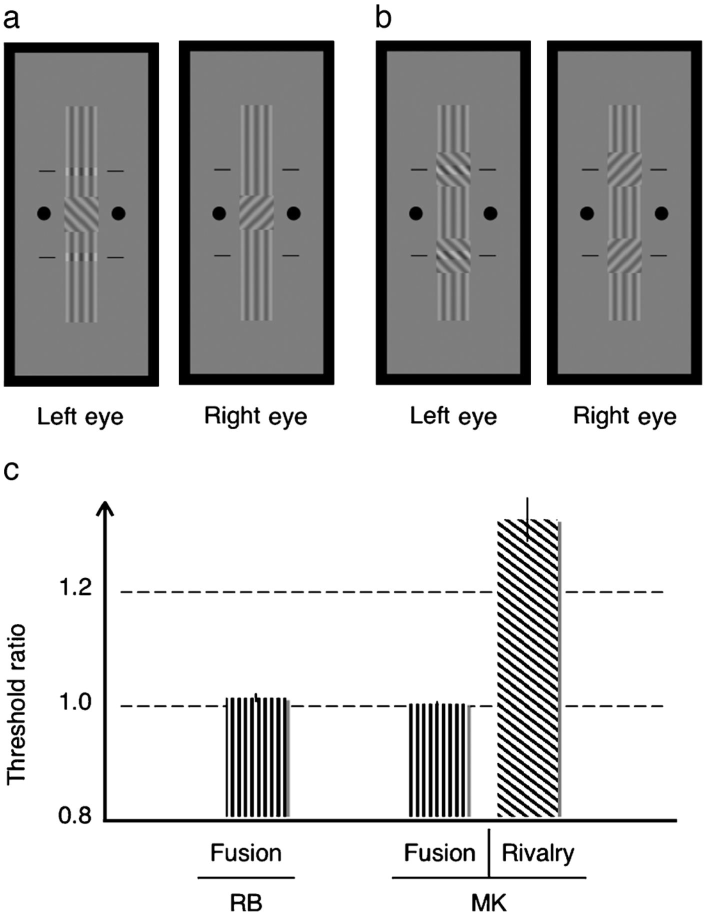

Figure 9. Probe experiments to determine whether suppression spreads from a region of rivalry to a region of fusion. (a) Stimulus configuration in which a brief probe (contrast increment) was presented to a region of fusion contingent on the rival state produced by a pair of rival targets within the central monitoring region. On each trial the probe appeared either above or below this monitoring region, some times when the left eye's central rival target was dominant and other times when that rival target was suppressed. During a given block of trials, two randomly interleaved staircases varied the magnitude of the contrast increment for the dominance and for the suppressed trials. (b) Stimulus configuration in which a brief probe (contrast increment) was presented to a region of rivalry contingent on the rival state for two pairs of rival targets located above and below a region of fusion. The observer triggered probes contingent on a given orientation being dominant (or being suppressed) within both regions of rivalry. Separate staircases varied the magnitude of the contrast increment for dominance and suppression trials. (c) Shown by the vertically filled histograms (two observers) are estimates of relative threshold elevation (suppression threshold/dominance threshold) for probes presented to a region of fusion (configuration shown in panel a); these estimates are based on eight staircases for each of the two rival states, and the results show no effect of rivalry state on sensitivity within the region of fusion where the probes were delivered. Shown by the diagonally filled histogram (one observer) is relative threshold elevation for probes presented to a region within which rival targets in both locations are dominant or are suppressed (configuration shown in panel b). As expected, thresholds during suppression are elevated significantly, relative to dominance, when delivered to a suppressed eye/target.

experiment (Figure 9a). A two up/one down staircase procedure was used to vary the magnitude of the contrast increment over trials, and the threshold level for a given staircase was estimated using a bootstrapping procedure after 13 reversals (Wichmann & Hill, 2001). Each test session consisted of two interleaved staircases, one devoted to contrast increments presented when the left-eye diagonal grating was dominant and the other devoted to increments presented when the left-eye diagonal grating was suppressed. Color bit stealing with range optimization was used to increase the luminance resolution of the monitor (Tyler, 1997). Trials for the two staircases were randomly interleaved, and thus, observers could not know whether the probe was being presented to the dominant or to the suppressed eye, nor were observers aware which eye received the probe when it did briefly appear, even when its contrast was well above threshold. To maximize statistical power, eight staircase threshold estimates were obtained for dominance and for suppression. Two of the authors participated in this grueling experiment.

For neither observer were increment detection thresholds during dominance and suppression significantly different [RB: $t(7) = 2.16$, $p = 0.07$; MK: $t(7) = 1.50$, $p = 0.18$], indicating that perceptual suppression within an eye did not spread to the region of binocular fusion (Figure 9c).

For one observer (MK) we measured increment thresholds at the same locations above and below the central region, this time with those upper and lower regions containing rival stimuli of 0.8° × 0.8° in size (Figure 9b); trials were triggered contingent on the state of dominance within both of those two rivalry regions (i.e., when a given orientation was dominant at both locations). Four staircases were devoted to trials on which a given grating was dominant and four other staircases were devoted to trials on which that grating was suppressed. Thresholds from these measurements showed that increment thresholds were elevated approximately 0.3 log units when the probes were delivered to the suppressed stimulus, relative to thresholds delivered to that same stimulus when it was dominant [$t(3) = 9.77$, $p < 0.01$]. This outcome merely confirms that a significant elevation in threshold should have been measurable under conditions of matched binocular inputs if suppression were spreading within those regions. In other words, we find no evidence for spread of suppression to the regions of the dioptic stimulus patterns where perturbations successfully produced entrainment of centrally viewed, dichoptic rival targets.

Discussion

Periodic perturbation provides an effective, sensitive technique for triggering perceptual waves that are evident in the dynamics of binocular rivalry. The technique is very easy for observers to understand and perform, for they are being asked to do nothing more than what a host of other rivalry studies require: track fluctuations in rivalry within a small region of the visual field. By merging the original trigger technique (Wilson et al., 2001) with rivalry tracking, periodic perturbation makes it possible to relate rivalry dynamics of waves to rivalry dynamics in the absence of triggers.

We discovered that the speed of traveling waves is correlated with alternation rate (the reciprocal of the mean dominance duration), a novel observation with implications for neural models of rivalry. Specifically, all recent models of rivalry account for the stochastic nature of rivalry alternations, and their dependence on stimulus strength (Levelt, 1965), using the concepts of neural adaptation and intrinsic noise (Kalarickal & Marshall, 2000; Kim, Grabowecky, & Suzuki, 2006; Laing & Chow, 2002; Lankheet, 2006; Lehky, 1988; Moreno-Bote, Rubin, & Rinzel, 2007). Traveling waves, on the other hand, have been successfully modeled using cooperative (excitatory) and competitive (inhibitor) connections among spatially distributed pools of neurons representing the two alternative rival stimuli (Stollenwerk & Bode, 2003; Wilson, 2003; Wilson et al., 2001). Based on the work presented here and elsewhere (Kang, 2009), we can now begin to see that these two aspects of rivalry—dynamics and transition states—are interdependent in ways that depend on the spatial extent of the region within which rivalry is occurring. And as discovered in Experiment 5, those spatial interactions may generalize beyond regions of the visual field in which rivalry is occurring.

Furthermore, we discovered that wave-like behavior can be generated within regions of the visual field where rivalry is not occurring. Specifically, we found that monocular triggers presented within regions of the displays containing matched binocular contours promote perceptual dominance of the rival stimuli within the central part of those displays. This outcome implies that a given trigger evokes neural events that propagate more strongly to the rival target imaged in the same eye receiving that trigger than to the rival target imaged in the other eye. Evidently, then, the neural events underlying entrainment carry eye of origin information. Otherwise, a given trigger would have impacted both rival targets equivalently, thereby, precluding eye-specific entrainment.

What is the mechanism responsible for the influence of a contrast increment delivered in one part of the visual field on the delayed change in perceptual dominance in another region of the visual field? It is natural to wonder whether shifts in attention caused by triggers might be the source of these periodic perceptual changes (Baylis & Driver, 1992; Egly, Driver, & Rafal, 1994). According to this hypothesis, attention is ordinarily focused on the dominant stimulus at the monitoring area, but the brief contrast increment above or below that stimulus provides an exogenous cue that draws attention to the location of the increment (Ling & Carrasco, 2006). This temporary removal of attention from the currently dominant stimulus, in turn, causes a switch in dominance by lowering the effective stimulus strength of that dominant stimulus. For several reasons, however, we are disinclined to attribute perceptual entrainment to putative switches in attention. For one thing, triggers occur repetitively throughout the extended tracking period and should, therefore, lose their novelty and, presumably, some of their power to commandeer exogenous attention (Theeuwes, 1991; Yantis & Jonides, 1990). In fact, however, entrainment does not dissipate throughout an observation period. For another, the attention hypothesis cannot explain why the exogenous cue in the binocular fusion condition (Figure 8) increases the perceptual dominance of the stimulus pattern presented within the same eye where the trigger is presented—in this condition, the feature receiving the trigger is different from either of the rival targets (ruling out differential feature-based attention), and moreover, the trigger's effect is specific to the eye receiving that trigger. Nor can the attention hypothesis explain the systematic phase shift in the switch function with the location of the trigger, unless one posits that it is the return of attention to the monitoring region that triggers a switch in dominance. This is not to say, however, that attention plays no role in the instigation of traveling waves. Perhaps observers need to see the trigger for it to generate a dominance wave, in which case failure to see the trigger (e.g., because of inattentional blindness) would weaken or abolish its effectiveness. In our experiments we did not explicitly instruct observers to attend to the trigger events, but that does not mean they ignored them. Attention's influence on a trigger's effectiveness remains to be determined, and with the addition of a distracting task the periodic perturbation technique should be suitable for answering that question.

Rather than shifts in attention, we are inclined to believe that the triggers' influence on rival stimuli is carried by a wave of excitatory activity propagating from the trigger point to the monitoring region. This kind of propagation has been invoked by Grossberg and Mingolla (1985) to account for traveling waves during perceptual filling-in, neon color spreading, and illusory contour formation, and it is the mechanism posited by Wilson et al. (2001) to explain traveling waves in binocular rivalry (see also Lee et al., 2005, 2007). Our results go beyond those earlier rivalry studies in suggesting the existence of waves under conditions of binocular fusion. In general, propagation within interconnected neurons is broadly consistent with the neural diffusion process proposed by Ermentrout and Kleinfeld (2001), and it embodies the essence of the field theory proposed by Gestalt Psychology. Viewed in this way, traveling waves of dominance offer a unique opportunity for studying dynamics of contextual effects and their role in perceptual organization.

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