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Overlapping features can be parsed on the basis of rapid temporal cues that produce stable emergent percepts

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Abstract

When two overlapping displays alternate rapidly, it is difficult to resolve the temporal coincidence of objects, parts, or features. However, under certain conditions (at least for luminance-based stimuli) rapid temporal coincidence can be detected on the basis of stable emergent percepts in which parts that oscillate in phase appear more strongly grouped than (or appear distinct from) parts that oscillate out of phase. These emergent percepts appear as depth segregation, enhanced slow orientation rivalry, and oriented shimmer (a new phenomenon that cannot be explained in terms of conventional apparent motion or temporal contrast illusions). These percepts resulted in up to an eightfold decrease in the coincidence detection threshold (alternations as fast as 20 ms/frame or 25 Hz) relative to control conditions that did not yield them; these sensitivity enhancements are unlikely to be due to temporal probability summation. The results provide psychophysical evidence that temporal-phase information can contribute to the parsing of overlapping patterns.

Keywords: Flicker; Orientation; Oscillation; Rivalry; Shimmer; Synchrony; Temporal phase

1. Introduction

Temporally correlated responses occur among cortical cells that have similar receptive field properties (e.g., cells that share orientation tuning, color opponency, and ocular dominance) as well as among cells that respond to image parts that share common motion (e.g., Gilbert, 1992; Gray, Konig, Engel, & Singer, 1989; Ts'o & Gilbert, 1988; see Gray, 1999, and Singer, 1995, for reviews). The neural response synchronization measured in these studies (e.g., using the cross-correlation technique with "shuffle correction") is presumably intrinsic in that it is not driven by the dynamics of the stimuli. The role of intrinsic response synchronization has received a great deal of research attention because it might potentially contribute to processes underlying perceptual binding and the grouping of visual features by way of temporally tagging cells responding to various features of the same object (potentially across different cortical visual areas). Indeed, if it could be conclusively shown that neural responses are generally more correlated (synchronized) for perceptually grouped features than for perceptually separate features, then this would suggest that intrinsic synchronization of neural responses plays a critical role in generating the conscious perception of image grouping. However, the evidence to date linking intrinsic neural response synchronization and perceptual grouping is both indirect and controversial (e.g., Lamme & Spekreijse, 1998; see Shadlen & Movshon, 1999, for a review).

Though it would be most interesting to directly test the potential role of intrinsic neural response synchronization in human perception, it is impractical to measure neural response synchronization as a function of the degree of perceptual grouping using human observers. Researchers instead have taken an indirect approach by using temporally modulated stimuli, attempting to simulate synchronized neural responses. Since cortical cells (in V1 and V2) tend to follow rapid stimulus oscillations (even beyond 20 Hz or

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25 ms/frame; e.g., Foster, Gaska, Nagler, & Pollen, 1985; Hawken, Shapley, & Grosof, 1996; Levitt, Kiper, & Movshon, 1994), synchronized neural responses can be induced by rapidly oscillating stimuli. However, it must be emphasized that there is no evidence that the coherent modulation of neural responses induced by oscillating stimuli in any way resembles the intrinsic response synchronization which may not be oscillatory, and which presumably mediates perceptual grouping of *static* stimuli. Despite this fundamental uncertainty, oscillating stimuli have been used in psychophysical studies to determine whether stimulus-driven neural response synchronization can at least potentially contribute to image grouping and segmentation.

Specifically, it has been hypothesized that parts that oscillate synchronously (or in phase) should tend to group together, whereas parts that oscillate asynchronously (or out of phase) should tend to segregate. This hypothesis has been tested primarily by examining whether feature-based (e.g., orientation-based) figure–ground segregation was facilitated when the texture elements in the figure and the ground regions were oscillated in opposite phase relative to when both regions (or arbitrarily chosen regions) were oscillated in phase. The results have been equivocal; figure–ground segregation was modulated by stimulus oscillation in some studies (e.g., Leonards, Singer, & Fahle, 1996; Usher & Donnelly, 1998, 2001) but not in others (e.g., Beaudot, 2002; Kiper, Gegenfurtner, & Movshon, 1996). Observers' ability to group and segment images on the basis of temporal information was also measured more directly. For example, Forte, Hogben, and Ross (1999) had observers detect a local texture region that oscillated (in contrast polarity) in opposite phase from the rest of a texture field, demonstrating that observers could segment a region on the basis of opposite temporal phase (also see Fahle, 1993; Leonards & Singer, 1998; Rogers-Ramachandran & Ramachandran, 1998). Parton, Donnelly, and Usher (2001) biased a square array of discs into grouping as rows or as columns by oscillating (on and off) alternate rows or columns of discs out of phase. However, as suggested by the authors, both of these results can be explained on the basis of selective activation of early spatiotemporal-separable detectors (e.g., Adelson & Bergen, 1985; DeAngelis, Ohzawa, & Freeman, 1993) and of orientation detectors (likely involving colinearity-based integration; e.g., Field, Hayes, & Hess, 1993; Kapadia, Ito, Gilbert, & Westheimer, 1995; Polat & Sagi, 1993), without requiring an explanation based on neural response synchronization.

In the present study, we also examined the potential role of temporal information in image grouping and segregation. However, our investigation differed from the previous studies in that we examined the role of temporal phase [1] in segregating spatially *overlapping* patterns. We hypothesized that because overlapping patterns cannot be readily segregated by spatial coding (i.e., assigning separate spatial regions to separate objects), temporal coding may be particularly important for these patterns.

In a relevant study, Holcombe and Cavanagh (2001) demonstrated fast-rate binding of color (or brightness) to orientation when the two features rapidly coincided *within a single entity*. For example, when a red (or light) grating tilted to the right was alternated with a green (or dark) grating tilted to the left (the sum being a checkerboard pattern with diamond-shaped elements), the orientation of the red (or light) grating could be detected even when the alternation rate was rapid (27–14 ms/frame or ~18–36 Hz for 75% accuracy). This fast-rate binding of color to orientation occurred presumably because the binding could be accomplished by V1 and V2 neurons locally tuned to specific combinations of color and orientation, multiplexing color and orientation (e.g., Ts'o & Gilbert, 1988; Ts'o & Roe, 1995); for example, binding of red to rightward tilt (within a red rightward tilted bar) could be signaled by activation of a cell that prefers both red color and rightward tilt. Similarly, brightness and orientation could be encoded simultaneously (as light bars or dark bars) by ON- and OFF-type orientation-tuned cells in V1 and V2 (e.g., Foster et al., 1985; Hubel & Wiesel, 1968). Indeed, Holcombe and Cavanagh (2001) found that orientation–color (or brightness) coincidence detection required a relatively slow frame rate (approximately 200 ms/frame or 2.5 Hz) when orientation and color (or brightness) alternated in adjacent regions, where multiplexing cells could not mediate performance. Here we demonstrated that even when feature grouping was unlikely to be mediated by specific cells that multiplex the features to be bound, rapid and repeated coincidences of overlapping shapes could be detected, under appropriate conditions, on the basis of stable emergent percepts.

Basically, the stimuli we used coupled alternating achromatic orthogonal gratings with discs that coincided with only one of the two gratings (Fig. 1a). Because the discs were colored red against the gray bars, were orientation neutral (thus, orientation–color multiplexing cells should not differentially respond to these stimuli), and were presented at intersections of the two gratings, they should not have preferentially grouped with either grating on the basis of feature similarity or proximity. Consequently, repeated temporal coincidence

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[1] Here we use the term "temporal phase" to refer to the fact that image onsets were in phase for features presented within the same display frame, but out of phase for features presented in alternate display frames. Though all of our stimuli were periodic, whether periodicity played any critical role in generating the reported emergent percepts beyond the synchrony and asynchrony of onsets (and offsets) is an empirical question for future studies.

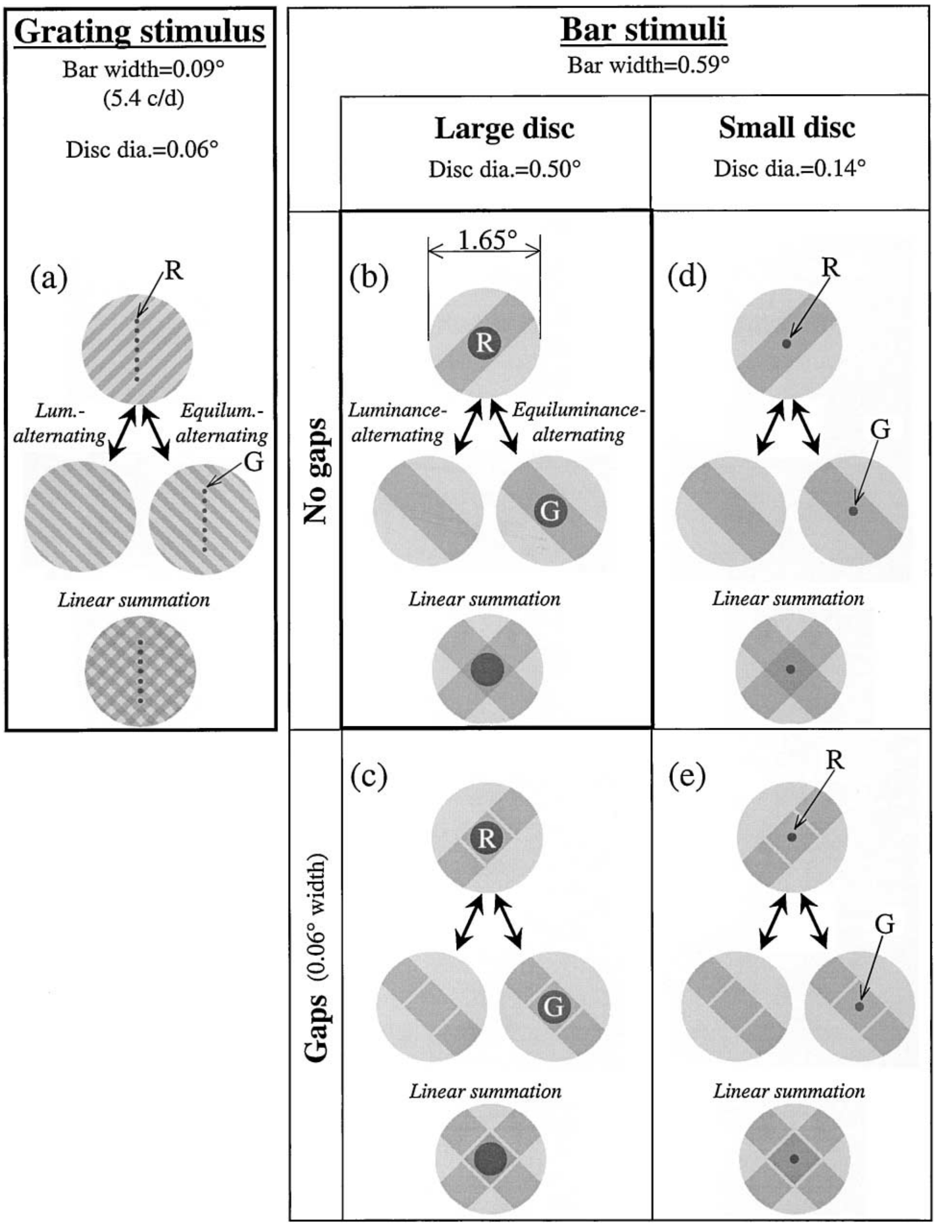

Fig. 1. The stimuli: (a) grating-with-vertical-array-of-small-discs, (b) continuous-bar-with-large-disc, (c) gapped-bar-with-large-disc, (d) continuous-bar-with-small-disc, and (e) gapped-bar-with-small-disc. For each stimulus, the bar (or grating) containing the red disc(s) either alternated with the bar (or grating) with no disc (luminance-alternating condition; see left arrows), or alternated with the bar (or grating) containing the green disc(s) (equiluminance-alternating condition; see right arrows). Note that the disc(s) was always presented in the intersection(s) of the bars, which remained static because there was no inter-stimulus-interval between the display frames (see illustrations under *Linear summation*).

(or temporal phase) provided the only information for deciding which grating orientation coincided with the discs. We hypothesized that repeated coincidences might be integrated into some form of stable emergent percept (e.g., a grouping of parts that oscillate in coherent phase), allowing observers to detect the disc-orientation coincidence (i.e., detection of which grating orientation repeatedly coincided with the discs) even when alternation rates were too fast to resolve individual frames. We would then take the existence of such emergent percepts as evidence that the visual system could utilize information carried by rapid temporal phase to facilitate stable image grouping and segregation. Here, we report two cases of these emergent percepts, one induced by rapidly alternating gratings (Fig. 1a) and the other induced by rapidly alternating single bars (Fig. 1b–e). Though the two stimuli were similar except for the number of bars and their spatial frequency contents, they produced qualitatively different forms of emergent percepts, (1) *enhanced orientation rivalry* for the orthogonal gratings and (2) *oriented shimmer* for the orthogonal bars.

When two orthogonally oriented gratings (e.g., a left diagonal and a right diagonal) of moderate spatial frequency are statically (and monocularly) superimposed, one or the other orientation tends to appear stronger (i.e., to appear higher in contrast) at any given moment. The relative strengths of the two orientations slowly and spontaneously alternate over time (e.g., Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973; Campbell & Howell, 1972; Wade, 1975). We found that this slow monocular orientation rivalry was enhanced, such that the perceptual dominance of each grating appeared more salient, when the two gratings were rapidly alternated (60–40 ms/frame or ∼8–12 Hz); a similar observation was also noted by Holcombe and Cavanagh (2001). This phenomenon is consistent with the possibility that alternation of overlapping patterns might facilitate the grouping of parts that oscillate in phase and the segregation of parts that oscillate out of phase. For example, rapid alternation might facilitate orientation rivalry by enhancing image coherence within each orientation component due to synchronized onsets while reducing image coherence between the two orientation components due to out-of-phase onsets. Enhanced slow orientation rivalry might thus indicate that the visual system keeps the two overlapping gratings separated by utilizing the opposite neural temporal phase corresponding to the two gratings; perceptual dominance might shift from one orientation to the other when visual awareness shifts from being more attuned to one temporal phase to being more attuned to the other. If this enhanced orientation rivalry is indeed due to grouping by coherent temporal phase, when the disc-present orientation is in the dominant phase, the discs may appear to be grouped with, or firmly fixed on, the grating oscillating in phase, whereas when the disc-absent orientation is in the dominant phase, the discs may appear less visible or weakly associated with the grating bars (see Fig. 2b).

The second stable emergent percept was a novel perceptual phenomenon which we term "oriented shimmer". This phenomenon occurred when alternating single bars were used instead of alternating gratings. Unlike orthogonal gratings, statically superimposed orthogonal bars are poor stimuli for producing monocular orientation rivalry; they overlap only at the center and the global perception of an "X" is stable. Thus, when orthogonal single bars were rapidly alternated, no apparent orientation rivalry was observed. Instead, the bars appeared to shimmer due to rapid flicker. Interestingly, when the central disc was presented synchronously with one of the bars, a portion of this shimmer became oriented, rapidly jittering along a specific bar (i.e., the bar having heterodirectional changes in luminance; see Experiments 2 and 3, and Section 7). The phenomenon was thus termed oriented shimmer. Although oriented shimmer does not explicitly generate a perceptual grouping of the disc with the coincident bar orientation as in the case of the enhanced slow orientation rivalry, the results reported here suggest that oriented shimmer is also a stable emergent percept that reliably covaries with the disc-orientation association defined by temporal phase (see Fig. 2c).

We hypothesized that if enhanced orientation rivalry (for the grating stimulus) and oriented shimmer (for the bar stimulus) indeed represented stable emergent percepts based on rapid processing of temporal phase, they should allow effective detection of disc-orientation coincidence even when the display alternation rate was too rapid to resolve individual frames.

2. Experiment 1A

2.1. Detection of rapid coincidence using stable emergent percepts

Stimuli consisted either of alternating orthogonally oriented gratings or of single bars (left diagonal and right diagonal). Multiple discs (for the grating stimulus to enhance the visibility of small discs; Fig. 1a) or a single disc (for the bar stimulus; Fig. 1b) repeatedly coincided with one of the two orientations (Fig. 3a). Observers were required to determine which grating or bar orientation coincided with the discs. The frame rate was varied from slow (where individual frames were clearly visible) to fast, the point where performance dropped to chance levels. The frame rate was varied from slow to fast rather than randomly because we wished to measure the effectiveness of the temporal-phase-based stable emergent percepts when observers were optimally attuned to the appearance of those percepts. The frame rate yielding 75% correct performance was used as the threshold frame rate for detecting the disc-orientation coincidence. We note that discs were always presented at the intersection(s) of the alternating bars (see illustration under "*Linear summation*" in Fig. 1a and b). Because display frames were alternated with no inter-stimulus interval, the diamond-shaped region(s) immediately surrounding the disc(s) remained static. Thus, in order to determine which orientation contained the discs, observers had to group the discs with the non-intersecting parts of the coincident bar(s) using only temporal information. The particular orthogonal gratings and single bars shown in Fig. 1a and b were used as the primary stimuli because pilot studies indicated that these stimuli reliably produced the emergent percepts of enhanced orientation rivalry (for the grating stimulus), and oriented shimmer (for the bar stimulus).

Because oriented shimmer appeared to be a novel phenomenon, we performed some basic parametric manipulations to begin to understand its potential mechanisms (see Experiment 3 and Section 7 for its potential relations to other phenomena such as bistable motion,

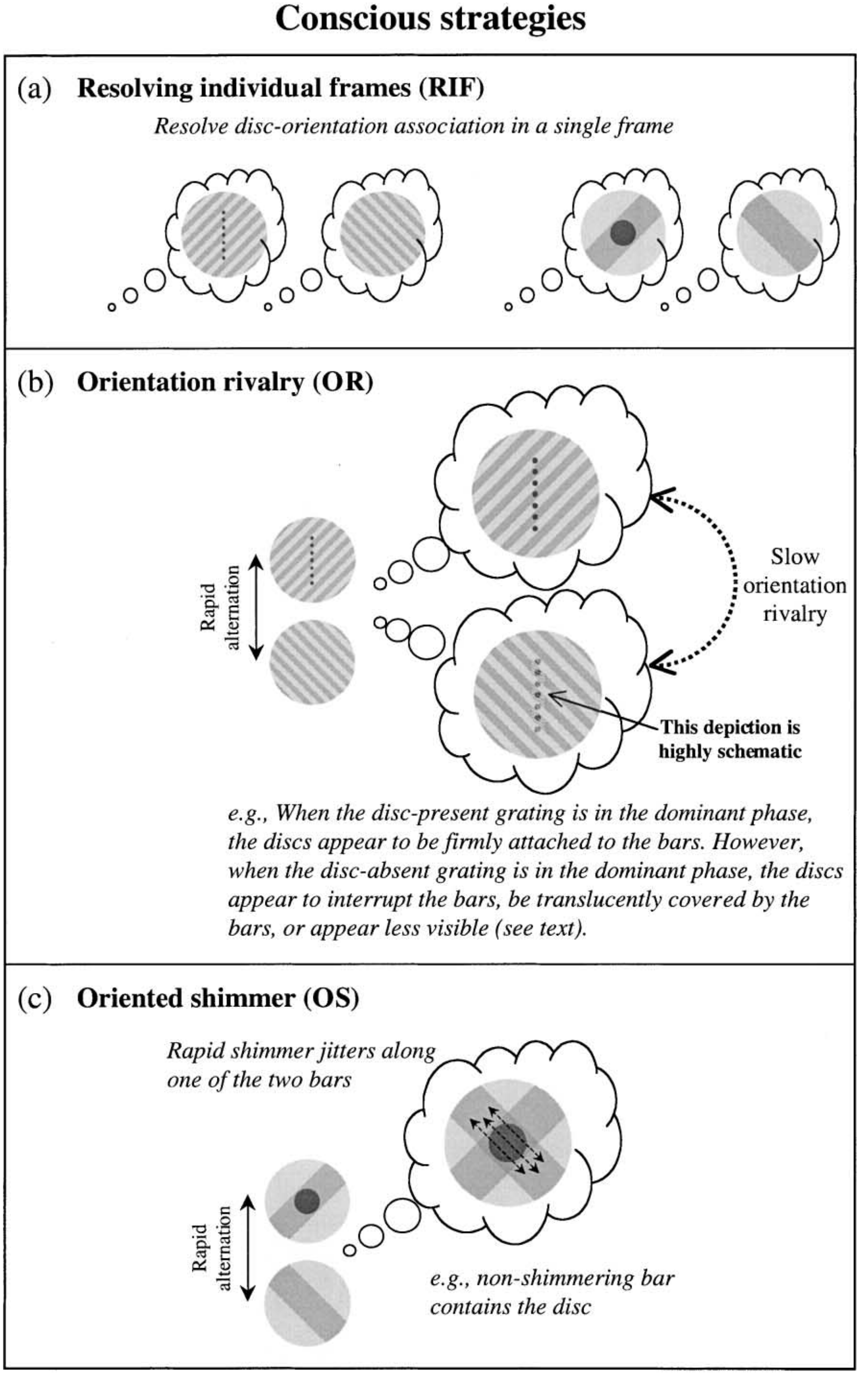

Fig. 2. Conscious strategies used to determine the bar (or grating) orientation that rapidly coincided with the disc: (a) Resolve individual Frames (RIF), (b) Orientation rivalry (OR). Note that the actual orientation rivalry was generally not as exclusive as it is shown in this figure. Instead, the dominant orientation tended to appear stronger (higher-contrast) than the non-dominant orientation: (c) Oriented shimmer (OS).

apparent motion, and flicker-induced contrast illusions). We used smaller discs, added gaps in the bar, or both (Fig. 1c–e). If oriented shimmer depended on the degree to which the bar appeared to be occluded by the disc, a smaller disc might produce weaker oriented shimmer. If oriented shimmer was the result of short-range interactions, it might be reduced when gaps separated the wings and the middle section of the bar. Altogether, there were five stimuli, (1) grating-with-vertical-array-of-discs (Fig. 1a), (2) continuous-bar-with-large-disc (Fig. 1b), (3) gapped-bar-with-large-disc (Fig. 1c), (4) continuous-bar-with-small-disc (Fig. 1d), and (5) gapped-bar-with-small-disc (Fig. 1e).

These five stimuli were tested in two conditions. In the *luminance-alternating* condition, the dark red discs appeared and disappeared (synchronized with one of the

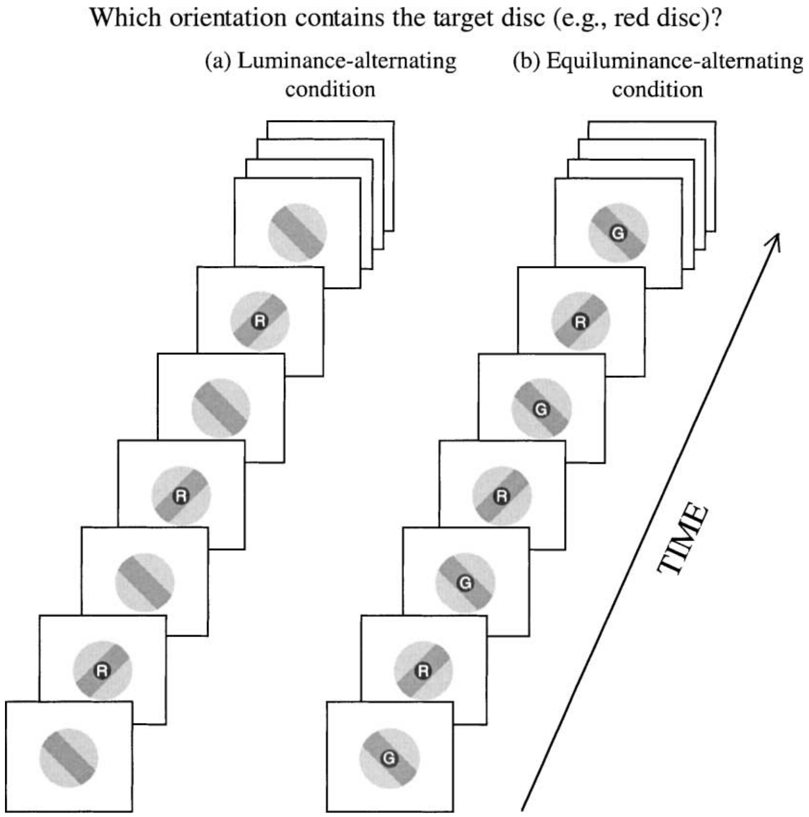

Fig. 3. Schematic depiction of the two trial conditions; the continuous-bar-with-large-disc stimulus is shown as an example. (a) The luminance-alternating condition (all experiments) in which the target-disc-present bar alternated with the disc-absent bar (Experiments 1A–C and 2) or alternated with the bar containing a motion-control disc (Experiment 3; see Fig. 9b); the disc oscillated in luminance. (b) The equiluminance-alternating condition (Experiment 1A only) in which the red-disc- (target-disc-) present bar alternated with the green-disc-present bar; the red and the green discs were set to be equiluminant. The onset of the bars was luminance ramped in Experiments 1A and 3. The observer determined either directly (by resolving individual frames) or indirectly (using emergent percepts) whether the target disc (dark red in Experiments 1A–C, dark or bright green in Experiment 2, and dark green in Experiment 3) coincided with the left tilted bar or the right tilted bar; the display continued until the observer responded (except in Experiments 1B, C and 3).

two orientations) against the static intersection(s) of the bars. Observers viewed the alternating display continuously until they responded as to which grating (or bar) orientation coincided with the discs (Figs. 1 and 3a). Pilot results indicated that this luminance-alternating condition produced both types of emergent percepts, disc-orientation grouping during enhanced orientation rivalry (for the grating stimulus) and oriented shimmer (for the bar stimulus).

In the *equiluminance-alternating* condition, each disc-absent bar was replaced with a bar containing a green disc which was identical to the red disc except for the color. The task was again to determine which grating (or bar) orientation coincided with the red discs (Figs. 1 and 3b). A pilot observation indicated that neither rivalry-based grouping nor oriented shimmer was observed under this condition despite the fact that the red–green flicker was salient for all frame rates in which the emergent percepts were observed in the luminance-alternating condition. The equiluminance-alternating condition thus provided a baseline measure of coincidence detection when observers' only strategy was to resolve individual frames (see Fig. 2a). It is possible that even in the luminance-alternating condition, observers might actually detect the disc-orientation coincidence by accruing evidence from consciously resolving individual display frames; the emergent percepts would then be merely epiphenomenal (inefficacious by-products). If this were the case, performance in the luminance-alternating condition using the emergent percepts should be equivalent to that in the equiluminance-alternating condition in which the emergent percepts were unavailable.

2.1.1. Method

Observers: The first author (SS), a volunteer (YS), and a paid observer (ET) participated; the latter two were naïve as to the purpose of the experiment, but both were experienced psychophysical observers. All had normal or corrected-to-normal vision. All observers went through a number of practice trials with feedback (typically 10–20 trials for each exact stimulus presentation) until they stabilized their conscious strategies for each stimulus in each condition (luminance-alternating or equiluminance-alternating) at each frame rate. The set of strategies eventually adopted were the same for all observers. When the frame rate was sufficiently slow or when no stable emergent percept was observed (i.e., for all frame rates in the equiluminance-alternating condition), observers attempted to consciously resolve individual frames (Fig. 2a). When enhanced orientation rivalry (Fig. 2b) or oriented shimmer (Fig. 2c) were seen at fast frame rates, observers relied on these emergent percepts.

Apparatus: The stimuli were presented on a 17 in. color monitor (75 Hz). The experiments were controlled by a Macintosh PowerMac 8600/300 MHz with Vision Shell software (Micro ML, Inc.).

Stimuli: The dimensions of the five stimuli are shown in Fig. 1. The viewing distance was 72 cm. The circular aperture had a luminance of 72.8 cd/m^2 against a lighter general background (93.5 cd/m^2). The bars were darker than the aperture (65.2 cd/m^2; contrast $= -0.06$). All of these regions were achromatic. The disc was red (CIE[0.60, 0.35]) and darker than the bars (22.5 cd/m^2; contrast $= -0.49$). The luminance of the green disc (CIE[0.33, 0.55]) used in the equiluminance-alternating condition was set to have the same luminance as the red disc for each observer, using flicker photometry at 18 Hz.

Procedure: Pilot observations showed that when the frame rate was relatively slow, the presence or absence of the disc was apparent in the initial frame (which had no forward masking). To avoid this problem, the onset of the bar (or grating) was luminance ramped. The observer initiated each trial by pressing a computer key. The computer then sounded a beep and displayed the circular aperture for about 2 s.

The luminance-alternating condition: Following the aperture-alone display, the disc frame (aperture + disc(s)) and the aperture-alone frame alternated 6–8 times (random in each trial). The single bars (or gratings) then gradually emerged over the 10 successive frames in equal luminance steps. The disc-present bar (or grating) and the disc-absent bar (or grating) then alternated until the observer made a response as to which orientation was synchronized with the discs (Fig. 3a).

The equiluminance-alternating condition: Following the aperture alone display, the red-disc frame (aperture + red disc(s)) and the green-disc frame (aperture + green disc(s)) alternated 6–8 times (random in each trial). As in the luminance-alternating condition, the single bars (or gratings) then gradually emerged over the 10 successive frames in equal luminance steps. The red-disc-containing bar (or grating) and the green-disc-containing bar (or grating) then alternated until the observer made a response as to which orientation was synchronized with the red discs (Fig. 3b).

The five stimuli (Fig. 1) were tested in each of these two conditions. For each stimulus, the initial frame rate was sufficiently slow to allow individual frames to be resolved easily (250–135 ms/frame or ~2–4 Hz depending on the condition and the observer). The frame rate was then increased in small steps (in 26 ms/frame steps up to ~80 ms/frame or ~6 Hz and in 13 ms/frame steps thereafter) until performance dropped to chance levels. Each observer performed a block of 10 trials per frame rate. Response accuracy and latency were recorded for each trial with feedback to the observer at the end of the block. Following each block, observers also recorded their conscious strategies. A minimum 2 min break was given before moving on to a new block (i.e., to a new frame rate). The entire range of frame rates was swept 4 times, resulting in 40 trials per frame rate per stimulus per condition; all five stimuli were tested once before they were tested again.

On the basis of these data, the frame rate yielding 75% correct performance was estimated for each stimulus for each condition by linearly interpolating the corresponding psychometric function (proportion correct vs. frame rate).

2.1.2. Results

Fig. 4 summarizes the threshold (75% correct) frame rates for the five stimuli under the luminance-alternating and the equiluminance-alternating conditions; the data from the three observers are plotted separately. The psychometric functions used to compute these thresholds are shown for SS in Fig. 5 as an example.

2.1.2.1. Equiluminance-alternating condition. The striped bars in Fig. 4 represent the equiluminance-alternating condition. For all observers, the five stimuli (i.e., grating vs. bar, large vs. small disc, and presence vs. absence of gaps) made little difference under this condition. It took 150–180 ms per frame (or about 3 Hz) to detect the coincidence of the red discs with the grating (or bar) orientation. As indicated by "RIF" (resolving individual frames), the only strategy available (at threshold) under this condition was to attempt to perceive the red disc(s) and the coincident bar(s) together by consciously resolving individual frames (Fig. 2a). We note that these threshold frame rates were well above flicker fusion for the equiluminant discs used; the strong perception of flicker disappeared only at the fastest frame rate (13 ms/frame or ~38 Hz) for the equiluminant flicker of the discs as well as for the achromatic flicker of the bars. For comparison, the on/off flicker of the red disc in the luminance-alternating condition was still faintly visible at 13 ms/frame. The examination of the relationship between the detection of disc flicker and the detection of oriented shimmer will be reported in Experiment 3.

There are several possible reasons as to why the emergent percepts were not effective in the equiluminance-alternating condition. Because the luminance of the red and the green discs was equated using a minimum flicker method, responses of phasic ganglion cells

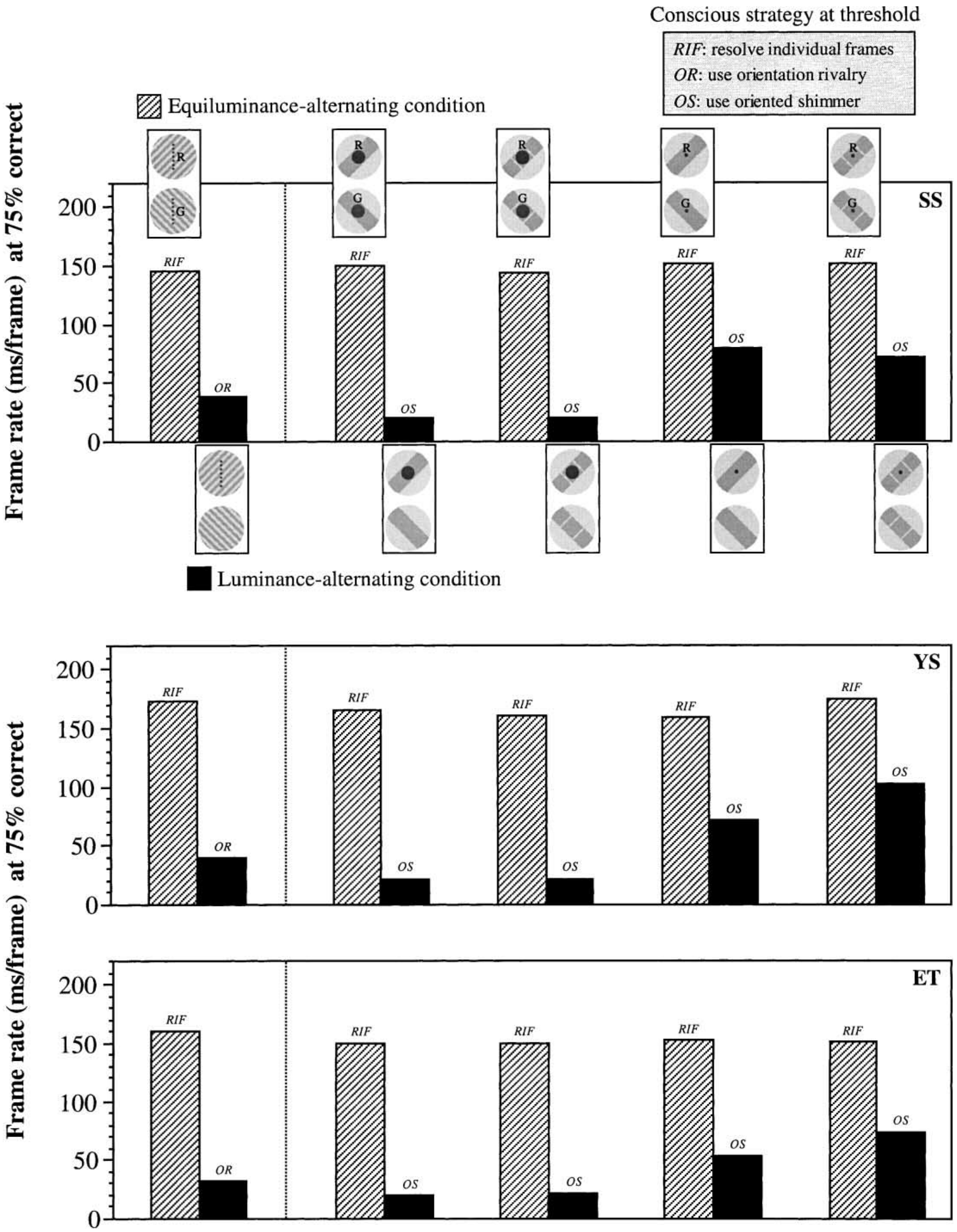

Fig. 4. The threshold (75% correct) frame rate for disc-orientation coincidence detection obtained for the five stimuli (shown schematically for SS) under the two conditions (observers SS, YS, and ET; Experiment 1A). The striped bars represent the equiluminance-alternating condition, and the filled bars represent the luminance-alternating condition. The conscious strategy used at threshold is indicated for each stimulus as RIF, OS, and OR (see the legend).

were minimized for the equiluminant disc oscillation (e.g., Lee, Martin, & Valberg, 1988). The color changes on the disc were thus presumably detected by red–green-opponent tonic ganglion cells whereas the bar alternation (a luminance oscillation) was primarily detected by phasic ganglion cells. It is possible that the emergent percepts require fairly synchronized responses to the disc and the bar regions; if so, the phase lag of the tonic ganglion cells relative to the phasic ganglion cells (e.g., Lee, Martin, & Valberg, 1989; Lee, Pokorny, Smith, Martin, & Valberg, 1990) might have caused enough asynchrony to disrupt the emergent percepts. In a future study this possibility could be tested by varying (with high temporal resolution) the relative phase of the disc oscillation and the bar alternation; if lack of the emergent percepts was due to relatively constant phase lag of the tonic ganglion cells, the emergent percepts should be reinstated when this lag was compensated by appropriately advancing the phase of the equiluminant disc oscillation relative to the phase of the bar alternation.

Alternatively, the fact that the equiluminance-alternating condition reached threshold at rather slow frame rates (about 3 Hz) suggests that the performance limit was reached due to the temporal limit of attention (e.g., 4–8 Hz, Verstraten, Cavanagh, & Labianca, 2000, 7 Hz, Rogers-Ramachandran & Ramachandran, 1998, or below 10 Hz, Forte et al., 1999) rather than due to phase lag of the tonic ganglion cells. The fact that the disc-orientation coincidence-detection thresholds did not depend on the stimulus manipulation is consistent with this idea. Regardless of the exact mechanism that renders the emergent percepts ineffective in the equiluminance-alternating condition, the thresholds in this condition provided a baseline level of performance when the only effective conscious strategy was to try to consciously resolve individual frames.

2.1.2.2. Luminance-alternating condition. Data from the luminance-alternating condition are indicated by the filled bars in Fig. 4. As seen in the figure, the thresholds for disc-orientation coincidence detection dropped substantially (up to eightfold) in this condition relative to the equiluminance-alternating condition for all stimuli and for all observers. The observers indicated that they were unable to consciously resolve individual frames for frame rates beyond about 80 ms/frame (~6 Hz); they then began to use the stable emergent percepts to perform the task, using slow orientation rivalry for the grating and oriented shimmer for the bars.

2.1.2.2.1. Slow orientation rivalry. For the grating stimulus, the orientation rivalry strategy (OR) was effective for rapid frame rates. When the frame alternation rates were in the range of 80–40 ms/frame (~6–12 Hz), the apparently stronger orientation of the grating slowly alternated (at about 0.5–2 s intervals), producing a salient orientation rivalry. For the gratings and the discs used in this study, when the disc-present orientation was in the dominant phase, the discs appeared to be firmly fixed on the grating bars, whereas when the disc-absent orientation was in the dominant phase, the discs appeared to interrupt the bars (or the bars appeared to translucently pass over the discs) (Fig. 2b). We note that the exact phenomenology of the grouping of the discs with the synchronized grating varied depending on the contrast of the discs (relative to the grating bars). For example, when the discs were low contrast (in a pilot observation), the disc-grating association was seen as slight changes in the visibility of the discs; they were more visible when the synchronized grating was in the dominant phase. We also note that the combination of the bar contrast and the frame rate need to be appropriate for generating salient orientation rivalry. Careful examinations of these and other stimulus factors need future study. The current result, however, demonstrates that synchronization can enhance perceptual grouping during orientation rivalry under appropriate conditions.

As orientation rivalry was not always stable and was at times interrupted by mixed percepts (e.g., a flickering grid and/or local islands of dominant orientations), the task was difficult. Observers SS and YS in particular needed to observe many cycles of slow orientation rivalry, resulting in substantially elevated response latencies, before they could determine to which grating the discs appeared to be firmly attached; their response latencies climbed sharply at around 80 ms/frame (~6 Hz) when they began to rely on the orientation rivalry strategy (mean correct latencies increased from 3.3 to 15.5 s for SS and 4.7–15.9 s for YS). The response latency, however, did not elevate for ET; she indicated that when she focused her attention on the discs, the disc-present grating tended to be initially in the dominant phase and she was able to reliably judge the discs to be strongly associated with that grating most of the time.

We note that the low-contrast square-wave gratings we used failed to produce monocular rivalry when the frame rate was increased to the point where the grating appeared static (13 ms/frame or ~38 Hz). This is consistent with the previous finding that statically superimposed stimuli that contain high-spatial-frequency harmonics (such as square-wave gratings and unblurred bars) tended to produce little or no monocular rivalry (e.g., Atkinson, Campbell, Fiorentini, & Maffei, 1973; Campbell & Howell, 1972). Although this spatial-frequency dependence of static monocular rivalry may be consistent with a potential contribution of afterimages

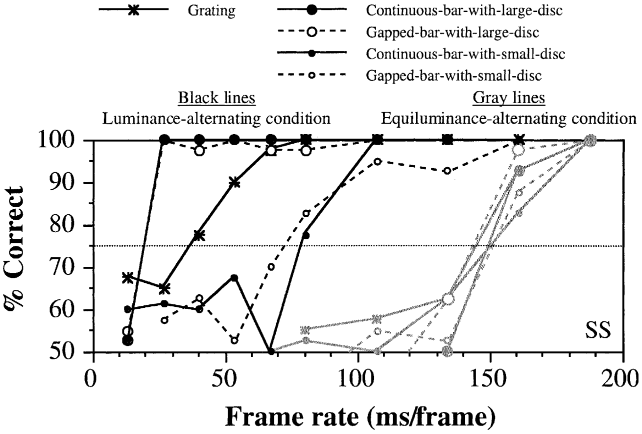

Fig. 5. The psychometric functions (% correct in disc-orientation coincidence detection as a function of frame rate) used to compute the 75% thresholds presented in Fig. 4 (shown for observer SS as an example; Experiment 1A). The black lines represent the luminance-alternating conditions, whereas the gray lines represent the equiluminance-alternating conditions.

(randomly masking either grating component due to small and slow random shifts in eye fixation; Georgeson, 1984), the degree to which this artifact might contribute to static monocular rivalry is unclear (e.g., Bradley & Schor, 1988). Here we used low-contrast (0.06) gratings to minimize afterimages. In addition, the afterimage hypothesis does not explain why rapid alternation imparted rivalry to our grating stimulus that produced little monocular rivalry when presented statically. Above all, since the discs were presented only at the intersections of the grating bars, even if drifting afterimages had occurred, they would have been uninformative as to the disc-orientation coincidence.

2.1.2.2.2. Oriented shimmer. For the bar stimuli, a faint shimmer appeared to jitter consistently along the *disc-absent* bar, and observers effectively used this oriented shimmer (OS) to determine the disc-orientation coincidence (Fig. 2c). Subjectively, this rapid shimmer did not in any way resemble conventional motion or apparent motion. All components of the stimulus, the red disc and the crossed bars, appeared to rapidly flicker in fixed positions; an amorphous shimmer then appeared to jitter along one of the two orientations over the length of the bar or primarily in the region of the disc. The oriented shimmer strategy was extremely effective with the large disc, providing reliable coincidence detection with alternation rates as rapid as 20 ms/frame (25 Hz), but this strategy was less effective with the smaller disc (Fig. 4). Overall, the presence of gaps made relatively little difference for the coincidence detection threshold, but did somewhat increase response latencies [2] (mean correct latencies for above-threshold frame rates were 2.7 s (no gap) vs. 3.5 s (gap) for the large disc, and 4.4 s (no gap) vs. 6.5 s (gap) for the small disc; the same trend for all observers).

Interestingly, for slightly slower frame rates (about 150–100 ms/frame or ~3–5 Hz) than those that produced oriented shimmer, observers reported an *apparent depth segregation* occurring with the continuous-bar-with-large-disc stimulus (Fig. 1b); the disc-absent bar appeared to hover in front of the disc-present bar.

These results indicate that information carried by rapid temporal phase can be seen as stable emergent percepts (orientation rivalry and oriented shimmer) which facilitate detection of feature coincidences when the frame rate is too fast to consciously resolve individual frames. The mechanism that generates these emergent percepts must keep the two half-cycles (disc present and disc absent) separate within each cycle or sum the two half-cycles non-linearly such that the sum is different depending on whether the disc(s) coincides with the left or the right tilted bar (or grating); obviously, if the two half-cycles are summed linearly, the information about the disc-orientation coincidence is lost (see illustrations under *Linear summation* in Fig. 1).

An interesting question is whether the stable emergent percepts contributed to the enhanced sensitivity to temporal phase beyond what would be expected from probability summation. Though observers viewed the stable emergent percepts for a prolonged time to determine the disc-orientation coincidence, it might be that the critical information about the disc-orientation coincidence was accrued independently from each cycle (a pair of consecutive disc-present and disc-absent frames). In other words, observers might simply be performing probability summation while using the repeated cycles as independent sources of information. Alternatively, the disc-orientation coincidence detection based on the emergent percepts might require *temporal integration of phase-specific information* beyond probability summation.

3. Experiment 1B

3.1. Do the emergent percepts reflect non-linear temporal integration beyond probability summation?

If an appropriate stimulus condition (e.g., appropriate contrast and frame rate) can be found where disc-orientation coincidence detection is at chance when only one cycle is viewed, but is reliably above chance when many cycles are viewed (thus enabling the stable emergent percepts to be used), the hypothesis of probability summation can be rejected. Any number of summations of chance cannot result in above-chance performance.

We thus tested a *one-cycle* condition in which the disc(s) used in the luminance-alternating condition was presented only once. The orthogonal single bars or gratings initially alternated with no disc(s); the disc(s) was then presented in a single frame, followed again by alternations of the single bars or gratings. Observers thus had to make their decisions about disc-orientation coincidence on the basis of viewing just one cycle. The frame rate was varied in the same way as in Experiment 1A to determine whether performance in the one-cycle condition reduced to chance levels at frame rates for which the use of the stable emergent percepts generated reliable performance in Experiment 1A.

3.1.1. Method

Observers: SS, YS, and ET participated.

Stimuli: Same as in Experiment 1A.

Procedure: Following the 2 s aperture-alone display (as in Experiment 1A), the two bars (or gratings) alternated 6–8 times (with no disc) within the aperture. Then, the red disc(s) was presented once, followed again by alternations (with no disc) of the two bars (or gratings)

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[2] We note that instructions emphasized accuracy and the task was not time pressured.

until the observer made a response as to which orientation coincided with the disc(s). The five stimulus types (Fig. 1) were tested in the same way as in Experiment 1A, except that the entire range of frame rates was swept 8 times (rather than 4 times), yielding 80 trials per frame rate per stimulus. Because the single presentation of the disc was not masked by the preceding and the subsequent discs as in the repeated-presentation condition (Experiment 1A), performance in the one-cycle condition might overestimate the degree to which the disc-orientation coincidence information could have been extracted from each cycle in the repeated-presentation condition in Experiment 1A. This made our potential rejection of probability summation more conservative.

3.1.2. Results

For all stimuli (the grating and the four bar stimuli) and for all observers, performance in the one-cycle condition reduced to chance levels (i.e., not statistically different from chance) at frame rates slower than the rates at which the performances using the emergent percepts of slow orientation rivalry (for the grating stimulus) and oriented shimmer (for the bar stimuli) were still at the 75% level in Experiment 1A (Table 1; note all numbers in the left column are larger than the corresponding numbers in the right column). In other words, performances based on the emergent percepts were reliable even when the frame rates were too rapid to extract any (above-chance) information about the disc-orientation coincidence from a single cycle. The results thus provide evidence against the possibility that the performance based on the emergent percepts demonstrated in Experiment 1A was due to probability summation from individual cycles.

For the grating stimulus, this conclusion was corroborated for SS and YS because they needed to observe many dominance phases of slow orientation rivalry. The fact that they relied on the different appearances of the disc-grating association that arose during the slowly alternating dominance phases is evidence against simple probability summation across individual stimulus cycles. ET, however, often saw the disc-containing grating to be initially dominant. Moreover, for the continuous-bar-with-large-disc stimulus (though not for the rest of the bar stimuli), SS and ET (but not YS) were sometimes able to observe oriented shimmer even in the one-cycle condition. They reported that oriented shimmer was seen as a kind of "after-ripple" immediately following the presentation of the disc. We thus evaluated probability summation for these cases using a more rigorous statistical procedure. The method of analysis that we used to formally evaluate probability summation will be introduced below for ET's performance on the grating stimulus. The same statistical procedure will be used to evaluate probability summation for oriented shimmer in Experiment 1C.

3.2. A formal test of probability summation for slow orientation rivalry: Introduction of the statistical procedure

A formal rejection of probability summation requires a quantitative model of probability summation to show that the lower confidence limit of the emergent-percept-based performance was beyond the upper confidence limit of performance predicted by probability summation. In Experiment 1A, ET was 100% correct at 40 ms/frame (~12 Hz) for the grating stimulus, and her average

Table 1
Comparison of performance based on one-cycle viewing (Experiment 1B) and that based on multi-cycle viewing using emergent percepts (Experiment 1A)

Observer	Stimulus	One-cycle performance reducing to *chance* (ms/frame)	Emergent-percept-based performance reaching 75% *threshold* (ms/frame)
SS	Grating	80	38
	Continuous-bar-with-large-disc	26	20
	Gapped-bar-with-large-disc	53	20
	Continuous-bar-with-small-disc	80	80
	Gapped-bar-with-small-disc	107	73
YS	Grating	160	41
	Continuous-bar-with-large-disc	53	21
	Gapped-bar-with-large-disc	107	22
	Continuous-bar-with-small-disc	107	72
	Gapped-bar-with-small-disc	134	103
ET	Grating	80	33
	Continuous-bar-with-large-disc	40	21
	Gapped-bar-with-large-disc	67	22
	Continuous-bar-with-small-disc	80	54
	Gapped-bar-with-small-disc	107	74

response latency was equivalent to 37 cycles (note that the actual number of cycles which contributed to the disc-orientation coincidence detection should have been less because the 37 cycles also included the time necessary to perform a key press). Because ET's one-cycle performance reduced to statistical chance at 80 ms/frame (~6 Hz) (Table 1), we thought it likely that ET's one-cycle performance would probably be truly chance at 40 ms/frame (~12 Hz). To confirm this and to obtain the necessary statistical power, ET was tested in the one-cycle condition at 40 ms/frame for 500 trials (10 trials per block with 2 min breaks between blocks to maintain the previous procedure). Her performance was 51.0% correct with the upper 97.5% confidence limit reaching up to $p_{97.5\%\ \text{upper conf. limit}} = 55.4\%$. This confidence limit was obtained by numerically solving the following formula (note that the integrands are binomial functions),

$$\frac{\int_{p=0}^{p_{97.5\%\ \text{upper conf. limit}}} \frac{N!}{r!(N-r)!} p^r (1-p)^{N-r}\, \mathrm{d}p}{\int_{p=0}^{p=1} \frac{N!}{r!(N-r)!} p^r (1-p)^{N-r}\, \mathrm{d}p} = 0.975 \tag{1}$$

where N is the total number of trials ($N = 500$), and r is the number of correct responses ($r = 0.51 \times 500 = 255$).

The expected performance due to probability summation was computed as follows. To be conservative, we assumed that *a correct response would result whenever correct judgments were made in more than half of the total number of cycles viewed* (the disc-orientation coincidence judgment would be either correct or incorrect in each cycle). Thus, if the total number of cycles (N_c) is odd, a correct response should result when correct judgments are made in $(N_c + 1)/2$ or more cycles. If the total number of cycles is even, a correct response should result when correct judgments are made in $(N_c + 2)/2$ or more cycles, and half of the time when correct judgments are made in $N_c/2$ cycles. More formally, we have,

$$p_{\text{probability summation}}(\text{for odd } N_c) = \sum_{k=(N_c+1)/2}^{N_c} \frac{N_c!}{k!(N_c-k)!} p_c^k (1-p_c)^{N_c-k} \tag{2}$$

and

$$p_{\text{probability summation}}(\text{for even } N_c) = \sum_{k=(N_c+2)/2}^{N_c} \frac{N_c!}{k!(N_c-k)!} p_c^k (1-p_c)^{N_c-k} + \frac{1}{2} \frac{N_c!}{(N_c/2)!(N_c/2)!} p_c^{N_c/2} (1-p_c)^{N_c/2}, \tag{3}$$

where p_c is the probability of correct judgment per cycle (% correct obtained in the one-cycle condition).

For ET, $N_c = 37$ (average number of cycles viewed or summed), $p_c = 51.0\%$, and $p_{c(97.5\%\ \text{upper conf. limit})} = 55.4\%$ (Eq. (1)). Thus, the expected probability summation is 54.9% (substituting $p_c = 51.0\%$ into Eq. (2)) and the upper 97.5% confidence limit of probability summation is 74.6% (substituting $p_c = 54.9\%$ into Eq. (2)). ET's actual performance using the slow orientation rivalry percept was 100% correct with the lower 97.5% confidence limit reaching down to, $p_{97.5\%\ \text{lower conf. limit}} = 91.3\%$. This confidence limit was obtained by numerically solving the following formula,

$$\frac{\int_{p=1}^{p_{97.5\%\ \text{lower conf. limit}}} \frac{N!}{r!(N-r)!} p^r (1-p)^{N-r}\, \mathrm{d}p}{\int_{p=1}^{p=0} \frac{N!}{r!(N-r)!} p^r (1-p)^{N-r}\, \mathrm{d}p} = 0.975, \tag{4}$$

where N is the total number of trials ($N = 40$ in Experiment 1A), and r is the number of correct responses ($r = 1.00 \times 40 = 40$). The fact that the lower 97.5% confidence limits for the actual performance (91.3%) is above the upper 97.5% confidence limit for the probability summation (74.6%) indicates that the probability that the true performance based on the orientation rivalry is equal to or worse than expected from probability summation is less than 0.05. Thus, probability summation can be formally rejected as an explanation for ET's disc-orientation coincidence detection using slow orientation rivalry at the conventional statistical criterion of $p < 0.05$.

Next we applied this statistical procedure to formally evaluate probability summation for oriented shimmer.

4. Experiment 1C

4.1. A formal test of probability summation for oriented shimmer

We used the continuous-bar-with-large-disc stimulus which most strongly produced oriented shimmer. To maximize the statistical power for potentially rejecting probability summation, we adjusted the stimulus parameters (i.e., luminance and frame rate) so that continuous observations of a relatively small number of cycles yielded near 100% correct performance based on oriented shimmer (i.e., oriented shimmer appearing along the disc-absent bar), but so that performance was at chance when only one cycle was shown.

4.1.1. Method

Observers: SS and ET participated.

Stimuli: The bar stimulus was identical to the continuous-bar-with-large-disc stimulus used in the preceding experiments (Fig. 1b) except for some minor changes in luminance. The background was 75.4 cd/m^2, the circular aperture was 59.1 cd/m^2, the bar was 52.3 cd/m^2 (all these were achromatic as in Experiments 1A and B); the contrast of the bar against the aperture was still −0.06. To make disc-orientation coincidence more difficult to detect in the one-cycle condition, the luminance of the dark red disc was increased to 47.6 cd/m^2 (and its color was de-saturated, CIE[0.34, 0.31]), reducing its contrast against the bar to 0.05. The frame rate was 26 ms/frame (~18 Hz).

Procedure: Three conditions varying in the number of presented cycles were tested for each observer, 1, half-maximum, and maximum. On the basis of a pilot study, the minimum number of continuous cycles required to generate 90–100% performances based on oriented shimmer was determined for each observer (16 cycles for SS and 32 cycles for ET); this was the maximum number of continuous cycles used. Thus, SS was tested for 1, 8, and 16 cycles, and ET was tested for 1, 16, and 32 cycles. Different conditions were tested in blocks of 10 trials; at least a 2 min break was inserted between blocks. These blocks were tested repeatedly; for example, SS went through, 1-cycle block → 8-cycle block → 16-cycle block → 1-cycle block → 8-cycle block → 16-cycle block → and so on. SS performed 200 trials per condition; due to higher variability in performance, ET performed 300 trials per condition.

As in Experiment 1B, a trial began with the aperture-alone display for 2 s. The two orthogonal bars then alternated within the aperture (with no disc) for about 1 s (38–40 alternations). The disc was then presented for the prescribed number of cycles, followed again by alternations of the two bars (with no disc) until the observer made a response as to which orientation coincided with the disc.

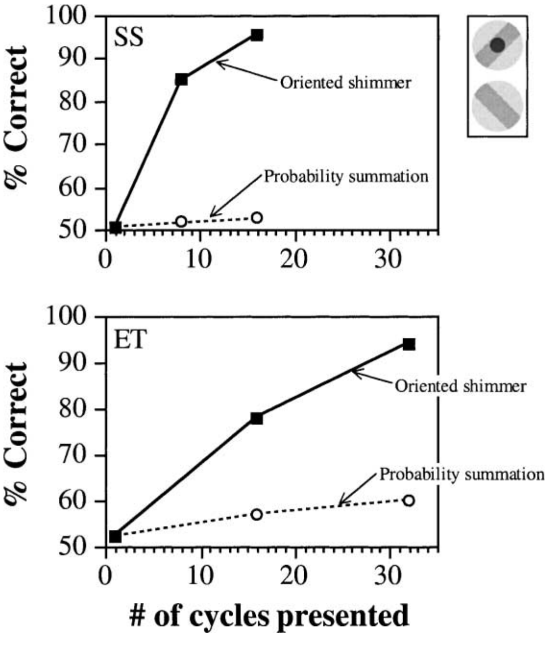

Fig. 6. The disc-orientation coincidence detection (% correct) based on perception of oriented shimmer (■) is contrasted with the levels of performance expected from probability summation (○) (observers SS and ET; Experiment 1C). The continuous-bar-with-large-disc stimulus was used as depicted. For both observers, the performance based on oriented shimmer was significantly greater than expected by probability summation (for both 8- and 16-cycle presentations for SS, and for both 16- and 32-cycle presentations for ET).

4.1.2. Results

SS's performance yielded 51.0% correct with 1 cycle, 85% correct with 8 cycles, and 95.5% correct with 16 cycles. These values are plotted in the upper panel of Fig. 6 (filled squares) along with the correct performance expected on the basis of probability summation computed for the 8- and the 16-cycle conditions using Eq. (3) (with $p_c = 0.510$, and $N_c = 8$ and 16) (open circles). As it is apparent in Fig. 6, the actual disc-orientation coincidence-detection performance based on perception of oriented shimmer was much greater than expected from probability summation. According to the statistical analysis described above (Eqs. (1)–(4)), these differences were significant for both the 8- and the 16-cycle conditions. Similar results were obtained for ET whose performance yielded 47.7% correct with 1 cycle, 78% correct with 16 cycles, and 94% correct with 32 cycles. To be conservative in rejecting probability summation, we used 52.3% (i.e., 100% – 47.7%) rather than 47.7% as the performance on the 1-cycle condition, assuming that the 2.3% deviation from chance provided potentially useful information. Again, as shown in Fig. 6 (the lower panel), the actual performances based on perception of oriented shimmer were much greater than the performances expected on the basis of probability summation (computed using Eq. (3) with $p_c = 0.523$, and $N_c = 16$ and 32). The differences were statistically significant for both the 16- and the 32-cycle conditions (Eqs. (1)–(4)).

Oriented shimmer thus facilitated the disc-orientation coincidence detection beyond probability summation from individual cycles. This provides evidence that oriented shimmer is indeed a stable emergent percept which requires a non-linear temporal integration mechanism that preserves temporal phase.

So far, we have described two stable emergent percepts, slow orientation rivalry and oriented shimmer, which can enhance detection of rapid feature synchronization beyond probability summation when the frame rate is too fast to consciously resolve individual frames. As discussed in the introduction, it is relatively straightforward to interpret the effectiveness of slow orientation rivalry; the discs tend to group more strongly with the coincident grating than with the other grating and the slow rivalry between the two gratings helps make this association salient. The origin of oriented shimmer, however, is unclear especially because it was consistently seen along the *disc-absent* bar. Based on the fact that the subjective impression of the phenomenon is one of "shimmer", we expected that the perception of oriented shimmer should depend critically on luminance relationships. We thus examined how the perception of oriented shimmer was affected by the relative contrasts of the disc, the bar, and the aperture. The results provided a simple dynamic rule that predicted the appearance of oriented shimmer.

5. Experiment 2

5.1. Oriented shimmer is induced by "heterodirectional" changes in luminance

The luminance of the disc was varied from brighter than the bar to darker than the bar (or in the reverse order) passing through the equiluminant point. The continuous-bar-with-large-disc stimulus (Figs. 1b and 3a) was again used because oriented shimmer was most strongly seen with this stimulus (Fig. 4). The disc was colored green and the bars were colored red; these colors were saturated so that the circle remained highly visible at equiluminance due to strong color contrast (green = CIE[0.33, 0.54] and red = CIE[0.60, 0.35]). The frame rate of 40 ms/frame ($\sim$12 Hz) was used because it appeared optimum for perception of oriented shimmer (for the stimuli we used) and was fast enough that oriented shimmer was the only effective conscious strategy for reliably determining the disc-orientation coincidence.

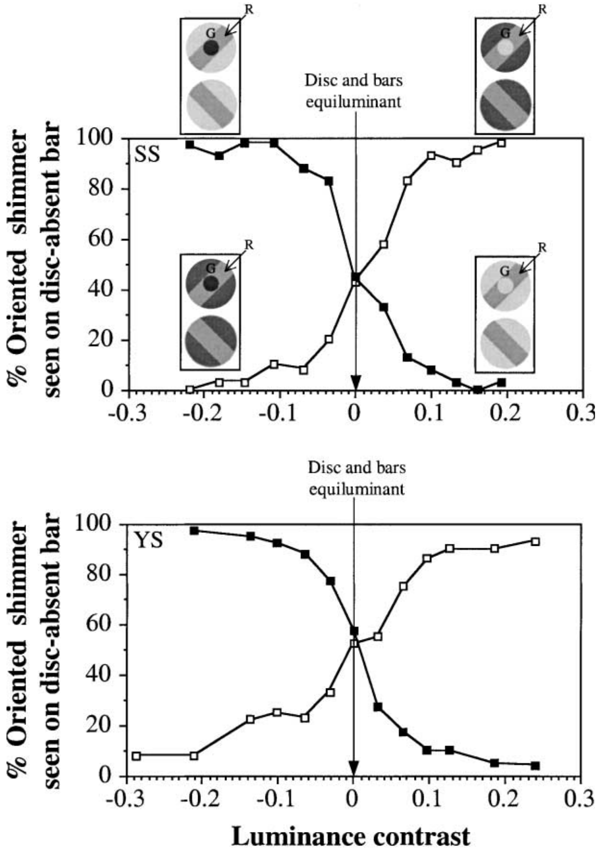

Fig. 7. Proportion of trials in which oriented shimmer was seen on the disc-absent bar (observers SS and YS; Experiment 2). On the abscissa, "0" indicates that the green disc was equiluminant with the red bars. Positive values indicate that the green disc was brighter than the red bars, whereas negative values indicate that the green disc was darker than the red bars. The red bars were either darker (■) or brighter (□) than the achromatic circular aperture. Note that oriented shimmer was always seen along the bar for which luminance changes were *heterodirectional* (see text for details).

5.1.1. Method

Observers: SS and YS participated.

Stimuli: The red bars (22.5 cd/m^2) were presented against a gray aperture which was either lighter (30.2 cd/m^2) or darker (16.4 cd/m^2) than the bars (see Fig. 7 for schematic drawings); the contrast of the bars was thus either +0.15 or −0.15 against the aperture.

Procedure: In each trial, the entire aperture was initially red (the same color and luminance as the bars). Following the 2 s aperture-alone display (as in all preceding experiments), the disc frame (red aperture + green disc) and the aperture frame (red aperture only) alternated 6–8 times (random in each trial). The portions of the aperture that did not belong to the red bar then became gray (lighter or darker), revealing the red bars alternating in orientation. Thus, the disc always appeared on the same red immediate background both before and after the emergence of the bars. As before, the bar alternation continued until the observer indicated the orientation of the bar that coincided with the disc. Specifically, the observer indicated the orientation of the bar that did not show oriented shimmer (the strategy found to be effective in Experiments 1A and C). Since the frame rate used was fast (40 ms/frame or $\sim$12 Hz) and oriented shimmer provided the only reliable conscious strategy, it was not necessary to use a ramped onset of the bars.

The lighter aperture and the darker aperture were tested in separate sessions. In each session, the luminance of the green disc was varied from lighter to darker or darker to lighter (relative to the bars) in blocks of 10 trials; at least a 2 min break was given before moving on to the next block of trials testing the next level of disc luminance. In the initial block in each session, the green disc was given sufficiently strong luminance contrast (i.e., it was sufficiently bright or dark) against the red bars so that oriented shimmer was reliably observed. In subsequent blocks, the luminance of the disc was gradually reduced or increased to be equiluminant with the red bars. The disc luminance was then further reduced or increased until the disc again acquired sufficiently strong luminance contrast against the red bars (equivalent in magnitude but opposite in polarity relative to the initial contrast). For each of the two aperture contrasts, the entire range of the disc luminance was tested four times (twice in the decreasing direction of disc luminance and twice in the increasing direction of disc luminance), yielding 40 trials per disc luminance per aperture luminance; both light and dark apertures were tested once before they were tested again.

5.1.2. Results

In Fig. 7, the proportion of trials in which oriented shimmer was seen on the disc-absent bar is plotted as a function of the contrast of the green disc (against the red bars of fixed luminance) when the red bars were darker than the aperture (filled squares) and when the red bars were lighter than the aperture (open squares) (see schematic drawings of the stimuli shown in Fig. 7); the data are plotted separately for the two observers.

The upper left part of the curve with filled squares shows the stimulus configuration comparable to that in Experiments 1A and C in which the disc was darker than the bars, and the bars were darker than the aperture. This result replicated the oriented shimmer result of Experiments 1A and C using a new set of luminance values (while maintaining the same contrast polarity relationships); oriented shimmer produced reliable performance (nearly 100% correct). As the luminance of the disc was gradually increased toward equiluminance, oriented shimmer became increasingly unreliable in indicating the disc-absent bar, resulting in ~50% correct when the disc was equiluminant with the bars though the green disc was always highly visible against the red bars due to strong color contrast. Interestingly, as the disc luminance was further increased past equiluminance, oriented shimmer then began to be seen on the *disc-present bar* rather than on the disc-absent bar (indicated by consistently "incorrect" performance). This pattern mirror-reversed when the bars were lighter than the aperture (open squares).

The particular manner in which oriented shimmer depended jointly on the contrast polarity of the disc (against the bar) and the contrast polarity of the bars (against the aperture), suggests the following principle. *Oriented shimmer is seen along the bar which oscillates with heterodirectional changes in luminance.*

When the disc was darker than the bars, and the bars were darker than the aperture (Fig. 8a), both the disc section and the wings of the disc-present bar appeared (labeled ONSET) as luminance decrements (relative to the corresponding locations of the preceding disc-absent frame) and disappeared (labeled OFFSET) as luminance increments (when replaced by the following disc-absent frame). The disc-present bar thus appeared and disappeared with unidirectional changes in luminance (i.e., with all parts either brightening or darkening). However, the disc-absent bar appeared and disappeared with heterodirectional changes in luminance (Fig. 8b); the central section that replaced the previous disc had a brightening onset and a darkening offset, whereas the wings had a darkening onset and a brightening offset. Oriented shimmer was seen on the *disc-absent* bar (left tilted bar in this example in Fig. 8a and b) along which changes in luminance were *heterodirectional* (i.e., brightening and darkening changes being inter-mixed). This *heterodirectional-change* rule applies to the remaining three combinations of luminances.

For example, when the disc was brighter than the bars, and the bars were darker than the aperture, it was the disc-present bar that appeared and disappeared with *heterodirectional* changes in luminance (the disc had a brightening onset and a darkening offset while the bar-wings had a darkening onset and a brightening offset) (Fig. 8c), whereas the disc-absent bar appeared and disappeared with unidirectional changes in luminance (all parts had a darkening onset and a brightening offset) (Fig. 8d). Thus, oriented shimmer was seen on the *disc-present* bar along which changes in luminance were heterodirectional (the right tilted bar in this example, Fig. 8c and d).

Various potential mechanisms underlying the perception of oriented shimmer (e.g., counterphase motion, as well as spatial and temporal contrast interactions) will be discussed later. The final experiment was conducted to assess (1) whether oriented shimmer is an apparent motion phenomenon, (2) whether the perception of oriented shimmer requires the appearance and disappearance of the disc contours, and (3) how detectability of oriented shimmer is related to detectability of flicker of the disc.

6. Experiment 3

6.1. Oriented shimmer is not an apparent motion phenomenon

The potential relationships between oriented shimmer and these phenomena (apparent motion, contour appearance and disappearance, and flicker detection) were examined in the same experiment, again using the continuous-bar-with-large-disc stimulus (Fig. 1b) which generated oriented shimmer most reliably (Fig. 4). At a very slow alternation rate, the bar stimulus appeared to switch orientations (or rock), but this apparent motion disappeared at high alternation rates. Moreover, the rocking motion did not specify the disc-orientation coincidence. Could other apparent motion percepts be supported by the bar stimulus? Consider the possible motion correspondences when the bar with the dark disc is replaced by the orthogonal bar with no disc (Fig. 3a). The bar clearly corresponds to the orthogonal bar in the subsequent frame, but the disc has no apparent pattern to which to correspond. It is possible that the dark disc might correspond to the dark wings of the following orthogonal disc-absent bar, generating an expansion-like apparent motion; a contraction-like apparent motion might occur when those dark wings correspond back to the dark disc in the following frame (Fig. 9a). It might be that at slow rates of alternation this expansion–contraction apparent motion was masked by the strong rocking motion of the bars, but it might manifest as

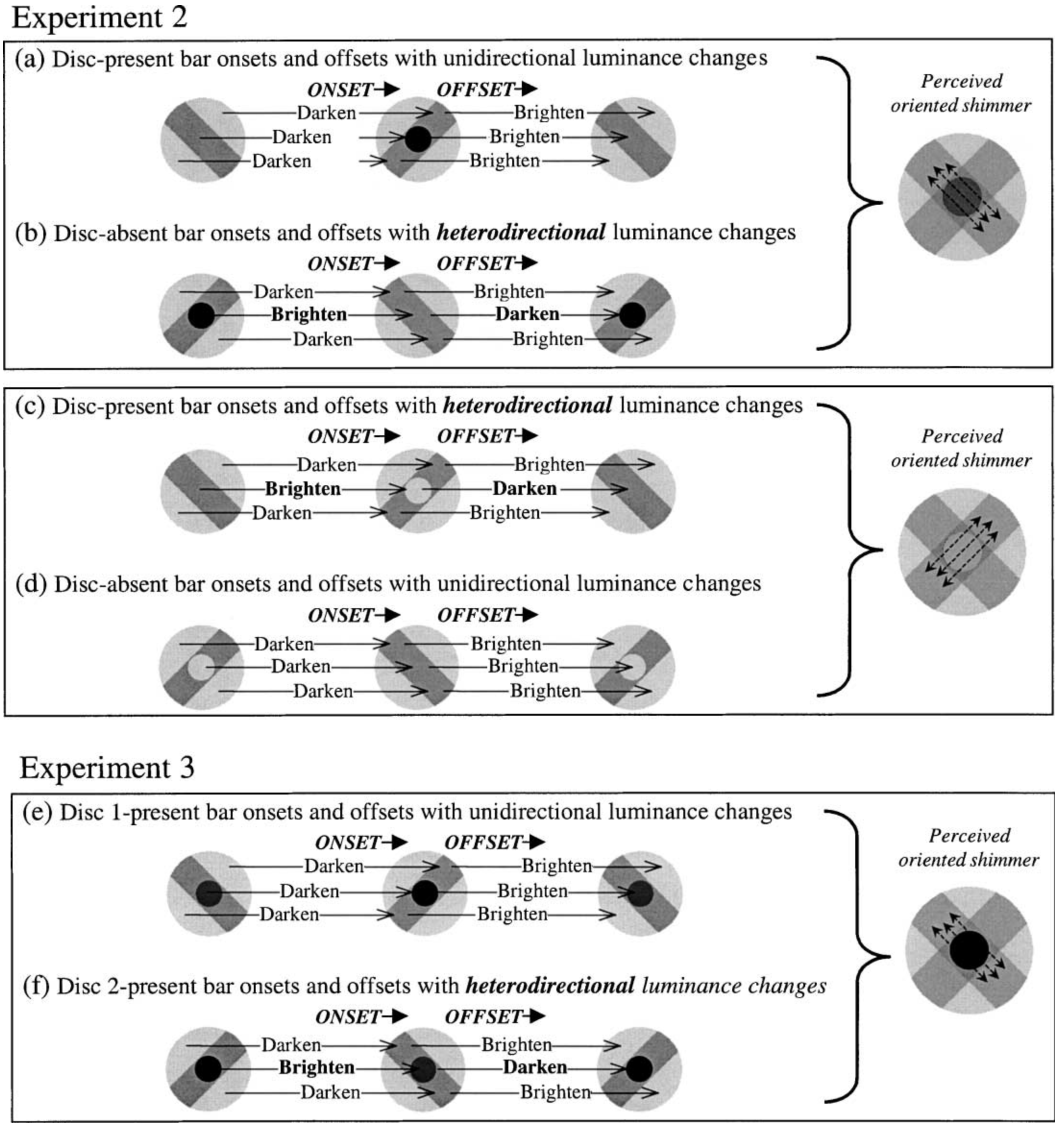

Fig. 8. An illustration of the heterodirectional-luminance-change rule of oriented shimmer. (a)–(d) Examples for Experiment 2. When the disc was darker than the bars and the bars were darker than the aperture, the disc-present bar appeared and disappeared with unidirectional changes in luminance (a), whereas the disc-absent bar appeared and disappeared with *heterodirectional* changes in luminance (b). In contrast, when the disc was lighter than the bars and the bars were darker than the aperture, the disc-present bar appeared and disappeared with *heterodirectional* changes in luminance (c), whereas the disc-absent bar appeared and disappeared with unidirectional changes in luminance (d). (e) and (f) Examples for Experiment 3. Even when a lower-contrast dark disc (disc 2) was added to the disc-absent bar shown in (a) and (b) to prevent expansion–contraction apparent motion, the original disc-present bar (labeled as disc 1-present bar) still appeared and disappeared with unidirectional changes in luminance (e), and the disc 2-present bar appeared and disappeared with *heterodirectional* changes in luminance (f). In all cases, oriented shimmer was observed along the bar which appeared and disappeared with *heterodirectional* changes in luminance.

oriented shimmer when alternation became too fast to support the rocking motion. Phenomenologically, however, oriented shimmer is not an expansion–contraction type motion; if any motion analogy were to be given to oriented shimmer, it is a rapid jitter that runs back and forth along one of the flickering bars. Nonetheless, we tested the expansion–contraction-apparent-motion hypothesis by modifying the stimulus such that the dark disc had a pattern to which to correspond across frames.

Note that in the prior experiments, the emergent percept of oriented shimmer was used by observers to infer the temporal coincidence between the target disc and the associated bar. The inclusion of a second disc to provide a motion-correspondence control required the task to change to orientation-discrimination of the oriented shimmer percept itself. However, the experience of the task was virtually identical on the part of observers because in the preceding experiments they also detected oriented shimmer except that they identified the shimmer orientation as the disc-absent orientation. On the previously disc-absent bar, we placed a motion-control disc (termed disc 2) which was the same size as the

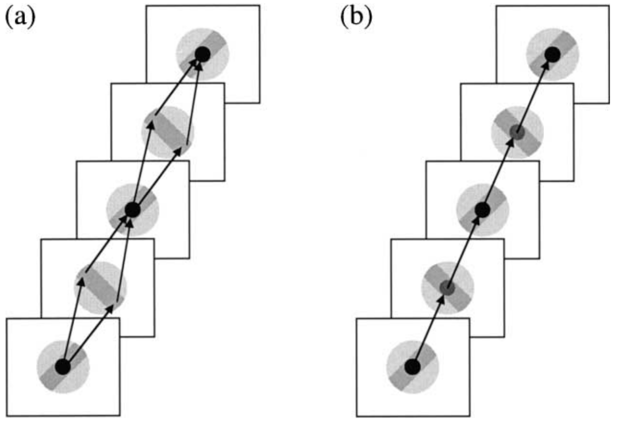

Fig. 9. (a) Expansion–contraction apparent motion that might potentially contribute to oriented shimmer. (b) The control condition used in Experiment 3 to eliminate expansion–contraction apparent motion (a slightly lighter disc being placed on the previously disc-absent bar).

original dark disc but slightly lighter in luminance. Now the original dark disc (here termed disc 1) clearly corresponded to disc 2 in the alternate frame, eliminating the possibility of expansion–contraction apparent motion (Fig. 9b). At slow frame rates, the bars still appeared to rock while the central disc oscillated subtly in luminance. At high frame rates, the bars appeared to flicker and the central disc appeared almost static. Expansion–contraction apparent motion was not observed at any of the frame rates tested. The addition of disc 2, however, did not alter the fact that the original disc 1-present bar still appeared and disappeared with unidirectional changes in luminance (compare Fig. 8e with a), whereas the original disc-absent bar (now with disc 2) still appeared and disappeared with heterodirectional changes in luminance (compare Fig. 8f with b). Thus, if oriented shimmer was indeed driven by heterodirectional changes in luminance rather than by expansion–contraction apparent motion, it should be reliably observed on the bar synchronized with disc 2 (the left tilted bar in this example in Fig. 8e and f). If oriented shimmer was reliably seen in this condition, we could also conclude that the appearance and disappearance of the disc contours was not critical in generating oriented shimmer because the disc contours were always present.

Because our pilot results indicated that oriented shimmer reliably indicated the disc-orientation coincidence in this condition, we also varied the relative luminance of the two discs to compare the detectability of oriented shimmer and the detectability of disc flicker using the same paradigm.

6.1.1. Method

Observers: SS, YS, and ET participated.

Stimuli: The stimulus dimensions were identical to the continuous-bar-with-large-disc stimulus used in the preceding experiments (Fig. 1b). The background was 86.5 cd/m^2, the aperture was 67.2 cd/m^2, and the bars were 59.2 cd/m^2 (all these were achromatic as in Experiments 1A–C); the contrast of the bar against the aperture was -0.06 (comparable to Experiments 1A–C). The two discs were both green (CIE[0.31, 0.57]). The dark disc (disc 1) had a fixed luminance of 21.1 cd/m^2 (contrast $= -0.47$ against the bar). The luminance of the lighter disc (disc 2) was varied from 32.7 cd/m^2 (contrast $= -0.29$ against the bar) to being nearly as dark as disc 1, 21.4 cd/m^2. The alternation rate was 40 ms/frame ($\sim$12 Hz) as in Experiment 2.

Procedure: Trials measuring detection of oriented shimmer. To measure detection of oriented shimmer and detection of flicker of the discs using the same paradigm, a two-interval-forced-choice method was adopted. Upon the observer's press of a computer key, the aperture-alone display appeared with a beep and remained for 2 s as in the preceding experiments. The disc 1 frame (aperture + disc 1) and the disc 2 frame (aperture + disc 2) then alternated 6–8 times. The bars then gradually emerged over the 10 successive frames in equal luminance steps. Subsequently, the disc 1-present bar and the disc 2-present bar alternated for 2 s (including the ramping period). The display was then terminated with a strong full-screen backward mask (403 ms; bright dots = 86.5 cd/m^2 and dark dots = 3.8 cd/m^2; dot size = $0.06° \times 0.06°$) so that the final frame was not any more visible than the other frames. The display then went blank for 2 s followed by the second interval which also began with a beep and a 2 s presentation of the aperture-alone display. The second interval was identical to the first interval except that the bar orientation was switched for the two discs. At the end of the second interval, the observer indicated the interval in which oriented shimmer was seen on the right-tilted bar.

Trials measuring detection of flicker of the discs. Upon the observer's press of a computer key, the aperture-alone display appeared with a beep and remained for 2 s. Disc 1 and disc 2 then appeared and began to alternate against a static version of the two bars (a linear time average of the two bars; see the illustration under *Linear summation* in Fig. 1b). The display then went blank for 2 s followed by the second interval. The two intervals were identical except that the disc was effectively static in one interval and flickered at 40 ms/frame (or $\sim$12 Hz) in the other. At the end of the second interval, the observer indicated the interval in which the disc appeared to be flickering.

The time-averaged luminances of the flickered disc and the static disc were matched by taking advantage of the fact that when the rate of flicker was increased to 13 ms/frame ($\sim$38 Hz) (the fastest possible rate obtained with our 75 Hz monitor), the disc flicker was well above fusion (appeared static) for the luminance modulation depths used in this experiment. In a pilot study, we

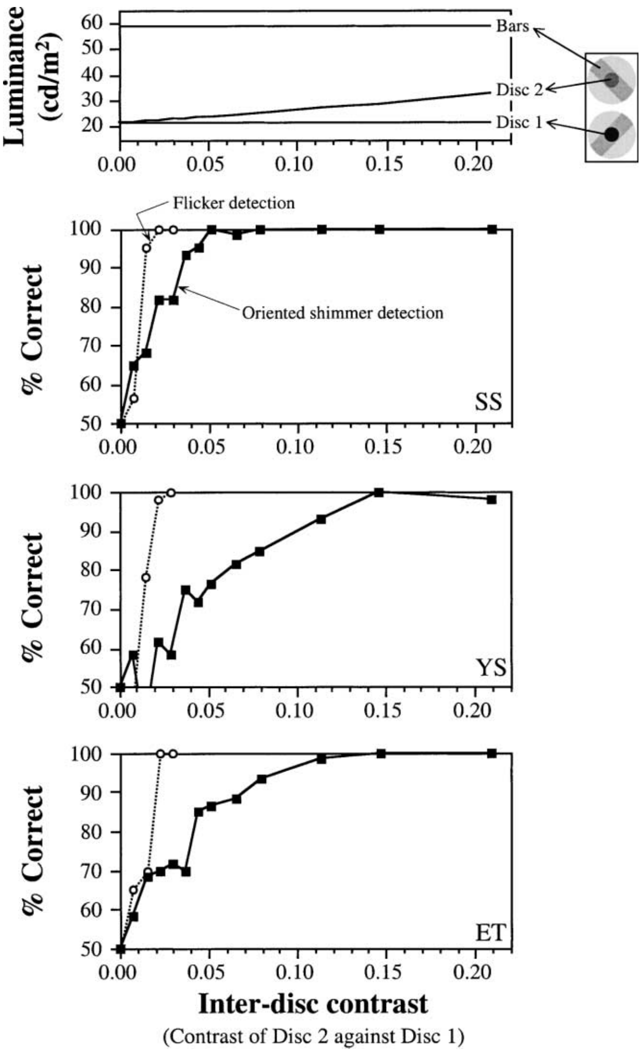

Fig. 10. Detection of oriented shimmer (■) and detection of flicker of the disc (○) are plotted as a function of the relative contrast of the two dark discs (disc 1 and disc 2) contained in the two bars (observers SS, YS, and ET; Experiment 3). The top panel shows the luminances of the bar and the two discs. Note that oriented shimmer was detected reliably when both discs were substantially darker than the bar, and when the luminance modulation of the discs was so small that it became difficult to detect the flicker of the discs (SS and ET).

determined that flicker was clearly visible when the disc 1 of 21.1 cd/m^2 and the disc 2 of 25.1 cd/m^2 (inter-disc contrast of 0.09) were alternated at 40 ms/frame (~12 Hz). We then verified that at 13 ms/frame (~38 Hz), this level of luminance modulation was above flicker fusion for all three observers. [3] Because 13 ms/frame (~38 Hz) flicker was already fused when the inter-disc contrast was 0.09, it could be safely assumed to be "static" for measurement of the contrast limit of 40 (~12 Hz) flicker, which occurred at the inter-disc contrast well below 0.09 (Fig. 10). Thus, we used 13 ms/frame (~38 Hz)-flickered discs as the static disc with matched time-averaged luminance.

Detection of oriented shimmer and detection of flicker were measured in alternate sweeps of the inter-disc contrast. In each sweep, observers detected either oriented shimmer or flicker while the inter-disc contrast was varied from 0.21 (yielding 100% performance) down to 0.007. Each inter-disc contrast was tested in a block of 10 trials with at least a 2 min break before moving on to a different contrast. Observers were tested in 12 sweeps (6 for oriented shimmer detection and 6 for flicker detection), yielding 60 trials per inter-disc contrast per task.

6.1.2. Results

Oriented shimmer was clearly detectable when the original dark disc (disc 1) was synchronized with one orientation while the motion-control disc (disc 2) was synchronized with the other orientation. Thus, even in the absence of any expansion–contraction type apparent motion and of any onset and offset of the disc contours, oriented shimmer was still reliably seen on the bar that appeared and disappeared with heterodirectional changes in luminance (Fig. 8e and f). As shown in the top panel of Fig. 10, both disc 1 and disc 2 were much darker than the bar, and the inter-disc luminance difference was relatively small. Remarkably, oriented shimmer was reliably detected (above 75% correct performance; see filled squares) when the inter-disc contrast was as little as 0.05 (only about 10% of the contrast of the discs against the bar). Furthermore, for SS and ET, oriented shimmer was still detected above chance when the flicker of the discs was barely detectable.

7. Discussion

The results of these experiments demonstrate that the visual system can take advantage of relative temporal phase, which was aligned for features presented within each frame, but shifted for features presented in alternate frames. [4] When orthogonal gratings were rapidly alternated, enhanced monocular orientation rivalry was perceived. Furthermore, when luminance-defined discs repeatedly coincided with one of these gratings, the disc-grating coincidence manifested as stronger grouping between the discs and the grating when the synchronized grating was perceived as dominant during orientation

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[3] The disc presented in the static interval had the arithmetic mean luminance of the flickered discs, but the luminance of the static disc was slightly varied from trial to trial to prevent mismatches between the actual time-averaged luminance of the flickered discs and the arithmetic mean luminance of the static disc from providing a clue to which interval contained the target.

[4] Though we demonstrated these emergent percepts using periodically oscillating stimuli, we have no evidence indicating that periodicity is critical. It is possible that repeated onsets without strict periodicity might be sufficient to induce these emergent percepts.

rivalry. In contrast, when orthogonal single bars were rapidly alternated, no apparent orientation rivalry was seen. However, when a luminance-defined central disc repeatedly coincided with one of these bars, oriented shimmer was seen consistently along the bar on which changes in luminance were heterodirectional. These emergent percepts substantially increased the sensitivity of disc-orientation coincidence detection beyond what can be achieved by consciously resolving individual frames or by probability summation. While the grating stimuli and the bar stimuli differed only in terms of the number of bars and spatial frequency contents, the two stimuli produced qualitatively different emergent percepts. Further investigation is necessary to understand how the mechanisms underlying enhanced orientation rivalry and oriented shimmer might be related. Here, we will separately discuss implications of the two seemingly different emergent percepts.

7.1. Enhanced orientation rivalry for orthogonally oriented gratings

Slow orientation rivalry was perceived for frame alternations in the range of 80–40 ms/frame (∼6–12 Hz), and was most salient at approximately 55 ms/frame (∼9 Hz) (for the particular grating stimulus we used). The discs appeared to be firmly attached to the grating bars when the disc-present grating was in the dominant phase, whereas the discs appeared to interrupt the bars, be translucently covered by the bars (or be less visible; pilot observations using low-contrast discs) when the disc-absent grating was in the dominant phase (see Fig. 2b). This apparent grouping between the discs and the synchronized grating was not epiphenomenal because it supported detection of disc-orientation coincidence when individual frames were no longer resolvable. Since the two gratings oscillated in opposite temporal phase and the discs oscillated in phase with only one of the gratings, the result is consistent with the interpretation that the discs and the synchronized grating were grouped on the basis of aligned temporal phase whereas the two gratings were segregated on the basis of shifted temporal phase. As discussed below, this result might add coherent oscillation of neural responses to the known set of factors that influence perceptual rivalry.

The most salient perceptual rivalry phenomenon is binocular rivalry; when a different image is presented to each eye, perception tends to alternate stochastically over time between the two images (for reviews, see Blake, 1989; Blake & Logothetis, 2002; Levelt, 1965; Logothetis, 1998). Broadly, two distinct mechanisms have been suggested to account for this phenomenon. The *eye suppression hypothesis* suggests that when a different image is presented to each eye, the visual system might select inputs from only one eye at any given moment while suppressing inputs from the other eye (thus any image would be suppressed if presented to the suppressed eye). In contrast, the *image suppression hypothesis* suggests that when confronted with two spatially overlapping images that are different from each other, the visual system might select one image at any given moment while suppressing the other image (irrespective of whether the two images are presented to the same eye or to different eyes). Empirical support for both hypotheses has been reported (e.g., Blake & Fox, 1974; Blake, Westendorf, & Overton, 1980; Blake, Yu, Lokey, & Norman, 1998; Lack, 1974 for eye suppression; and Logothetis, Leopold, & Sheinberg, 1996 for image suppression). Recently, Lee and Blake (1999) reported that while static dichoptic images produced binocular rivalry under a wide range of stimulus conditions, the special paradigm used by Logothetis et al. (1996) to produce image-based rivalry (swapping images between the two eyes every 333 ms while the stimuli flickered at 18 Hz) generated slow rivalry only when the rivaling gratings satisfied specific spatial and temporal constraints (also see Bonneh, Sagi, & Karni, 2001).

Instead of a dichotomy between eye-based and image-based rivalry, recent research on perceptual rivalry seems to suggest that during any rivalry (monocular or binocular), the visual system weights multiple factors in determining the optimum grouping of local features that could resolve an apparently incoherent image into two (or more) coherent images that then alternate in time. One set of factors involves perceptual grouping principles such as proximity, similarity in color, good continuation of local orientation, closure, and symmetry, all of which can facilitate grouping of features across the two eyes during binocular rivalry (e.g., Bonneh & Sagi, 1999; Bonneh et al., 2001; Kovács, Papathomas, Yang, & Feher, 1996; Logothetis, 1998; Suzuki & Grabowecky, 2002). Rivalry may also be influenced by global shape representations, mediated by high-level cells that are tuned to global shapes (e.g., IT cells; see Logothetis & Sheinberg, 1996; Tanaka, 1996, for reviews; Sáry, Vogels, Kovács, & Orban, 1995; Vogels & Orban, 1994, for responses to grating stimuli). There is evidence that these global-shape-tuned cells in IT, having large receptive fields (e.g., Desimone, Albright, Gross, & Bruce, 1984; Gross, Rocha-Miranda, & Bender, 1972; Ito, Tamura, Fujita, & Tanaka, 1995; Lueschow, Miller, & Desimone, 1994), act to inhibit one another (e.g., Miller, Gochin, & Gross, 1993), perhaps to help select or recognize particular shapes in a cluttered environment (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Usher & Niebur, 1996). Consistent with this high-level neural competition idea, activity of most cells in IT and STS (90%) is substantially modulated by binocular rivalry, whereas only a relatively small proportion of cells are modulated in V1 and V2 (20%) (e.g., Leopold & Logothetis, 1996; Logothetis, 1998; Sheinberg &

Logothetis, 1997, but see Polonsky, Blake, Braun, & Heeger, 2000 for human fMRI data to the contrary). Furthermore, Yu and Blake (1992) psychophysically demonstrated the influence of high-level representations on binocular rivalry by showing that recognizable figures (presumably activating high-level cells) dominated longer than feature-matched nonsense patterns.

Thus, basic perceptual grouping factors, detection of global shapes by high-level shape-tuned cells, as well as mutual inhibition of V1 cells based on eye of origin (e.g., Blake, 1989; Lehky, 1988; Sugie, 1982), might all contribute to determine which feature configurations end up rivaling. In this framework, whether binocular rivalry appears to be an eye rivalry or an image rivalry should depend on the relative contribution of these grouping factors in a given stimulus context. For example, making the two orthogonal gratings different in color (i.e., adding color-based grouping to orientation-based rivalry) enhances both monocular rivalry (e.g., Campbell et al., 1973; Campbell & Howell, 1972; Wade, 1975) and binocular rivalry (e.g., Wade, 1975). Our result suggests that coherent temporal phase of oscillatory neural responses may be another factor that can contribute to feature grouping during rivalry. Here we assume that in response to grating alternation, activations of cells that are responding to the same grating are modulated in phase (thus facilitating grouping of parts within each grating) whereas activations of cells that are responding to the orthogonal gratings are modulated out of phase (thus facilitating segregation of the two gratings). As discussed earlier, responses of cells in V1 and V2 can follow stimulus oscillations in the range of alternation rates that we used.

Some researchers have suggested that coherent neural oscillations constitute a general mechanism underlying basic perceptual grouping (e.g., grouping by feature similarity and common motion) even when stimuli are not oscillated (e.g., Gray, 1999; Gray et al., 1989; Singer, 1995). This view, however, is controversial (e.g., see Shadlen & Movshon, 1999, for a review). For example, when figure and ground regions were defined by a difference in texture orientation or motion, Lamme and Spekreijse (1998) failed to find stronger temporal correlation of responses in V1 among cells that responded to the same region (within figure or ground) than among cells that responded to different regions (across figure and ground). Psychophysically, some researchers reported that flickering the figure and the ground regions out of phase facilitated orientation- (and colinearity-) based figure–ground segregation (e.g., Leonards et al., 1996; Usher & Donnelly, 1998, 2001), but others reported null effects using similar stimuli (e.g., Kiper et al., 1996) or attributed the effect to priming from the unmasked stimulus onset (Beaudot, 2002). More relevant to the current study, some have demonstrated that texture segregation (e.g., Fahle, 1993; Forte et al., 1999; Leonards et al., 1996; Rogers-Ramachandran & Ramachandran, 1998) and perceptual organization (Parton et al., 2001) can be induced by temporal cues (opposite temporal phase) alone. However, these results can be explained without requiring a specialized synchrony mechanism. The texture-segregation result can be explained on the basis of early spatiotemporal-separable detectors (thought to be involved in the initial stage of motion processing; e.g., Adelson & Bergen, 1985; DeAngelis et al., 1993) being selectively activated at texture borders along which texture elements on the two sides were oscillated in a contrast-reversing manner (see discussion in Forte et al., 1999). The perceptual-organization result (seeing rows/columns in a square array of elements when alternate rows/columns were oscillated out of phase) can be explained on the basis of repeated activation of horizontally/vertically tuned orientation detectors because the array elements were consistently organized in each frame as rows or columns by grouping by proximity.

The phenomena reported here, that is, the temporal-phase-based enhancement of orientation rivalry as well as the apparent grouping of the discs to the synchronized grating during the rivalry, are difficult to explain on the basis of selective activation of motion- or orientation-tuned receptive fields. This is because (1) the orientation-neutral discs were presented at the static intersections of the alternating gratings, and (2) the task was detection of feature grouping rather than texture-border detection or orientation discrimination. As we pointed out in the introduction, it is possible that temporal coding might be primarily used for resolving overlapping stimuli because differences in temporal phase allow spatially overlapping patterns to be represented separately; some have also speculated that synchronization and desynchronization of neural responses might underlie the eye-of-origin effect in binocular rivalry (e.g., Alais & Blake, 1998; Fries, Roelfsema, Engel, Konig, & Singer, 1997). In contrast, when two patterns do not spatially overlap as in the case of figure–ground segregation, coding of temporal phase is not critical because patterns could be grouped and segregated spatially.

7.2. Oriented shimmer for orthogonally oriented single bars

Oriented shimmer was an effective strategy for frame alternations in the range of 80–20 ms/frame (~6–25 Hz) for the bar stimulus especially when the disc was relatively large. The small gaps, which made the disc-present middle region of the bar discontinuous from the wings of the bar, elevated response latencies somewhat but did not substantially affect threshold frame rates for the detection of oriented shimmer. The fact that the perception of oriented shimmer depended critically on *heterodirectional changes in luminance* (see Fig. 8) provides a clue for understanding the potential neural mechanism generating this phenomenon. We first discuss the possibility that oriented shimmer might be closely related to the perception of bistable (counterphase) motion, apparent motion, and/or flicker-induced contrast illusions.

7.2.1. *Is oriented shimmer bistable drifting motion?*

The bar that generated oriented shimmer, that is, the bar that oscillated with heterodirectional changes in luminance, contained a component of counterphase modulation along its length; the disc- and the wing-regions of the bar oscillated in luminance in opposite temporal phase. With the large disc, the oscillation consisted of a superposition of two approximately square-wave profiles (e.g., contrast = ±3%, wavelength ~2/3 bar length, and spatial frequency ~0.85 c/d) being shifted by a half wavelength per frame in opposite directions. This counterphase oscillation was superimposed on a static luminance step (time averaged luminance being lower or higher in the disc region relative to the wing regions of the bar) and residual luminance oscillation at the disc or at the bar. Although there is no net motion energy, counterphase modulations can appear to drift in one direction (rather than flicker at fixed positions) under appropriate conditions, presumably due to biasing of neural units tuned to one or the other direction of motion. The particular combinations of temporal frequency (up to 25 Hz) and spatial frequency (~0.85 c/d for the fundamental) that generated oriented shimmer, however, were beyond the range in which stable drifting can be observed in sinusoidal counterphase gratings (e.g., Gorea & Lorenceau, 1984). Furthermore, in Experiment 3, oriented shimmer was observed when counterphase modulation was only a tiny fraction of the static luminance profile. We also emphasize that the subjective percept of oriented shimmer was not a slow alternation of unidirectional drifts. Instead, at high frame rates, the bars and the disc appeared to flicker at fixed positions and a faint amorphous shimmer appeared to rapidly jitter along one of the two orientations along the entire length of the bar or primarily over the region of the disc.

7.2.2. *Is oriented shimmer a form of apparent motion?*

This possibility was examined and rejected in Experiment 3 by demonstrating that the bar having heterodirectional changes in luminance still generated oriented shimmer even when both bars contained discs that were clearly darker than the bar, that is, even when potentially informative expansion–contraction apparent motion was eliminated.

7.2.3. *Is oriented shimmer explained by flicker-induced contrast modulation or simultaneous contrast induction?*

Luminance flicker has been known to enhance perceived contrast or produce "luster" depending on the flicker frequency, and the relative luminance of the dark and the light phases of the flicker and the surrounding region (e.g., Anstis, 2000; Anstis & Ho, 1998; Magnussen & Glad, 1975a,b). These effects might make the apparent contrasts of the wing regions of the bars and the disc region differ from when they are static. However, these flicker-induced contrast illusions that modulate apparent brightness of flickered regions cannot explain oriented shimmer because oriented shimmer depends on the relative temporal phase (rather than relative apparent brightness) of flickered regions.

Alternatively, a simultaneous contrast effect (an identical spot appearing lighter in a darker surround and darker in a lighter surround) might be relevant. For example, when the dark red disc was used, the wings of the disc-present bar appeared next to the dark disc whereas the wings of the disc-absent bar had no dark neighbor. A simultaneous contrast effect might thus make the wings of the disc-present bar appear lighter than the wings of the disc-absent bar. Observers then might have used this apparent difference in brightness between the two bars to detect the disc-present bar, while oriented shimmer was an epiphenomenon. We have three pieces of evidence against this explanation. First, the hypothetical brightness difference between the two bars was not observed in our stimulus; when the bars were flickering rapidly, both bars appeared equal in luminance. Second, simultaneous contrast effects have a rather coarse temporal resolution (falling virtually to zero beyond a few hertz of light–dark oscillation of the surrounding luminance; De Valois, Webster, De Valois, & Lingelbach, 1986; Rossi, Rittenhouse, & Paradiso, 1996; but occurring at higher temporal frequencies (peaking at 2–5 Hz) under certain conditions (e.g., high mean luminance and/or high contrast modulations; Magnussen & Glad, 1975b)), whereas oriented shimmer was effective up to 25 Hz with low contrast modulation. Third, oriented shimmer was effective even when simultaneous contrast would have made little contribution, that is, even when both bars contained a dark disc, one being only slightly darker than the other (Experiment 3).

7.2.4. *What mechanism might be causing oriented shimmer?*

Oriented shimmer occurred when both bars contained dark discs (Experiment 3) as well as when only one bar contained a disc (Experiments 1A–C and 2). This indicates that the appearance and disappearance of the luminance edges of the disc were not critical for generating oriented shimmer (the dark disc was always present in Experiment 3). Thus, it is unlikely that on-center-off-surround and off-center-on-surround type ganglion cells (or any other mechanisms tuned to particular contrast-polarity profiles) responding to the luminance edge of the disc made critical contributions to oriented shimmer.

A key feature of oriented shimmer is that it was not induced by contrast relationships among parts of each alternating display, but it was induced by *heterodirectional changes* in luminance. It is known that luminance increments and decrements are detected by separate ON and OFF channels which appear to be segregated until the visual pathway reaches V1 (e.g., Schiller, 1984, 1992). Due to this early segregation, inputs coming through the same channel might preserve coherent temporal phase of stimulus oscillation more precisely than inputs coming separately through the two channels. Thus, the bar that oscillates with unidirectional changes in luminance might drive the responding cortical cells in a temporally coherent manner by virtue of activating ON or OFF channels exclusively along the length of the bar at onsets and offsets. In contrast, the bar that oscillates with heterodirectional changes in luminance might drive the responding cortical cells in a less temporally coherent manner by virtue of activating ON and OFF channels in different parts of the bar at onsets and offsets. These temporally incoherent responses might be detected as enhanced shimmer by higher-level mechanisms.

In conclusion, using rapidly alternating overlapping displays we found evidence that suggests that the visual system can translate coherent and incoherent temporal phase into stable emergent percepts so long as oscillations are defined by changes in luminance; these emergent percepts are not epiphenomenal because they can facilitate detection of repeated feature coincidences beyond the temporal resolution of individual display frames and beyond probability summation. We reported two examples of such emergent percepts. First, rapidly alternating orthogonal gratings with discs synchronized with one grating revealed that image grouping on the basis of in-phase oscillations and image segregation on the basis of out-of-phase oscillations can manifest as enhanced monocular image rivalry. Second, rapidly alternating orthogonal single bars with a synchronously luminance-modulated central disc revealed a mechanism that appears to translate subtle temporal incoherence in neural responses across contiguous regions into a percept of oriented shimmer. Together, the results suggest that the visual system has mechanisms to perform nonlinear temporal integration that can translate rapid temporal phase information into stable parsing of overlapping patterns.

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