

Competing Global Representations Fail to Initiate Binocular Rivalry

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Summary

A longstanding debate in binocular rivalry literature is whether the perceptual competition in rivalry occurs at an early or late stage of visual processing. Central to this debate is the determination of the source of the competition. Overwhelming evidence exists that local interocular differences can lead to binocular rivalry, but it is not yet clear whether interocular conflicts at the global level are sufficient to generate binocular rivalry. The current study adopted a novel stimulus that enabled the introduction of dramatic global differences between the two eyes with compatible local elements. Results show that global differences between the two eyes' images do not result in rivalry if local elements are compatible. The implication of these findings is that the registration of competing interocular information, necessary to generate binocular rivalry, is performed at an early stage of visual processing prior to global analysis of the image.

Introduction

Under normal viewing conditions, the information conveyed by the two eyes can often be matched and combined into a single coherent percept (Howard and Rogers, 1995). However, under some circumstances, the differences between the two eyes cannot be reconciled and the visual system is faced with the conflicting information from the two eyes. One solution to competing information between the two eyes is binocular rivalry, a perceptual alternation between the two eyes' images. The phenomenon of binocular rivalry has long intrigued philosophers, psychologists, and neuroscientists alike. More recently, the phenomenon has gained renewed interest because it provides a dissociation between the physical world and conscious perception, allowing scientists to investigate the factors important for visual awareness (Blake, 2001). A longstanding and unresolved debate in the binocular rivalry literature is whether rivalry is a "low-level" or "high-level" phenomenon (Blake, 2001; Tong, 2001). In recent years, there have been a number of influential findings showing that higher-level representations of stimuli can strongly influence the perceptual outcome during rivalry, such as experiments in interocular grouping (Kovacs et al., 1996) and the demonstration of rivalry between stimulus representations independent of the eye of origin (Bonneh et al., 2001; Logothetis, 1998; Logothetis et al., 1996).

Recently, Blake and Logothetis (2002), in an effort to

reconcile a large body of conflicting evidence between high- and low-level interpretations of rivalry, suggested that rivalry could be decomposed into multiple processes that may occur at different stages of visual processing. The authors' breakdown included: (1) the registration of competing information, (2) the promotion of dominance of one of the two sources of information, (3) the suppression of conflicting information, and (4) the mediation of perceptual switching. The aforementioned experiments by Logothetis et al. (1996) and Kovacs et al. (1996) have shown that high-level global representations of the stimulus pattern can influence the promotion of dominance and mediation of perception switching. The present study specifically focused on what types of competing information are sufficient to initiate rivalry within the context of the debate between high- and low-level interpretations of rivalry. While few would argue that low-level factors contribute to the induction of rivalry (e.g., color, local orientation differences), the contribution of the high-level factors has never been independently tested (Levelt, 1965b). Given the influence that high-level factors can have on the perceptual outcome during rivalry and that the perceptual alternations in rivalry often resemble other high-level multistable phenomena (Andrews and Purvis, 1997), coupled with the idea that the rivalry is a multistage process with competition occurring at multiple stages of visual processing (Leopold and Logothetis, 1996; Ooi and He, 1999; Wolfe, 1996), one may be inclined to believe that high-level global pattern representations also contribute to the induction of rivalry. The aim of the present study was to test this notion.

Evaluating the contribution of competing global patterns to rivalry is hindered by the fact that a pair of stimuli that have conflicting global patterns will also have different local image features. Our solution was a novel stimulus design with global patterns composed of a matrix of local elements. Stimuli of this type were pioneered by David Navon in testing global shape precedence (Navon, 1977). Critically, this type of compound stimuli can achieve a relatively high degree of independence between the local features and global representations. In our study, the stimulus has local elements in the two eyes' images that are matched in shape and have the same contrast polarity relative to the background (Figure 1). In this configuration, local conflicts are reduced to a simple luminance difference. It has been shown previously that when the two eyes' stimuli are of the same shape and contrast polarity, a wide range of interocular luminance differences between the two eyes do not lead to rivalry (Fry and Bartley, 1933; Levelt, 1965a). In the experiments, we made sure that the individual elements paired between the two eyes stayed within a luminance range so that they did not generate rivalry. At the same time, by assigning different luminance values within this range to specific elements in the image, we were able to generate distinct global patterns (e.g., the two orthogonal gratings or the letters X versus O shown in Figure 1). With stimuli generated using this method, we asked whether global form and

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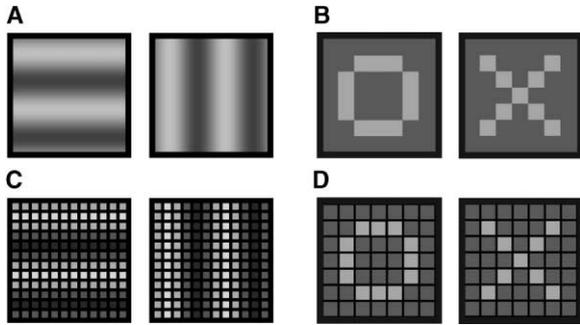


Figure 1. Examples of the Conventional Stimuli and Matrix Stimuli Used in the Study

- (A) Two orthogonal gratings.
- (B) Two different shapes (O and X).
- (C) Two orthogonal gratings at the global level defined by the matched local elements.
- (D) Two globally different shapes (O and X) defined by matched local elements.

global motion conflicts defined by the nonrivalrous local elements could generate binocular rivalry.

It is generally believed that two images with different forms presented on corresponding regions of the two eyes' retinae lead to binocular rivalry. Virtually all experiments involving binocular rivalry use stimuli that involve some variation of conflicting form, ranging from the simplest of stimuli (e.g., horizontal versus vertical gratings) through images with very complex structure (e.g., face versus house). It is not clear, however, whether conflicts at these different levels are all potent in generating binocular rivalry. As shown in Figure 1, the global conflicts between the two eyes arise after one integrates the local elements to form explicit representations of a horizontal and a vertical grating, or an X and an O. It is obvious that the X and the O have different forms, but can they generate rivalry when the elements themselves are not rivalrous? In the first series of experiments, we tested if competing global form representations of the two eyes' stimuli are sufficient to induce binocular rivalry. Specifically, we queried if at the neural site(s) of binocular rivalry, are the differences between X and O registered as such?

In the second set of experiments, we expanded our inquiry into the domain of motion. Numerous studies have documented interactions between motion and binocular rivalry. A number of studies have shown that motion signals tend to integrate between the two eyes even when other features of the stimuli were engaged in rivalry (Andrews and Blakemore, 1999, 2002; Carney et al., 1987). Based on these and other studies (Carlson and He, 2000; O'Shea and Blake, 1986), we advocated a hypothesis that signals processed in the magnocellular pathway may not be subject to interocular rivalry (He et al., 2005). Generally speaking, it is believed that the magnocellular pathway mediates fast temporal events such as motion perception, while the parvocellular pathway mediates the perception of form (Livingstone and Hubel, 1987, 1988; Schiller et al., 1990). An outstanding question that follows from this hypothesis is whether competing motion signals, in the absence of conflicting form, can generate binocular rivalry (i.e., can "pure mo-

tion" signals generate rivalry?). The prediction being that pure motion cannot induce rivalry, which was supported by the findings of Ramachandran (1991) but later challenged by Blake and colleagues (1998). The difficulty in answering this question again lies in the construction of the stimuli. The problem is that for most conflicting dichoptic motion stimuli, the two eyes also receive conflicting information along other dimensions, often form. Thus, it is difficult to assess whether motion rivalry is generated by competing motion signals, or if it is simply a dynamic version of form rivalry. The matrix stimuli introduced in this study provide an opportunity to test if conflicting motion, in the absence of other conflicting signals between the two eyes, is sufficient to generate binocular rivalry.

Results and Discussion

Many properties associated with binocular rivalry can be measured experimentally, such as the mean dominance time, rate of perceptual switching, etc. Since the goal of the present study is to determine whether competing global information between the two eyes can generate binocular rivalry, the variable of interest is the proportion of the time that rivalry is experienced for various stimuli. This measure provides an index of the effectiveness of a stimulus to generate binocular rivalry. If the rivalry mechanism is sensitive to a conflict in the stimuli, then the rivalry mechanism will engage and binocular rivalry will be experienced. If the rivalry mechanism is not sensitive to a conflict, then subjects will not experience rivalry and some sort of integration will occur.

Global Form Conflict and Binocular Rivalry

First, using two uniform squares presented to the two eyes on dark background, we determined experimentally an interocular luminance range that was insufficient to generate binocular rivalry. This range, however, was more than sufficient to generate a perceptually salient global pattern. The luminance of the elements that formed the letters was set to the maximum value of this range and the luminance of the remaining elements was set to the minimum value. As a control condition, the first pair of stimuli was an X and an O in their conventional form (Figure 2A). Not surprisingly, this pair of stimuli was effective in generating binocular rivalry. Subjects reported seeing rivalry about 90% of the time.

Next, we constructed the same X and O patterns with locally matched elements (matrix condition). This manipulation effectively removed the local contours' contribution to rivalry (Fry and Bartley, 1933; Levelt, 1965a). The result of this rather simple manipulation is a dramatic shift from rivalry to fusion (Figures 2B and 3). Subjects now predominantly reported seeing fusion (Figure 2). Apparently, the global X and O patterns in the two eyes were insufficient to generate binocular rivalry. Note, the differences between the images presented in the first experiment and the second experiment are very small (Figures 2A and 2B, top), yet the perceptual consequences are striking (Figures 2A and 2B, bottom). Figure 3 schematically shows the perceptual outcomes of the two stimulus conditions. Subjects perceived alternations of X and O or parts of the X and O in the conven-

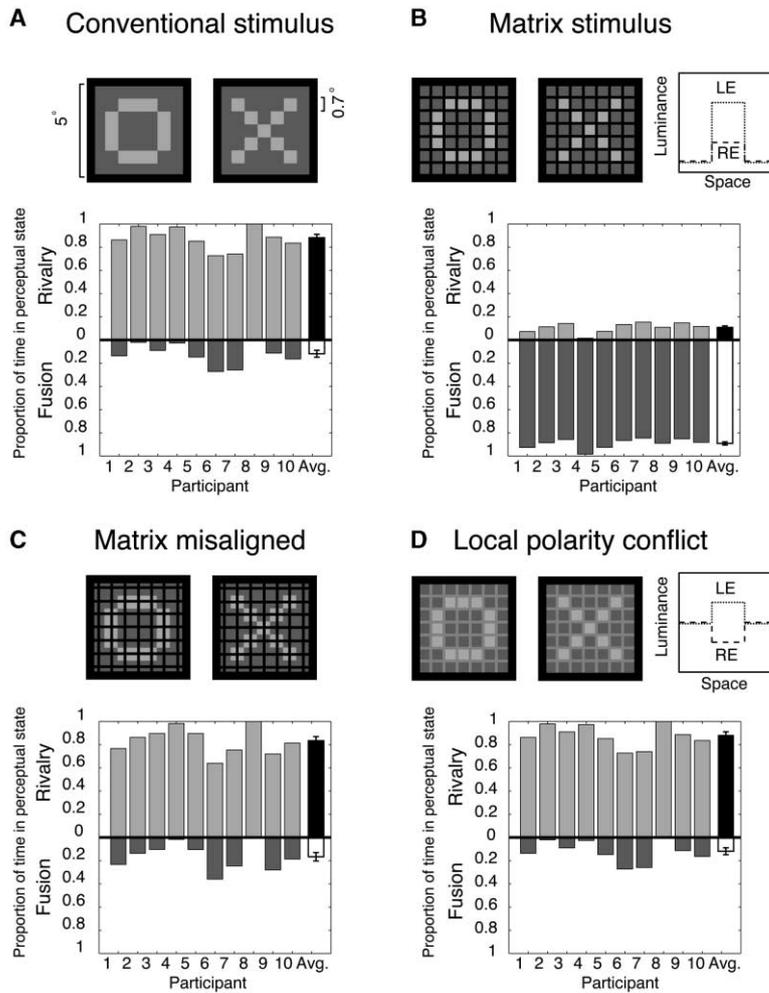


Figure 2. Stimuli and Results for Global Form Rivalry Experiments

Results are reported as the proportion of time subjects reported perceiving fusion and rivalry. Data from ten naive subjects as well as cross-subject average data are plotted. Error bars are \pm one SEM. Above the plots are example stimuli for each experimental condition.

(A) Conventional stimuli: stimulus with both local and global competition.

(B) Matrix stimulus: local competition is removed from the stimulus using occluders. (C) Matrix misaligned: occluders are misaligned, revealing local contours.

(D) Polarity conflict: occluders set to an intermediate luminance value, creating a local polarity conflict between matched elements.

Subjects perceived very little rivalry for the matrix stimulus (B) but perceived clear alternations (rivalry) most of the time for conditions (A), (C), and (D). To highlight the luminance polarity relations in conditions (B) and (D), the luminance profile from two matched elements between the two eyes are shown next to the example stimuli.

tional condition during most of the test period, but in the matrix condition they only occasionally saw indications of rivalry including mosaic rivalry. The results of these experiments indicate that conflicting global patterns are not capable of generating rivalry.

Introducing fusible contours to the two eyes' images has been shown to reduce the incidence of rivalry and promote fusion (Blake and Boothroyd, 1985; de Weert and Wade, 1988). Thus, one possible reason that little rivalry was perceived in the matrix condition was that the occluding lines provided a strong fusion cue that generally promoted fusion. This possibility was tested with a simple manipulation in which the occluding lines were shifted and misaligned with the boundaries of local square elements, thereby revealing the competing local contours (Figure 2C, top). With this manipulation, observers again perceived vigorous rivalry between the X and O patterns (Figure 2C, bottom). Clearly, simply having matched lines in the two stimuli that provide an additional fusion cue does not prevent observers from perceiving binocular rivalry, and it was not the reason that little rivalry was experienced in the condition shown in Figure 2B.

Finally, to demonstrate the critical importance of the local image feature conflicts to rivalry, as well as to further demonstrate that having matched lines does not

prevent global pattern rivalry, we performed an experiment in which the luminance of the occluding lines of the matrix was changed to an intermediate value (Figure 2D, bottom). This manipulation maintained the fusible grid lines but created competition between the local elements because the luminance of the local elements have the opposite polarity against the background, which would lead to rivalry between local elements. Not surprisingly, subjects again perceived vigorous rivalry between the X and O (Figure 2D, bottom). In addition to demonstrating the critical role of local competition to rivalry, this result also provides additional evidence that the result shown in Figure 2B was not merely due to the presence of fusible grid lines in the stimulus.

Global Motion and Binocular Rivalry

The issue of whether pure conflicting motion signals in two eyes can generate rivalry remains unresolved. The dichoptic matrix stimulus provides another opportunity to examine the contribution of motion, specifically global motion, to the induction of binocular rivalry. In the previous section, we have shown that conflicting global patterns in the two eyes do not generate binocular rivalry. In the next set of experiments, a motion component was added to the stimulus by sequentially modulating the luminance of local elements. Using this dynamic version

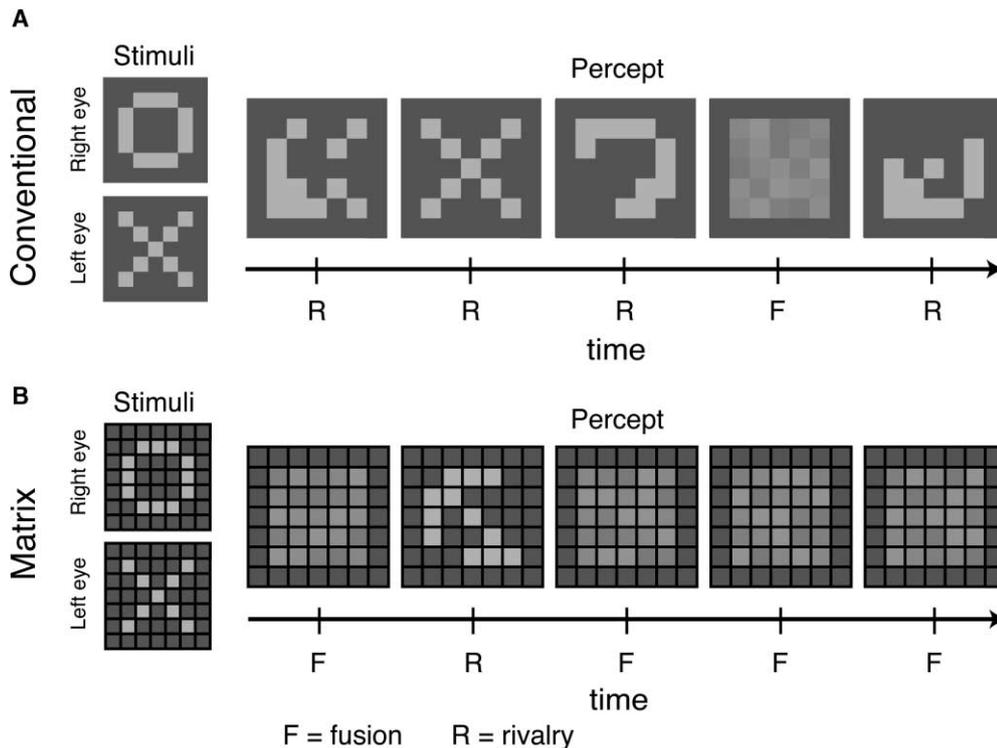


Figure 3. Schematic Depiction of Possible Perceptual Outcomes for Global Form Stimuli

Subjects indicated fusion or rivalry for the global form stimuli. Fusion (F) was reported when subjects perceived a relatively stable integration of the two eyes' images (the small luminance differences in the elements are shown to indicate nonuniform summation of the two eyes' images). Rivalry (R) was reported when subjects perceived alternations between left and right eyes' figures or their parts.

(A) A representative time series of a subject's percept of the conventional global form rivalry stimulus.

(B) A representative time series of a subject's percept of the matrix global form rivalry stimulus.

of the matrix stimulus, we tested if competing global motion signals could generate rivalry with the assurance that form conflicts in the stimulus were not a contributing factor.

We first verified that the form conflicts between the two grating stimuli would not generate rivalry if presented using the matrix. The stimuli were two orthogonal luminance sine wave gratings with or without the occluding grid lines (Figure 4A). Similar to what we found in the previous section, the results clearly show that the orthogonal grating stimuli composed of matched local elements did not engage in binocular rivalry, even though each local element has a small luminance gradient. Without the occluding lines, the orthogonal static luminance gratings generated rivalry, but with occluding lines, subjects perceived a fusion of the two eyes' stimuli.

We next tested the contribution of global motion to rivalry using drifting gratings with both orthogonal and opposing motion. Again, the incidence of binocular rivalry was measured both with and without the grid lines (i.e., matrix stimulus and a regular grating stimulus). As shown in Figures 4B and 4C, observers experienced very little perceptual alternations when the moving gratings were presented behind the occluding lines. In the matrix condition, when the two gratings moved in orthogonal directions, subjects frequently perceived motion of a plaid-like pattern in the vector sum direction (diagonal); when the two gratings moved in the opposing directions,

subjects mostly perceived a grating pattern that rocked back and forth, rarely traveling in one direction for more than half a cycle. The results of these experiments indicate that global motion signals also are not capable of generating binocular rivalry.

In addition to simple linear motion, we also tested complex motion patterns. Complex motion patterns, similar to linear motion, have often been used as rivalry stimuli, and rivalry can be experienced between different types of complex motion signals. However, there have been mixed reports of rivalry with complex patterns and differential outcomes between simple and complex motion in experiments investigating rivalry. Rivalry has been observed with complex motion (Wade and de Weert, 1986), and yet pairs of opposing complex motion such as expanding versus contracting, rotating clockwise versus counterclockwise, and opposite spiraling motion have also been reported to standstill instead of engaging in motion rivalry (de Weert and Wade, 1984). Furthermore, adaptation studies have also shown that simple linear motion signals can adapt during suppression (i.e., phenomenological removal of the stimulus) and subsequently induce a motion aftereffect (MAE) just as strong as nonsuppressed adaptation (Lehmkühle and Fox, 1975; O'Shea and Crassini, 1981). Adaptation to complex motion, however, is affected by suppression and produces a weaker MAE when adapted during binocular rivalry (van der Zwan et al., 1993; Wiesenfelder

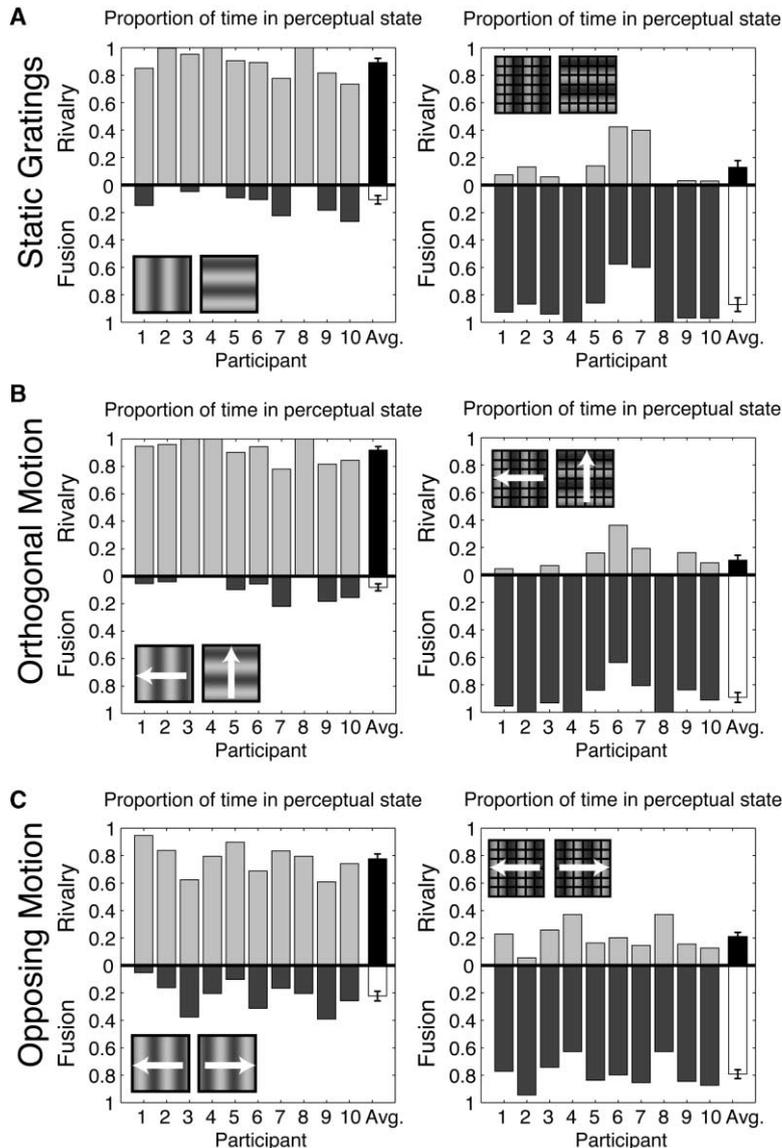


Figure 4. Results for the Global Motion Experiments

Data are reported as the proportion of time each subjects reported perceiving integrated motion and alternating (rivalry) motion. Data from ten naive subjects as well as their average are plotted. Error bars are \pm one SEM. An iconic depiction of the stimuli is shown next to each of the plots. Arrows denote the direction of motion.

(A) Static orthogonal gratings.

(B) Orthogonal motion.

(C) Opposing motion. Conventional stimuli generated very strong rivalry, but very little rivalry was perceived when stimuli were presented in the matrix format.

and Blake, 1990). The purpose of the next experiment was to test if complex global motion signals were capable of generating binocular rivalry (i.e., perceptual alternation between expanding and contracting or clockwise and counterclockwise motion). The results of the experiments using complex motion signals were consistent with that of the linear motion condition. Without the matrix, subjects experienced perceptual rivalry alternations about 70% of the time. They reported very little rivalry under the matrix condition (Figure 5). Competing complex global motion signals also appear to be unable to generate binocular rivalry.

As mentioned earlier, Ramachandran used the motion aftereffect (MAE) to generate competing motion signals in the two eyes (Ramachandran, 1991) and tested if observers perceived binocular rivalry. After adapting the two eyes to two different motion signals, subjects perceived a motion aftereffect in different directions when each eye was tested alone, but they experienced rivalry only if differently oriented gratings were presented to

the two eyes. Subjects did not perceive rivalry when both eyes were looking at the same stimulus. Our results are consistent with Ramachandran's observation that pure motion signals cannot generate rivalry. Using a dynamic test stimulus, Blake and colleagues reported that subjects could perceive rivalry between two eyes' MAEs following differential adaptation (Blake et al., 1998). However, the Blake et al. study used a very indirect measure of binocular rivalry (i.e., percept was categorized as rivalry when subjects perceived motion direction other than the mean of the left and right eye's MAE), which in our view casts doubts on whether binocular rivalry between MAE signals was really perceived.

The stimuli used in our motion experiments were of the spatial scale such that V1 neurons would unlikely to be sensitive to the global motion, but MT neurons would be capable of detecting the motion signals (Mikami et al., 1986a, 1986b). Thus, one interpretation of this result would be that competing motion signals need to be registered at the V1 level in order to initiate binocular

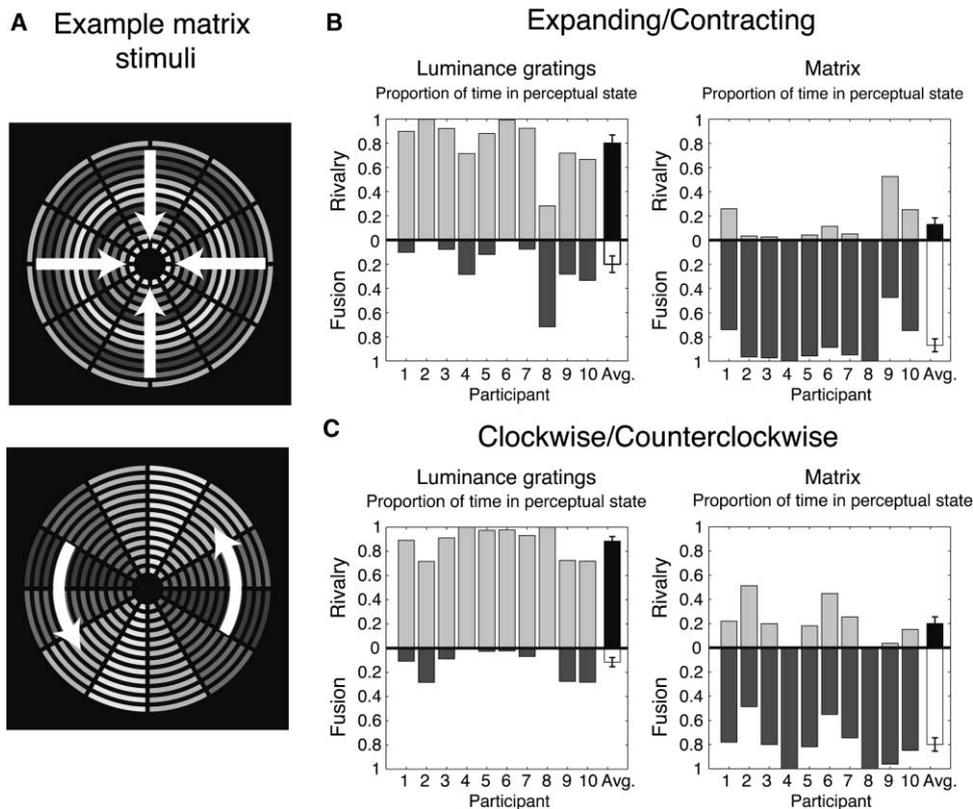


Figure 5. Results from the Complex Motion Experiment
 (A) Schematic depiction of complex matrix motion stimuli.
 (B) Results for competing expanding/contracting motion stimuli.
 (C) Results for competing clockwise/counterclockwise rotating motion stimuli. Results in (C) and (D) are plotted the same way as in Figures 2 and 4.

rivalry. With regard to the issue of why some studies show rivalry between complex motion while others show integration of the motion signal, our view is that the outcome critically depends on whether the moving pattern is trackable or not. With relatively coarse stripes and slow speed, each eye's features can be tracked, and this in turn can be seen as alternating (such as the case in Carlson and He, 2000, slow speed condition). When the features become dense and/or move relatively fast, feature tracking becomes difficult, and then motion cancellation becomes apparent (such as in de Weert and Wade, 1984; Carlson and He, 2000, fast speed condition).

Conclusions

Many factors can influence the characteristics of binocular rivalry, but not all of them are responsible for initiating rivalry. The present study investigated what types of interocular conflicts are sufficient to generate binocular rivalry. The results of our experiments show that when local conflicts are removed, conflicting global signals between the two eyes are insufficient to generate binocular rivalry. This was true for both conflicting global form and motion stimuli. The implications of these findings is that the mechanism responsible for generating binocular rivalry is likely based on local competition that occurs prior to the explicit representation of pattern infor-

mation. As a cautionary note, the conclusions drawn from this study bear more directly on binocular rivalry in the classic sense and may not generalize to other forms of perceptual rivalry (e.g., stimulus rivalry resulting from fast interocular stimulus switching).

In terms of the neural correlates of binocular rivalry, our results support the view that the mechanism that engages rivalry is at an early stage in the system, prior to the explicit representation of global information. Since the two eyes' images are locally compatible, the disparate information in the two eyes is fused. Thus, locally fusible but globally different patterns are not capable of generating rivalry because the local conflict has been removed. This view is consistent with recent fMRI studies showing that in a monocular patch in V1 (blindspot) as well as in extrastriate areas selective for faces and houses, fMRI-measured activity was fully modulated by the alternating perception (Tong and Engel, 2001; Tong et al., 1998). In addition, our results are also consistent with the neurophysiological finding that activity of neurons at high levels (e.g., inferotemporal and MT) tend to follow perception, while activity of V1 neurons are more likely to be stimulus driven (Logothetis, 1998), if one interprets the physiological finding as showing V1 to be the site for rivalry initiation and those high-level areas are receiving the outcome of the early competition.

A recent publication seems to contradict our claim

that global representation in the absence of local conflict will be unable to initiate binocular rivalry. Andrews and Lotto (2004) showed that two physically identical patches made to appear perceptually different by embedding them in different chromatic contexts can engage in rivalry. Their interpretation of these results is that rivalry is the result of competition between meaningful interpretations of the two eyes' images. Their claim is inconsistent with the conclusion reached in the current paper. In our experiments, the matrix stimuli (e.g., X versus O) could not be more different, yet they did not generate rivalry. In our view, Andrews and Lotto's observation could be interpreted as that the mechanisms responsible for color contrast and color constancy are early in the visual pathway (Moutoussis and Zeki, 2000) and may precede the mechanism that determines rivalry. This is similar to the demonstration that filling-in at the natural blindspot can contribute to rivalry (He and Davis, 2001), which suggests that the filling-in process is occurring at least partly before the rivalry mechanism. There is no evidence that indicates that meaningful interpretations have been generated for each eye's image and rivalry is between these meanings. On the contrary, the current study clearly demonstrates that when local conflicts are removed from two stimuli that have dramatically different meanings, there is no rivalry.

The idea that binocular rivalry is a multistage process has recently gained more popularity (Blake and Logothetis, 2002). This is in part an effort to reconcile the disparate evidence supporting early versus late rivalry (Tong, 2001). However, unless one can specify what type of information and under what conditions rivalry occurs, simply saying that rivalry is a complex phenomenon that occurs at multiple stages is not very satisfying. Although high-level and global information can strongly influence the dynamics and organization of binocular rivalry, based on the evidence presented in this paper, our view is that the mechanism that determines whether competing information would result in binocular rivalry is fundamentally a local and early process.

Experimental Procedures

Participants

Ten naive observers participated in the experiments. All observers had normal or corrected to normal vision. No formal stereo test was administered, but all could see stereo random-dot images.

Apparatus

Stimuli were generated on a Macintosh G4 computer with MATLAB and presented on a 19" Mitsubishi Diamond Pro monitor (1280 × 1024 at 85 Hz) using the psychophysical toolbox (Brainard, 1997; Pelli, 1997). The two eyes' images were displayed side-by-side on the monitor and fused using a mirror stereoscope mounted on a chinrest. A frame that extended roughly 0.2° beyond the outer border of the stimulus and fixation point were presented to facilitate stable convergence of the two eyes' images. The viewing distance was 57 cm.

Form Rivalry Stimuli

Stimuli in the form experiment were 7 × 7 matrices of local elements with the unique global configurations of the letters X and O for the left and right eye, respectively (see Figure 1). Local elements were 0.7° × 0.7°. The global pattern was 5° × 5°. Stimuli were presented on a dark background (1.2 cd/m²). Light and dark elements were 58.1 cd/m² and 13.1 cd/m², respectively. Occluder bars were 0.2° in width and of the same luminance as the background (1.2 cd/m²).

Example stimuli for each experimental condition are shown in Figure 2. In the matrix condition, dark occluders were arranged to cover the boundaries between the local elements. In the matrix misaligned condition, occluders, identical to those in the matrix condition, were positioned to pass through the center of the local elements, revealing the local contours. In the local polarity conflict, the luminance of the occluders was changed to 32.8 cd/m², creating the opposite luminance polarity for the light and dark square elements.

Motion Rivalry Stimuli

Linear motion stimuli were sine wave gratings at 0.8 cycles/° subtending 3° by 3°. Expanding and rotating motion stimuli were circular and radial gratings modulated at 1.6 cpd and 1 cycle/radian, respectively; both had a diameter of 3°. In both experiments, grating patterns had a mean luminance of 35.6 cd/m². Matrix stimuli were composed of a 12 × 12 array of elements (0.18° in height and width) generated by placing evenly spaced occluders 0.07° in width over the luminance gratings for experiments using linear motion. Elements for complex motion were generated using the polar coordinate system. Individual elements were 0.15 radians by .09°, and occluders were 0.05 radians by .02° with small amount of linear expansion added to elements in the periphery. All moving stimuli drifted at a rate of 2 Hz.

Procedure

Subjects were asked to maintain fixation and press one of two buttons to indicate their percept (fusion or rivalry). Since the purpose of the study was not to study the conditions for exclusive dominance versus mosaic rivalry, subjects were only asked to report between two perceptual alternatives, fusion and rivalry. Prior to the experiments, subjects were given an opportunity to view a physically fused version of the stimuli constructed by averaging the two eyes' images (image sequences for moving stimuli) and the two eyes' images (image sequences) individually. The instructions to the subject were to respond "rivalry" if they saw an alternating percept of the two eyes' images or fluctuating parts of the two eyes' images, and to respond "fusion" if they perceived no clear parts of the two eyes' images and no sense of alternation in percept. Data were collected in four 30 s trials for a total of 120 s for each experimental condition. The form and motion experiments were run in separate sessions, but different conditions within the form experiment and the motion experiment were run in an interleaved sequence. Results of the experiments are reported as the proportion of time subjects reported seeing rivalry versus fusion.

Acknowledgments

This work was supported by grants from the James S. McDonnell Foundation and National Institutes of Health (R01 EY015261). We thank the anonymous reviewers for their helpful comments and suggestions on an early version of this paper.

Received: March 23, 2004

Revised: June 28, 2004

Accepted: August 27, 2004

Published: September 15, 2004

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