

Binocular Rivalry and Motion Perception

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Abstract

■ In a series of experiments psychophysical techniques were used to study the relation between binocular rivalry and motion perception. An initial series of experiments confirmed that motion enhances the predominance of an eye during rivalry, although the direction of motion does not matter. The presence of an annulus of motion immediately surrounding one eye's rival target greatly enhances dominance of that target, but the influence of the annulus progressively decreases as the separation between disk and annulus increased. Opponent directions of motion in disk and annulus yield greater dominance than when dots in the disk and annulus moved in identical directions. In a second experiment the two eyes were adapted to

orthogonal directions of motion, generating strong, distinctively different monocular motion aftereffects (MAEs). Even though the two eyes view physically identical random-motion displays following differential adaptation, binocular rivalry of the discrepant MAEs can occur. Finally, using a stimulus replacement technique to measure detectability of translational and rotational motion, it was found that both types of motion were readily detected during periods of dominance but went undetected during periods of suppression. Taken together, these results bear on the process responsible for rivalry and its neural locus relative to the analysis of different types of motion. ■

INTRODUCTION

Visual perception is the culmination of information processing within hierarchically organized stages, with different qualitative aspects of the visual scene engaging populations of neurons distributed among numerous, distinct visual areas (e.g., Felleman & Van Essen, 1991). Given this conceptualization, a comprehensive account of visual perception must include not only details of specific aspects of vision (e.g., color perception) but also the interrelationships among different aspects of vision (e.g., the interaction of color and form). In this spirit, we have performed a series of experiments focusing on the broad question of the relation between visual motion perception and binocular vision, particularly binocular rivalry. The motivation for our interest in this problem comes from several sources:

1. Binocular rivalry itself is fascinating: Dissimilar monocular images, rather than coalescing into a stable binocular hybrid, undergo alternating periods of dominance and suppression. How the brain manages, for several seconds at a time, to block from consciousness an otherwise interesting, complex monocular image represents a mystery that has recently attracted the attention of visual neuroscientists (Logothetis & Schall, 1989; Sengpiel, Blakemore, & Harrad, 1995; Leopold & Logothetis, 1996) as well as computational theorists (Crick, 1996), who see

binocular rivalry as a paradigm case for studying visual awareness.

2. Binocular rivalry affords a powerful psychophysical technique for inferentially partitioning hierarchically organized stages of visual processing (Blake, 1995). In effect, one can use rivalry suppression as a neural landmark for determining what aspects of visual information processing remain effective during rivalry suppression and what aspects are blocked by suppression.

3. Studying the conditions that instigate rivalry sheds light on the stimulus features used in binocular matching and the establishment of stable binocular single vision. If suitable matches can be established between left- and right-eye views, binocular single vision results; otherwise, binocular rivalry ensues. Thus, the compatibility of the monocular stimuli must be assessed at some site of binocular interaction. The types of interocular differences capable of generating binocular rivalry inform us about the inputs to the binocular matching process.

4. Exciting developments in the field of motion perception have greatly refined our understanding of the neural mechanisms involved in registration of different types of motion information (Movshon, 1990). It is now generally agreed that motion perception is the culmination of hierarchically organized processes that start with local registration of uniform (i.e., translational) motion followed by integration of these local signals to represent more global forms of motion, including rotational and

radial motion (e.g., Morrone, Burr, & Vaina, 1995). It is possible to capitalize on the hierarchical nature of motion processing to draw inferences about the site of rivalry suppression.

Together these considerations led to the present experiments, the overarching goal being to detail how binocular rivalry and motion perception are interrelated. While others have addressed specific questions about rivalry and motion (Blake, Zimba, & Williams, 1985; Breese, 1899; Fox & Check, 1968; Fox, Todd, & Bettinger, 1975; Lehmkuhle & Fox, 1975; O'Shea & Crassini, 1981; Wade, de Weert, & Swanson, 1984; Wiesenfelder & Blake, 1990), this paper provides a comprehensive look at exactly how motion influences binocular rivalry and how rivalry influences the perception of motion.

RESULTS

Motion Predominates during Rivalry

In his seminal work on rivalry, Breese (1899) noted that a moving target viewed by one eye tended to dominate over a stationary one viewed by the other, a characteristic confirmed in more contemporary studies (Blake et al., 1985; Walker & Powell, 1979). In the experiments in this section, we have confirmed this observation and extended its generality.

Figure 1a documents the potency of motion, in this case an array of stationary dots pitted against a random-dot cinematogram (RDC) in which all dots moved in a given direction, with the particular direction varied over blocks of trials. During a series of 60-sec tracking periods, the moving dots were exclusively visible for an average total duration of 40 sec, and the stationary dots were dominant for only about a total of 10 sec; the remainder of the time was occasioned by mixed dominance in which portions of each eye's view were visible. In terms of predominance, all directions of motion appear equal in predominance strength—there is no evidence for an oblique effect of the sort established for pattern vision (Appelle, 1972). Nor, for that matter, does a single direction of coherent motion predominate more than random motion in which dots are free to move in all different directions (Figure 1b).

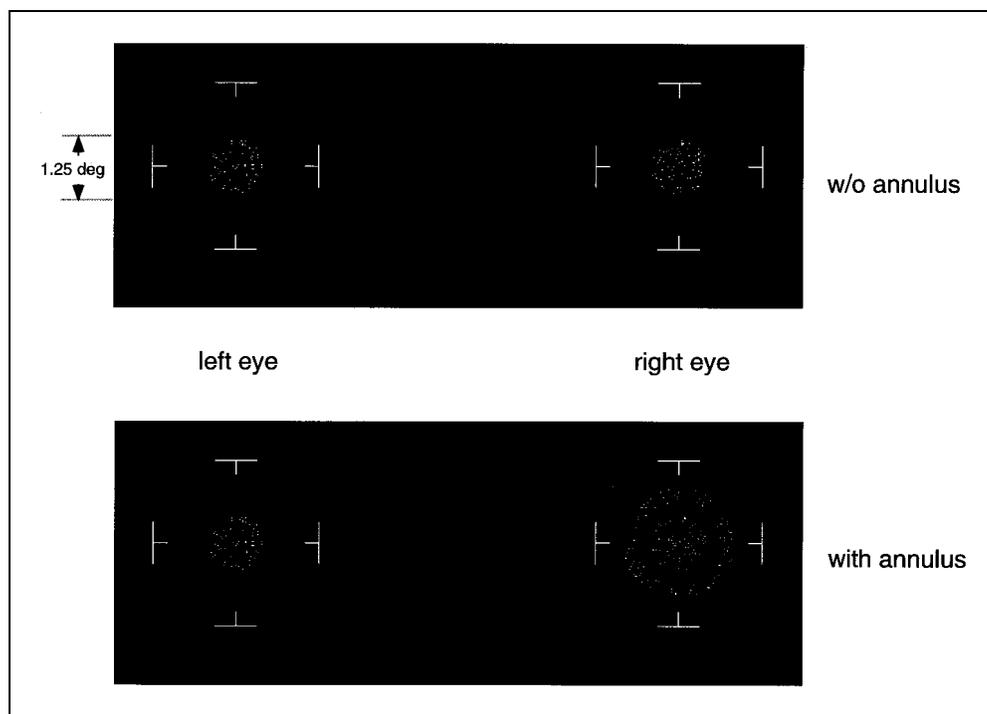
In contrast to motion direction, motion speed does strongly modulate the potency of motion in rivalry. For this experiment one eye viewed dots moving upward at a constant speed of 1.2° per sec and the other eye viewed downward moving dots whose speed varied over blocks of trials from 0.3 to 2.1° per sec. Each speed combination was tested in six 1-min tracking periods, with direction counterbalanced between eyes. The results, presented in Figure 1c, revealed that intermediate dot speeds predominated for a larger percentage of the viewing period compared to the slower and faster speeds. We also found that the rivalry alternation rate (i.e., the rate of fluctuations in dominance) increased

with dot speed, in large measure because the periods of suppression were more abbreviated with faster-moving dots.

One hallmark of rivalry between stationary targets is the increased incidence of mixed dominance (i.e., simultaneous visibility of portions of each eye's view) with larger rival targets. We wondered whether rivalry between opposite directions of motion would exhibit the same dependence on stimulus size. To find out, we measured periods of exclusive visibility and periods of mixed dominance for dots moving upward in one eye and downward in the other eye; the diameter of the circular patch of rival dots was varied over blocks of trials. Results, presented in Figure 2, show that the incidence of mixed dominance does indeed increase with rival target size. Extrapolating the best-fit regression line for the exclusive visibility data, one finds that this line intersects the 100% point (i.e., zero duration mixed dominance) at a diameter value of 9 arc min. This value is essentially identical to that found for foveally viewed, stationary rival targets (Blake, O'Shea, & Mueller, 1992). This equivalence of rival zone sizes for static and dynamic targets suggests that the underlying inhibitory circuitry thought to mediate rivalry between static targets (e.g., Blake et al., 1992) may be applicable to dynamic targets as well.

Motion falling *outside* a monocular area engaged in rivalry can boost the predominance of its rivalrous monocular neighbor. For these measurements, observers dichoptically viewed small circular disks within which dots moved upward in one eye's view and downward in the other, with dot speed fixed at 1.2° per sec. These conditions produced vigorous binocular rivalry with few periods of mixed dominance, and observers had no trouble tracking fluctuations in motion dominance during 60-sec rivalry epochs. On some trials, these two opposite directions of motion were viewed on their own, and the predominance of the two was roughly equal (i.e., each was exclusively visible for about 45% of the viewing period, with mixed dominance being experienced for the remainder of the time). On other trials, an annulus of dots moving in random directions surrounded one eye's rival target (Figure 3), and this monocular annulus greatly enhanced dominance of the moving dots surrounded by the annulus. However, as the separation between disk and annulus increased, the potency of the annulus was progressively weakened (Figure 4). Motion in the annulus was effective in enhancing dominance of the surrounded disk regardless of dot speed, which is rather surprising given that dot speed of the rival target itself has a pronounced effect on predominance. Moreover, unlike motion direction in the rival target itself (recall Figure 1b), the direction of motion in the nonrivalrous surround did matter (Figure 5). Opponent directions of motion in disk and annulus yielded significantly greater dominance than did identical directions of dot motion in disk and annulus; or-

Figure 3. Schematic of rival targets. One eye viewed 50 dots all moving upward and the other eye, 50 dots all moving downward; individual dots subtended approximately 2 arc min, and the circular area within which dots were confined subtended 1.25° . Dots were white against a black background, and four fusion contours were located symmetrically around the circular rival targets. Surrounding the moving dots in one eye's view was an annulus region filled with dots moving randomly; the width of this annulus was always 20 min arc, and the separation between the inner edge of the annulus and the outer edge of the circular rival area was varied over blocks of trials from 0 to 60 min arc in 10-min steps. Observers tracked rivalry between the two opposite directions of motion during 60-sec viewing periods. Each gap size was tested four times, twice with the annulus surrounding the upward-moving dots and twice with the annulus surrounding the downward-moving dots.



Rivalry Is Engaged by “Illusory” Motion Signals

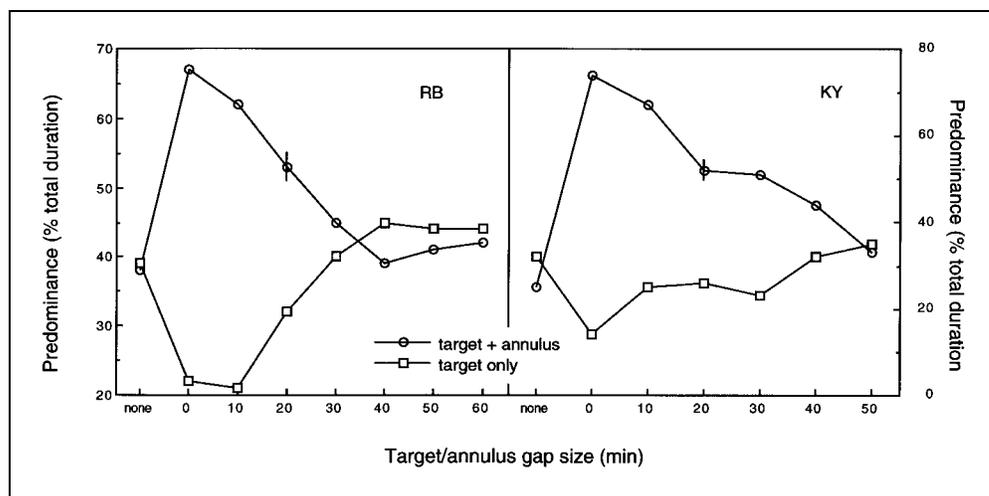
We know that rivalry is triggered when left- and right-eye views are simply too dissimilar to promote binocular fusion; rivalry, in other words, is the default outcome when binocular matching fails (Blake & Boothroyd, 1985). But what transpires when physically identical monocular stimuli *appear* dissimilar by virtue of differential adaptation of the two eyes? First we will explain how this can be accomplished and then describe what actually happens and why the result is significant.

To start, imagine a pair of identical RDCs portraying completely random motion. Upon viewing the two members of the pair separately with the two eyes, observers perceive a single, stable motion sequence—the members of the pair are fused binocularly (middle portion of Figure 6). Moreover, this stable binocular view contains no sense of coherent motion in any particular direction, which is understandable given the totally random distribution of local motion vectors. But now suppose the two eyes are separately adapted to different directions of coherent motion for an extended period of time, say motion down and to the left (DL) for the right eye and motion up and to the left (UL) for the left eye (upper portion of Figure 6). Now upon viewing the *random*

motion sequence, observers temporarily perceive semi-coherent motion up and to the right (UR) when viewing with the right eye and motion down and to the right (DR) when viewing with the left eye (lower portion of Figure 6). This *illusory* sense of directional motion represents a dynamic version of the classic motion aftereffect, and it is thought to arise directly from neural adaptation of motion-selective neurons (Hiris & Blake, 1992; Tootell et al., 1995). So by differential monocular adaptation, it is possible to create dichoptic differences in perceived direction of motion from physically identical monocular stimulation. Do observers experience binocular rivalry from these physically identical but perceptually dissimilar stimuli? Before disclosing the answer, let us comment on why the question is worth asking in the first place.

An answer to this question sheds light on the site within the visual nervous system where the stimulus conditions triggering binocular rivalry are registered. The motion aftereffect itself is certainly cortical in origin, because adaptation to motion transfers interocularly (e.g., Steiner, Blake, & Rose, 1994) even when the adapted eye is pressure-blinded to remove any retinal contribution (Barlow & Brindley, 1963). Moreover, there is physiological evidence (e.g., Movshon & Lennie, 1979)

Figure 4. Predominance scores (i.e., percentage of time during the 60-sec viewing period) for the target-plus-annulus and the target alone as the function of gap size. For both RB and KY the annulus significantly increased predominance ($F(1, 42) = 72.847$ for RB and 331 for KY, both values $p < 0.001$) and the interaction between gap-size and annulus was highly significant ($F(6, 42) = 25.380$ for RB and 42.1 for KY). Only for KY was the effect of gap-size significant ($F(6, 42) = 5.49$, $p < 0.001$; $F = 0.28$ for RB). The short vertical lines denote the average SE for these observers.



that neurons in visual cortex, but not subcortical areas, show temporary reductions in responsiveness following prolonged stimulation to visual motion. Given, then, that the motion aftereffect is cortical in origin, think again about the situation where a motion stimulus viewed by the right eye looks different from that same stimulus viewed by the left eye. If the cortical site of motion adaptation occurs prior to and provides input to the rivalry process, dichoptic motion aftereffects should yield binocular rivalry. On the other hand, if the site of motion adaptation occurs after (or in parallel with) the neural site of rivalry, there is no reason to expect rivalry of dichoptic aftereffects.¹

Now, if interocular transfer of the MAE were complete, it would be impossible to generate dissimilar monocular MAEs. The MAE, however, shows only partial interocular transfer, meaning that the strength of the MAE is weaker in the unadapted eye than in the adapted one. Thus, in

principle, it is possible to induce opposite direction MAEs in the two eyes. Before performing the critical experiment, however, we needed to establish that these dissimilar monocular MAEs were sufficiently robust, in principle, to trigger discriminable binocular rivalry. This involved two steps: (1) determining the minimum level of motion strength sufficient to generate rivalry and (2) determining whether differential monocular adaptation could produce MAEs equivalent in strength to that value. To determine the strength of the physical motion signals necessary to generate discriminable binocular rivalry, we presented separate RDCs to the two eyes, one containing a given percentage of dots moving UR and the other containing the same percentage of dots moving DR. Over blocks of trials we varied the percentage of signal dots in these two dichoptic RDCs, sampling values from 0 to 40% in 10% steps. Observers viewed these pairs of rival motion for 4-sec intervals and then indicated by

Figure 5. Predominance (expressed as total percentage of time during the 60-sec viewing period) for the target-plus-annulus and the target alone for four different annulus conditions. In each condition, the monocular annulus was 20 arc min in width and the gap between the inner edge of the annulus and the outer edge of the circular rival area was 20 arc min. For the Stationary condition dots in the annulus were stationary; for the RDVN condition, they moved randomly in direction from frame to frame; for the Same condition the dots in the annulus moved in the same direction as the dots in the rival target they surrounded; for the Opposite condition the annulus dots moved in the direction opposite of those in the rival target they surrounded. For each condition the observer tracked rivalry during four 60-sec viewing periods, with direction of motion counterbalanced within trials of a block.

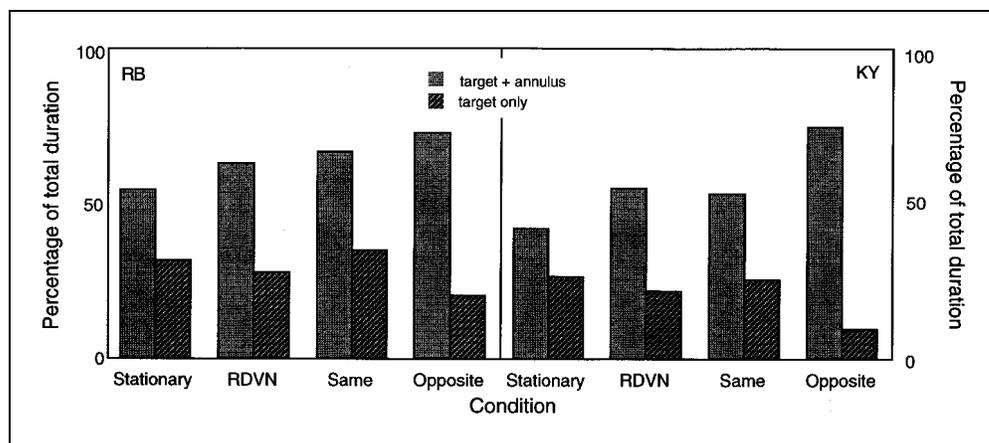
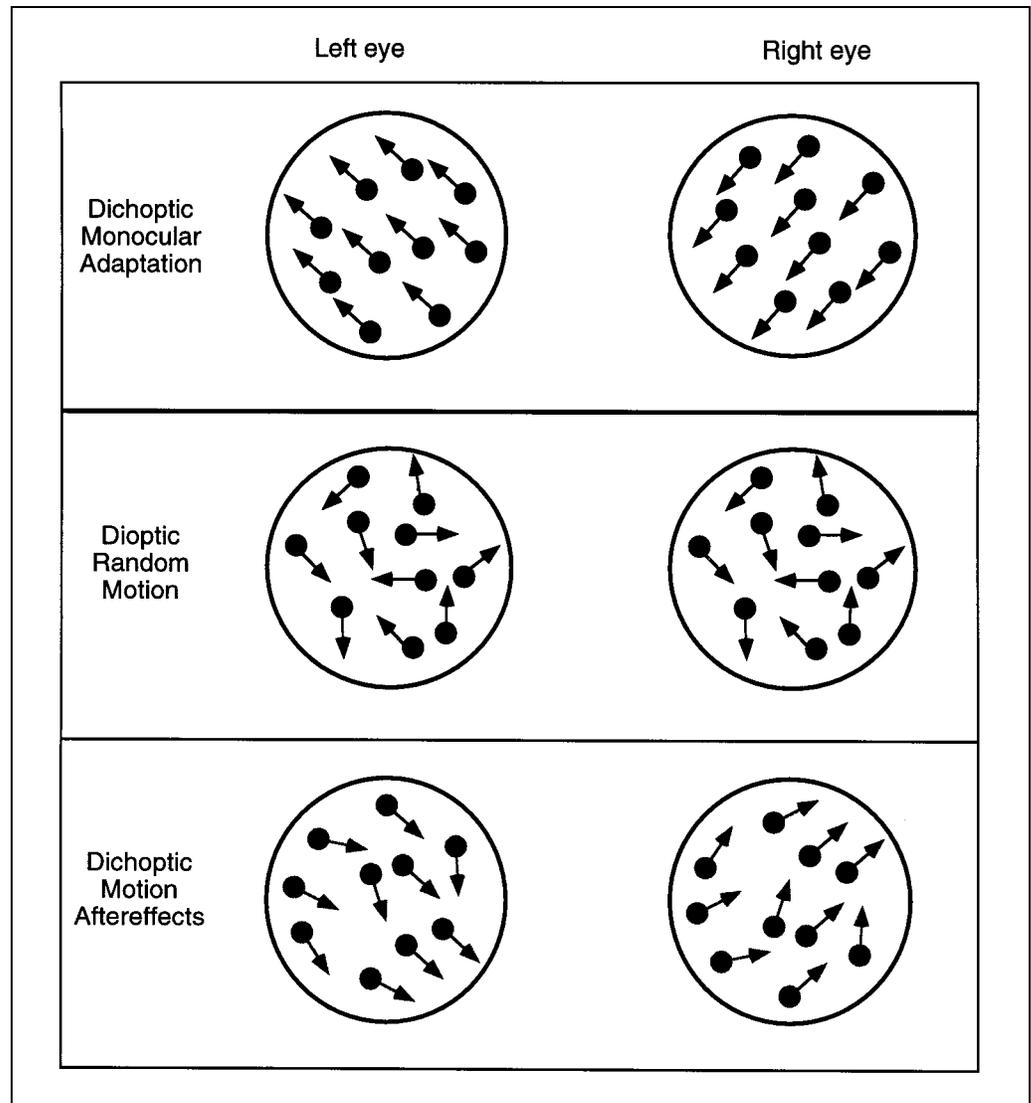


Figure 6. Schematic illustrating how adaptation (upper panel) of one eye to motion up and to the left (left eye in this example) and adaptation of the other eye to motion down and to the left (right eye) causes identical random motion (middle panel) to appear to drift in different directions for the two eyes (lower panel).

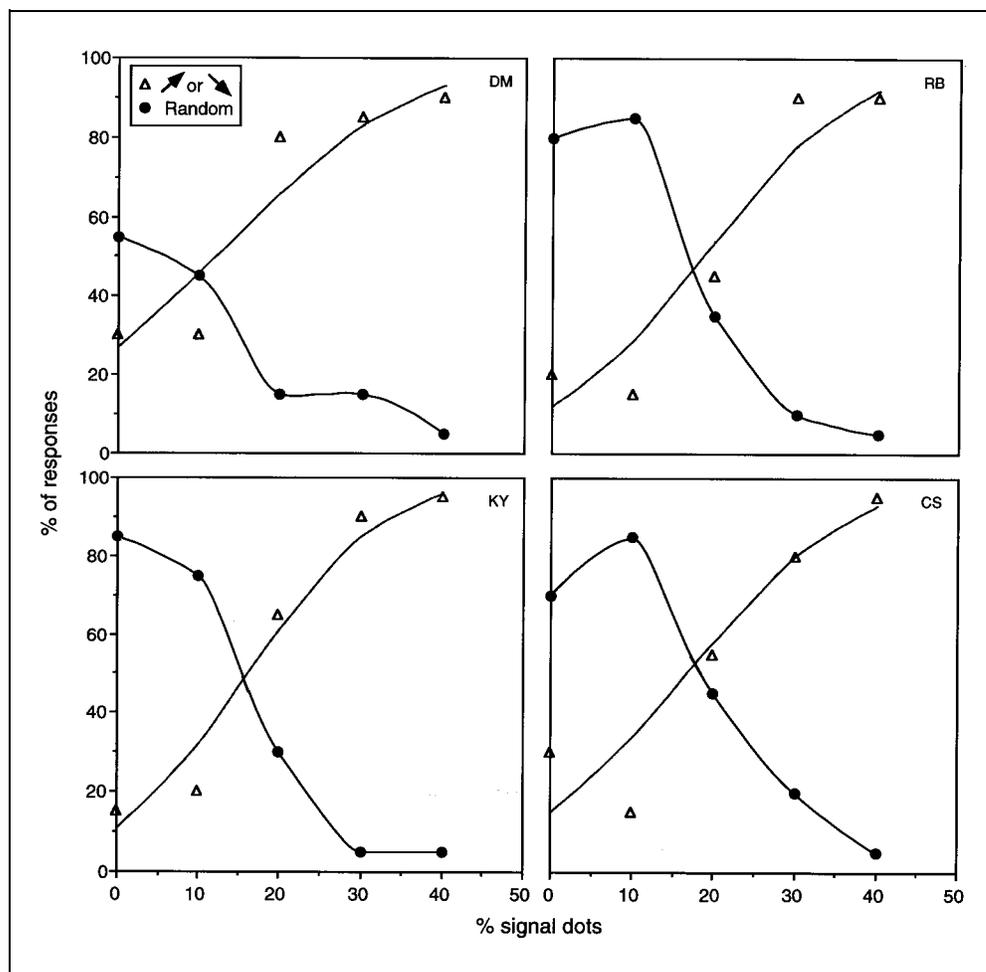


keypress whether the dominant direction of motion was UR, DR, or random; reports of UR and/or DR were taken as evidence that binocular rivalry was experienced. As summarized in Figure 7, at signal strengths of 30% or greater, binocular rivalry was predominantly experienced.²

So having established that dichoptic RDCs of 30% signal strength engage in binocular rivalry, we next determined whether it was possible to generate monocular, orthogonal motion aftereffects whose perceived coherence was at least this strong. (We opted for orthogonal, not opposite, directions of motion so as not to cancel one eye's MAE by the other's.) To tackle this question, we used a nulling technique (Blake & Hiris, 1993) to quantify the magnitudes of the left- and right-eye MAEs following an extended period of adaptation. During an initial 10-min adaptation period, the left eye viewed 200 dots moving DL and the right eye simultaneously viewed 200 dots moving UL. During adaptation the observer fixated the center of the circular region, without track-

ing rivalry.³ Following the initial 10-min adaptation period, the observer received a 4-sec test period during which the left eye viewed a RDC containing either 0, 10, 20, 30, or 40% signal dots moving DL; the corresponding region in the other eye's view was blank during this test period. At the end of this 4-sec test period, the observer judged whether motion in the random RDC was DL or UR (a response of UR indicates that the real motion signal was insufficient to counteract the illusory motion produced by adaptation). After each 4-sec test period, the observer received an additional 20 sec of exposure to the dichoptic adaptation display, to "refresh" the level of adaptation. Interspersed between each of these refresh periods of adaptation was another 4-sec test period, with the order of signal values randomized over trials. These conditions of dichoptic adaptation cause an illusory impression of semicoherent motion in the random RDC: The random motion appears to be semicoherent motion flowing in a direction opposite that experienced by that eye during adaptation. Moreover, we found for each of

Figure 7. For this experiment, left- and right-eye RDCs were presented within circular apertures subtending 1.8° of visual angle. These apertures were presented against a patterned surround (a gridlike pattern of white dots on a black background), viewing conditions designed to maximize MAE strength (e.g., Bell, Lehmkuhle, & Westendorf, 1976). Any given frame in the motion sequence consisted of 200 white dots (each 1 pixel \times 1 pixel), each of which was displaced by 3 pixels in a direction that could be independently specified for each individual dot. Dot speed was 0.4° per sec. Two signal directions were used: 45° clockwise from vertical, and 135° clockwise from vertical. For each observer, a given direction of signal motion was presented to the left eye and the other direction to the right eye. The percentage of signal dots varied from 0% (RDVN) to 40% in steps of 10%. Each observer completed a total of 100 trials (20 for each of the five signal strengths, which randomly intermixed within a block of trials). The two eyes viewed orthogonal directions of signal motion, but signal strength (i.e., the percentage of signal dots) was always equivalent for the two eyes on any given trial. Observers initiated each trial via keypress, triggering a 4-sec test display. Observers were given four possible response alternatives: 45° clockwise from vertical (corresponding to the monocular directions of motion), 135° clockwise from vertical (corresponding to the vector sum of the monocular directions of motion), and random. Observers indicated the response that corresponded most closely to the perceived direction of global motion of the test stimulus. Reports of 45° and 135° were taken to indicate the occurrence of binocular rivalry. Observers were instructed to respond based on the final appearance of the display if the perceived direction of motion fluctuated during the 4-sec test period. Observers were instructed to fixate the center of the circular aperture at all times. The four panels plot for each observer the percentage of responses falling into a given response category plotted against the percentage of signal dots. Open triangles represent responses of 45° and 135° ; filled circles represent responses of "random." Note that 45° and 135° responses are combined, given that both of these responses are indicative of the occurrence of binocular rivalry.



four observers tested that to nullify this monocular MAE required coherent motion containing more than 30% motion signal (see Table 1). Thus the monocular MAEs produced by dichoptic adaptation are sufficiently strong, in principle, to produce observable binocular rivalry. So, do competing monocular MAEs produce binocular rivalry?

For this critical condition, we repeated the adaptation regime described in the previous paragraph (i.e., 10-min of initial adaptation to DL for the left eye and UL for the right eye, with 20-sec periods of readaptation interspersed with 4-sec test periods). Now, however, the 4-sec test periods involved presentation of one of three test conditions: left-eye monocular test trials, right-eye monocular test trials, and binocular test trials. On the mo-

Table 1. Signal strength necessary to nullify the monocular motion aftereffect produced by simultaneous dichoptic stimulation with opposite directions of motion. These values represent the coherence strength associated with 50% response level (i.e., signal values that yield an equal number of responses in the two opposite directions of motion).

Observer	Signal strength (%)
DM	35
RB	38
KY	40
CS	32

ocular trials, an RDC was presented to one eye and the corresponding region in the other eye's view was blank; on the binocular trials, identical RDCs were presented to the two eyes. Following each test trial, observers indicated by keypress whether the perceived direction of global flow was UR, DR, directly rightward (i.e., the vector sum of UR and DR), or random. Observers were instructed to base their responses on the perceived direction at the end of the 4-sec test period. The monocular test trials were included to verify that the appropriate monocular MAEs were perceived as well as to promote uncertainty about what would be experienced on any given trial, thereby discouraging response bias.

Results, summarized in Figure 8, reveal that all four observers experienced monocular MAEs in the predicted directions, and three of the four experienced binocular rivalry when those dichoptic MAEs were pitted against one another during binocular stimulation. For these three, responses on binocular test trials were distributed between the two monocular MAE directions over trials, implying that observers sometimes perceived the left-eye's MAE and other times, the right-eye's MAE. The fourth observer, however, predominantly experienced motion in a rightward direction (i.e., the vector

sum of the two monocular MAEs). We have no ready explanation for this individual's results because he is equivalent to the other observers in other respects.

Intrigued by this finding, we repeated this experiment in all respects except that the 4-sec test periods involved presentation of static dots during the three test conditions: left eye test only, right eye test only, and binocular test. For the binocular condition, the two eyes viewed identical static dot patterns. With monocular viewing during the 4-sec test period, the stationary dots appeared to move in a direction opposite that presented to that eye during adaptation, as expected. With binocular viewing, however, the stationary dots appeared to move in a direction corresponding to the vector-sum of the two monocular MAEs. This pattern of results (Figure 9) was found for all four observers, and it is in agreement with earlier experiments (Anstis & Duncan, 1983; Anstis & Moulden, 1970; Ramachandran, 1991; Riggs & Day, 1980).

So, orthogonal monocular MAEs yield different phenomenal outcomes under binocular viewing conditions, depending upon the nature of the test patterns. When the left and right eyes view identical *static* test patterns, binocular viewing yields an MAE in the vector-sum direction of the two monocular MAEs. When the two eyes

Figure 8. Bars indicate the percentage of trials falling into each of the four response categories. Results from monocular trials—the filled bars shown in the bottom half of each graph—indicate that observers saw MAEs in the expected direction when the random motion was presented monocularly. Results from binocular trials—hatched bars in the top half of each graph—indicate that three of four observers experienced binocular rivalry on a large fraction of trials (i.e., binocular responses are frequently in the UR or the DR direction, implying rivalry). Observer CS primarily experienced the vector sum of the two monocular aftereffects.

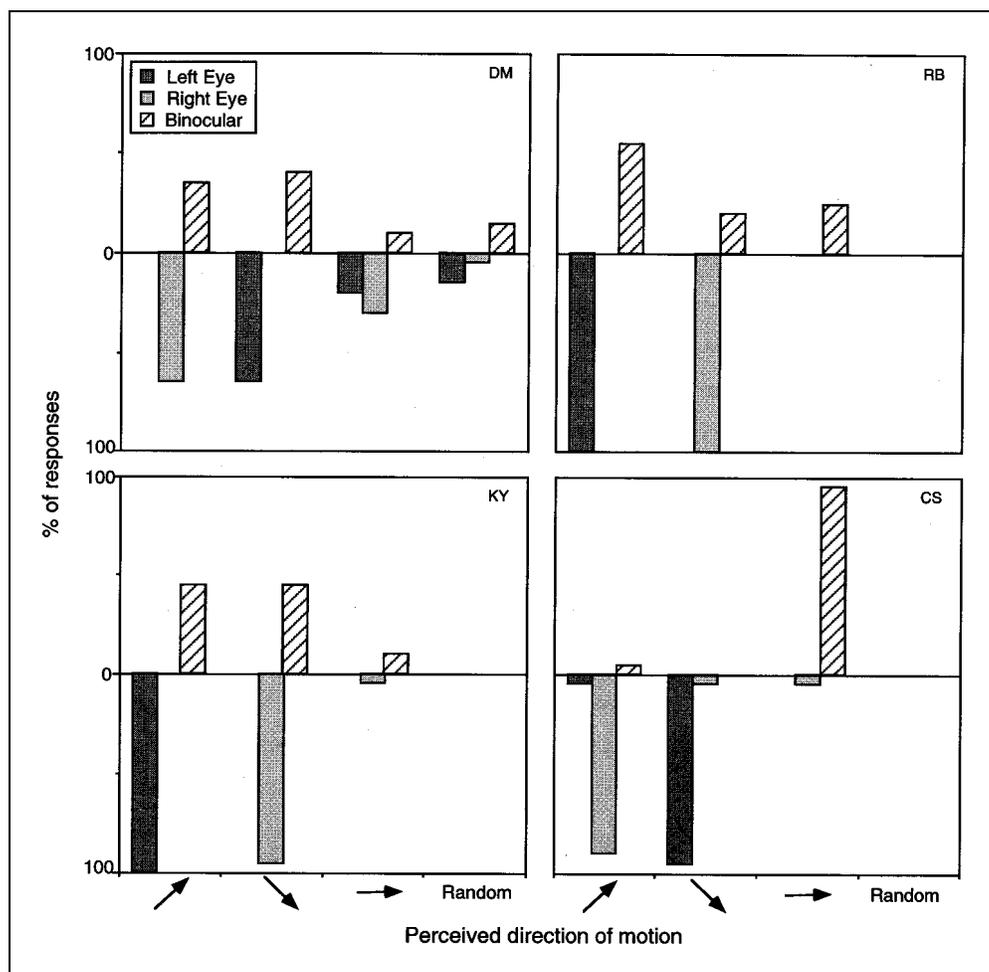
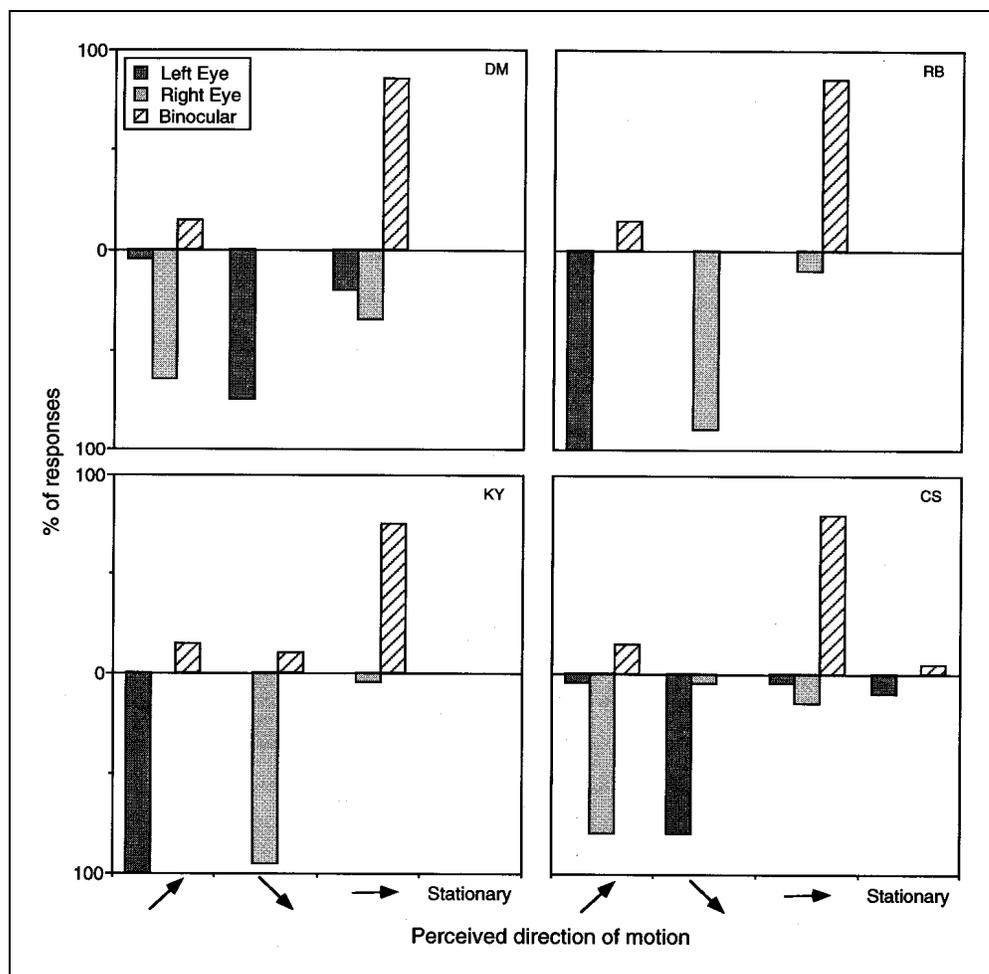


Figure 9. Same convention as previous figure. Results from monocular trials—the filled bars shown in the bottom half of each graph—indicate that observers saw MAEs in the expected direction when static dots were viewed monocularly. Results from binocular trials—hatched bars in the top half of each graph—indicate that all observers experienced the vector sum of the two monocular after-effects.



view identical *dynamic* test patterns, however, binocular rivalry of the monocular MAEs may ensue. The latter finding argues against the proposal that binocular rivalry depends upon the existence of interocular form differences per se (Ramachandran, 1991). Indeed, our results indicate that “pure” motion rivalry can occur. Binocular rivalry is triggered when the process responsible for binocular combination receives incompatible monocular information; the neural inputs to this binocular process evidently include those adapted by motion. At the same time, binocular rivalry of discrepant monocular MAEs does *not* result when static form information specifies the conditions for fusion (i.e., when the two eyes view identical, static patterns).

Why is it, then, that matched *dynamic* test displays trigger binocular rivalry, whereas matched *static* displays do not? Knowing that physically weak dichoptic stimuli do not engage in rivalry (Liu, Tyler, & Schor, 1992), perhaps the static MAEs are simply too weak to trigger rivalry. After all, a dynamic test display presumably engages the same (adapted) neural elements activated during motion adaptation, because both displays contain common motion vectors. It is unlikely, however, that stationary features activate as effectively the neural ele-

ments responsive during adaptation to stimuli that actually move. This account could be tested if it were possible to create physically moving stimuli that mimic the static MAE, but efforts to this end have failed (Hiris & Blake, 1992). Another possibility is that the motion system itself does not register the presence of fusible stimuli to the two eyes but instead relies upon the form system to signal interocular compatibility. Note that this speculation is related to Ramachandran’s suggestion. However, rather than positing that the motion system relies upon the form system to trigger *rivalry*, it may be that the motion system defers to the form system to register *fusion*. As a final possibility, the conditions for rivalrous MAEs may be present only when dynamic test patterns are viewed. According to this possibility, when the two eyes view identical *static* patterns, the neural representation of those patterns is not altered by adaptation of neural elements registering motion information; from the standpoint of the process underlying binocular combination, the static patterns remain static and identical. When, however, the two eyes view identical *dynamic* patterns, the neural representation of those patterns is altered by adaptation to motion, and this alteration is different for the two eyes. Consequently,

from the standpoint of the process underlying binocular combination, the left- and right-eye dynamic patterns signal different directions of motion, which triggers rivalry.

Rivalry Suppression Nonselectively Disrupts Motion Perception

When one eye's view is suppressed during rivalry, it is patently obvious that information processing associated with that eye's stimulus is temporarily disrupted in some fashion, producing phenomenal invisibility. But is that disruption limited to just the suppressed stimulus itself? The answer seems to be No. In an important series of experiments, Fox and colleagues have shown that new visual information presented to an eye during rivalry is more difficult to detect when the eye receiving that information is suppressed (Fox & Check, 1968; Wales & Fox, 1970). Similarly, large-scale changes in a suppressed rival stimulus itself may go completely undetected for several seconds, until that eye spontaneously achieves dominance (Blake, 1988; Blake & Fox, 1974). As characterized by Fox (1991), rivalry suppression operates nonselectively over a broad range of stimulus dimensions encompassing more than just the information represented in the suppressed stimulus. Just how extensively suppression operates, however, is debatable, and for two reasons we were motivated to test the nonselectivity of suppression in the case of motion perception.

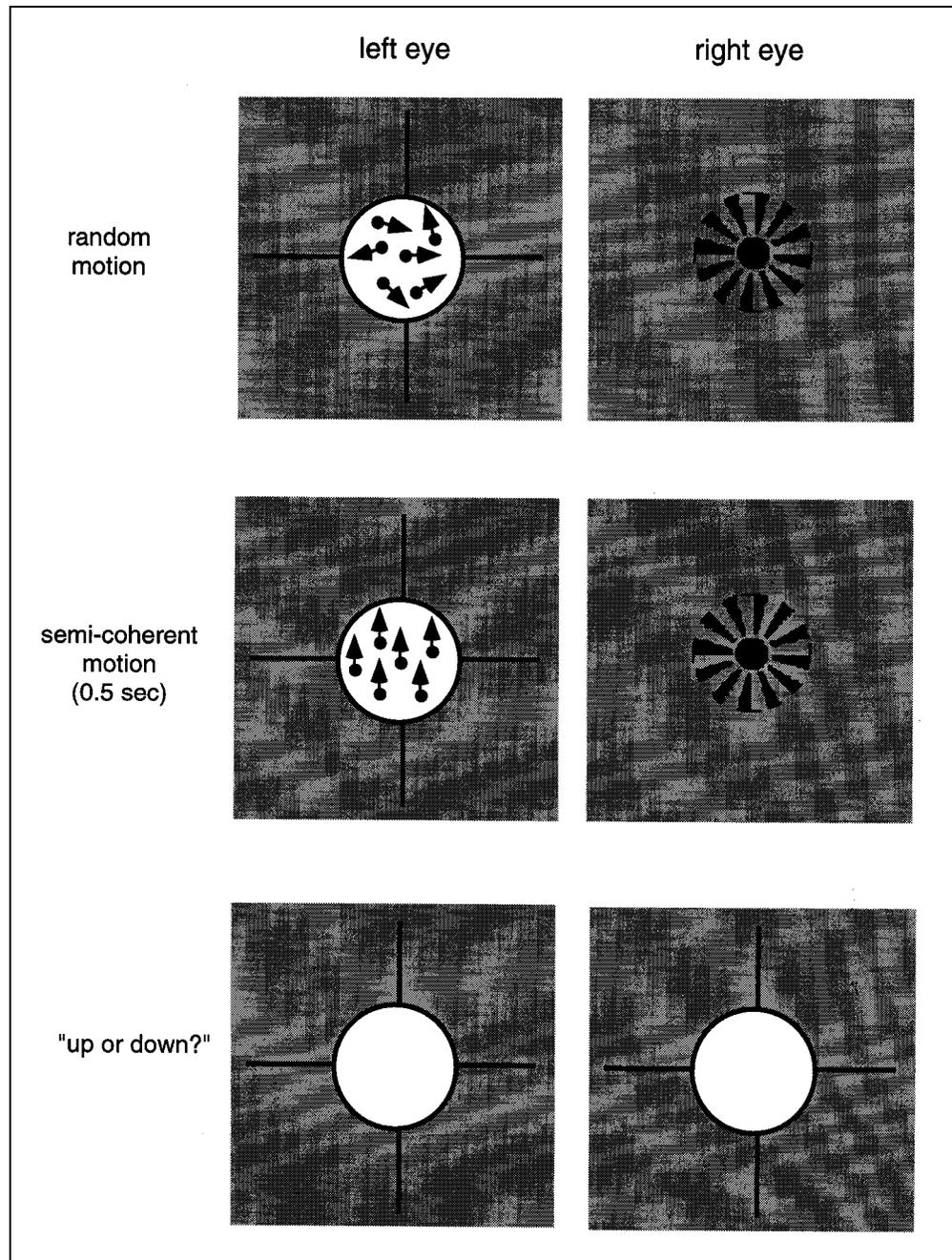
The first reason for our interest in this question stems from psychophysical studies indicating that suppression affects color-sensitive mechanisms more than luminance mechanisms (Ooi & Loop, 1994; Smith, Levi, Harwerth, & White, 1982). To the extent that these two classes of mechanisms are associated with parvo- and magno-pathways, these results could be construed to mean that rivalry suppression's influence within the magno-pathway is weaker. Moreover, it has been reported that rivalry does not occur with very low contrast dichoptic stimulation (Liu et al., 1992), a stimulus condition that would favor magno-pathway activation. These findings led us to wonder to what extent suppression phases of rivalry nonselectively affect motion perception, an aspect of vision often ascribed to the magno-pathway? Secondly, we were particularly interested in comparing the detectability of translational and rotational motion, because of evidence pointing to the hierarchical extraction of optic flow information specifying these different forms of motion (Morrone et al., 1995). To summarize this idea briefly, complex optic flow (created either by object motion or by observer locomotion) is initially registered as local translational motion signals in parallel across the visual field. These signals, which are ambiguous with respect to motion speed and direction, are integrated at higher processing stages by neurons responsive to global speed and direction of motion, including coherent motion in RDCs. At still higher processing

levels, neurons are responsive to more complex vector fields, including rotation. Given the hierarchical nature of motion processing, we wondered whether rivalry suppression would differentially affect the putative stages of this hierarchy. To learn the answer, we determined whether observers could detect presentation of translational motion and presentation of rotational motion during periods of suppression.

The observer initially viewed a pair of circular rival targets, one consisting of an RDC portraying random motion (i.e., 100 dots moving haphazardly in all directions) and the other a stationary pattern resembling a starburst (Figure 10). On each trial, the observer depressed a key when one of the two rival targets was exclusively dominant, with no hint of the other target. Key depression caused a fraction of the randomly moving dots to begin moving in a prescribed manner, which depended on the motion condition under test. For translational motion, the specified fraction of dots (the so-called signal dots) moved either upward or downward, with the direction varying randomly from trial to trial. In other blocks of trials, the motion was rotational and the specified fraction of signal dots moved either clockwise or counterclockwise. For both motion types, the percentage of signal dots moving coherently was 10, 20, 30, or 40% of the total dot population, and the particular coherence level (i.e., percentage of signal dots) varied randomly over trials. The presentation duration of semicoherent motion was 0.5 sec, after which both rival targets were removed. The observer made a forced-choice judgment, guessing if necessary, about the direction of motion (up or down for blocks of translational motion; CW or CCW for rotational motion). Error feedback was not given. On some blocks of trials, the transition from random to semicoherent motion occurred when the random dots were dominant, whereas in other blocks of trials the transition occurred during suppression. This experiment thus consisted of 16 conditions (4 levels of coherent motion \times 2 rival states \times 2 motion types), which were counterbalanced over observers; 30 trials were administered at each of the 16 conditions.

The percentage of correct performance is summarized in Figure 11. For all seven observers, the brief introduction of semicoherent motion during dominance was easily detected at all but the weakest, 10%, signal level. During suppression, however, detectability of translational and rotational motion was significantly impaired for six of the seven observers (results for those six are shown in the left-hand panel of Figure 11), even at the strongest signal levels tested. The performance of the seventh observer (right-hand panel, Figure 11), in contrast, was essentially equivalent for dominance and suppression. We think this could be attributable to this observer's remarkably rapid alternations between dominance and suppression—when simply tracking rivalry alternations, he typically experienced 40 or more reversals during a 60-sec observation period, meaning that the

Figure 10. Schematic of motion substitution technique used to measure detectability of coherent motion during dominance and suppression phases of rivalry. On each trial one eye initially viewed random, incoherent motion (100 dots each moving in random directions from frame to frame) and the other eye viewed a stationary starburst pattern. These two dissimilar targets engaged in binocular rivalry, with substantial periods of exclusive visibility of one target or the other. During the “dominance condition” the observer depressed a computer key when the random motion display was dominant in its entirety—this action caused the random motion to be replaced for 0.5 sec by semi-coherent motion in which a fraction of the 100 dots moved in a given direction (up vs. down for the translation condition; clockwise vs. counterclockwise for the rotation condition), with the degree of coherence (i.e., the percentage of dots moving in the specified direction) varied over trials from 10 to 40% in 10% steps. The observer made a forced-choice judgment about the direction of motion. The exact same set of events occurred during “suppression condition” trials except that now the observer triggered the substitution of random motion by semicoherent motion when the sunburst target was dominant in its entirety, with no hint of the moving dots.

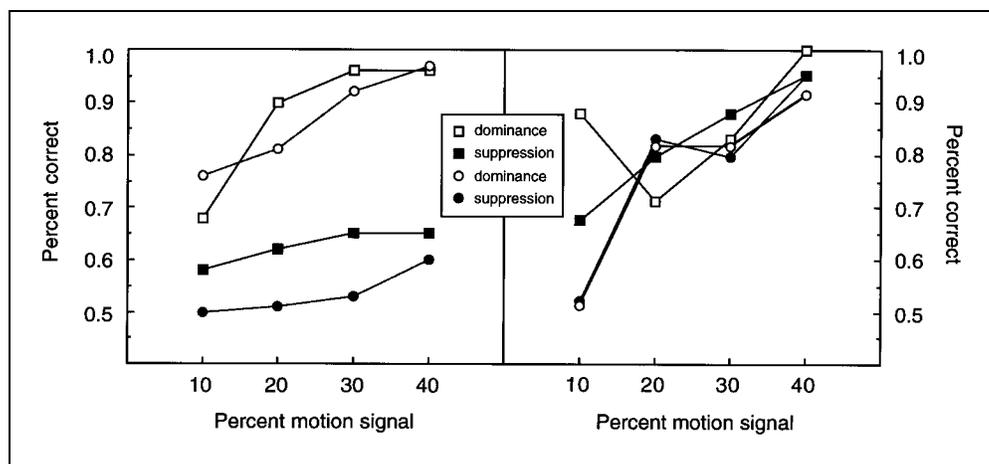


durations of single episodes of dominance were quite brief. We suspect that many of the transitions from random to semicoherent motion were spanning two rivalry states, the consequence being that most presentations were at least partially visible during a dominance phase. None of the other observers evidenced alternation rates nearly this rapid, and consequently, the 0.5-sec presentations of signal motion were usually confined to the desired rivalry state.

These results extend the notion of suppression’s non-selectivity to forms of motion believed to be registered at different neural stages. This pattern of results could

arise for one of several possible reasons. Perhaps the neural events responsible for suppression transpire at a stage of visual processing after the registration of both uniform and complex motion, effectively disrupting transmission of fully processed motion information to subsequent stages of vision. Alternatively, suppression may occur quite early in visual processing, intermittently blocking input to neural sites responsible for analysis of uniform and complex motion. In fact, existing evidence points to a third conclusion: Suppression occurs after the extraction of information about uniform motion but before analysis of information about complex motion.

Figure 11. Percentage of correct performance for detection of translational motion (square symbols) and rotational motion (circular symbols) of varying signal strengths presented during dominance (open symbols) or during suppression (filled symbols). The left-hand panel summarizes results from six observers, all of whom exhibited comparable patterns of results; the panel on the right summarizes results for the one observer, whose performance was markedly different from the others. For all observers except this one, differences between dominance and suppression are statistically significant as confirmed by paired samples *t* tests.



That evidence comes from studies showing that intermittent suppression of translational motion has no influence on the strength of the motion aftereffect generated by that motion, implying that translational motion is fully analyzed even during periods of suppression (Lehmkühle & Fox, 1975). In contrast, intermittent suppression of spiral motion (which comprises two complex forms of motion, i.e., rotation and expansion) dilutes the strength of the resulting spiral aftereffect, implying that complex motion signals are not registered during suppression (Wiesenfelder & Blake, 1990).

The hypothesis that rivalry suppression occurs at an intermediate stage, sandwiched between two stages of motion processing, receives support from an even more stringent test (Blake, 1995). That test was based on a procedure whereby observers were adapted to translational motion and to rotational motion under conditions where they never consciously experienced the adapting motion: These structured motions were only presented during suppression phases of rivalry. A clear MAE was produced by adaptation during suppression to translational motion, but there was no hint of a rotational MAE following adaptation to rotational motion during suppression. These results, too, point to a locus of rivalry suppression intermediate between two stages of motion processing.

Given this hierarchical ordering of motion stages with suppression sandwiched between, how do we account for suppression's profound effect on *both* translational motion and rotational motion, the finding in Figure 10? The answer, we believe, turns on the distinction between registration of motion information and perception of motion—we envision these processes occurring at different sites within the visual pathways. At a relatively early stage, translational motion is registered locally throughout the visual field; this registration process is

accomplished by mechanisms often identified with direction-selective neurons in primary visual cortex (e.g., Emerson, Bergen, & Adelson, 1992). The responses of these mechanisms adapt upon prolonged stimulation with translational motion, and this adaptation constitutes the neural basis for the conventional MAE. Outputs from these local mechanisms are fed to higher processing stages where units, possibly with larger receptive fields, respond to global translational motion (e.g., Britten, Shadlen, Newsome, & Movshon, 1993) and to rotational and radial motion (e.g., Graziano, Andersen, & Snowden, 1994). Those mechanisms show adaptation effects as well when stimulated with their preferred motion. We assume that behavioral judgments concerning motion—regardless of type—are crucially dependent on neural events transpiring at these higher stages. When inputs to those stages are disrupted, as they are during suppression phases of rivalry, those judgments are compromised.

Before leaving this discussion, one point deserves elaboration. It is generally recognized that visual areas are interconnected by feed-forward and by feedback pathways. Thus an area (e.g., V1) innervating another (e.g., MT) also receives feedback from the cortical area it innervates. This looping arrangement means we must clarify what is meant by “higher” visual stages and suppression's relation to those stages. We conceptualize a “stage” as an aggregate of neurons whose connections—both intrinsic and extrinsic—allow those neurons to represent explicitly some component of the visual scene that was only implicitly contained within the activity of neurons at some other (“earlier”) stage. An example should help.

Imagine a light/dark border imaged on the fovea. The existence and location of that border is implicitly contained in the distribution of signals among the cone

photoreceptors on which that border is imaged. But it remains for the ganglion cells connected to those cones to register that border explicitly, which they are able to do by virtue of their receptive field organization. Of course those ganglion cells do not explicitly represent the orientation of that border; that task remains for the cortical cells that collate inputs from an array of thalamic neurons whose activity implicitly contains orientation information. The cortical cells accomplish that task by virtue of *their* receptive field properties. So it is in this sense that we identify the primary visual cortex as the stage where orientation information is made explicit. Neurons in the primary visual cortex, of course, receive afferents not only from the thalamus but, as well, from the midbrain and from those higher areas that it innervates. Presumably, those extra-thalamic inputs play important roles in shaping the orientation selectivity of cortical neurons and, perhaps, modulating those responses in a context-dependent way. But the fact remains that orientation information is made explicit at this stage, not earlier.

The same line of reasoning applies to motion signals. The visual cortex registers spatio-temporal fluctuations in luminance within small regions of the visual field—this information is somewhat akin to the light-level information registered by the cones. There is, however, insufficient information in those local motion signals to specify unambiguously the nature of the event producing them. That job falls to groups of neurons at higher stages, where local motion signals are recombined to synthesize an explicit representation of object motion.

The data presented in this paper combined with earlier work on rivalry implies, then, that suppression operates at a point in visual processing after spatiotemporal fluctuations in luminance have been explicitly registered but prior to the stage where complex global motion is made explicit.

Conclusions

Several general conclusions can be drawn from the present experiments. First, our results further document that motion enhances predominance during binocular rivalry. Why are moving stimuli more salient than stationary stimuli? In general, it is known that motion readily captures attention, so to the extent that rivalry represents a form of selective attention (e.g., Lack, 1978), the potency of a moving rival target may simply be a manifestation of attention's focus on things that move. For reasons detailed elsewhere (Blake, 1988), however, we are somewhat skeptical of an attentional account of rivalry. Instead, we believe the salience of moving rival targets has to do with the transients associated with motion. Flickering a rival target also significantly increases its predominance (e.g., Blake & Fox, 1974), as can blinking one eye that receives a stationary rival target. Both of these actions produce transient stimula-

tion on the retina, and their effects are comparable to those of target motion.

Second, the present results extend the notion of rivalry suppression's nonselectivity (Fox, 1991) to motion signals specifying translation, rotation, and radial motion. It seems rather remarkable that a transition from unstructured, random motion to highly coherent motion goes undetected during suppression, because the informational content in the latter is much higher than in the former. Speaking metaphorically, the visual system seems to be completely illiterate with respect to optical events imaged on the suppressed region of an eye. We believe this adds further weight to the idea that suppression operates on a given region of the eye, not a particular stimulus or class of stimuli. This idea, however, is not without controversy (Logothetis, Leopold, & Sheinberg, 1996).

Third, the present results—particularly those dealing with suppression's nonselective effect on motion perception—provide no support for the idea that suppression is exclusively a parvo-pathway function. It is true that rivalry can be instigated by stimulus conditions that primarily activate parvo-pathway mechanisms (e.g., O'Shea & Williams, 1996), but our results with RDCs would seem to implicate magno-pathway involvement, too. In this respect it is noteworthy that Logothetis and Schall (1989) found modulations in single neuron activity within visual area MT that corresponded to the phenomenal state of rivalry. Area MT, of course, is a major processing station within the magno-cellular pathway. Whether rivalry suppression's influence within the magno-pathway is weaker remains to be determined.

Finally, it is particularly striking that rivalry can be triggered by physically identical stimuli (RDCs) presented to the two eyes, when adaptation is used to make those identical stimuli *look* different when imaged in the left vs. right eye. This represents an intriguing dissociation between physical stimulation and perceptual experience, and it implies that the process responsible for binocular matching operates on monocular information that has been altered by neural adaptation. Whether the same pattern of results would be found using more complex forms of motion adaptation (e.g., rotational motion) remains to be learned.

GENERAL METHODS

In all experiments, observers viewed random-dot cinematograms (RDC), that is, animation sequences consisting of a random array of small moving dots whose direction and speed can be accurately specified from frame-to-frame of the sequence (Williams & Sekuler, 1984; see Hiris & Blake, 1995, for details of the creation of RDCs in our laboratory). These RDCs were presented on a video monitor (Apple, 66.7-Hz frame rate, P4 phosphor, 480 × 640 pixels, 76 dpi) under control of an accelerated Macintosh II computer. For any RDC, a given

percentage of dots (*signal dots*) could be specified to move in a given direction while the remaining dots (*noise dots*) were free to move in any direction; increasing the percentage of signal dots (i.e., those moving in a given direction) increases the perceived coherence in these RDCs (Hiris & Blake, 1995).

Except where noted, RDCs were presented on the left- and right-halves of the video monitor, and these two half-images were viewed dichoptically through a mirror stereoscope from a viewing distance of 114 cm. The dots themselves always appeared within two small circular regions, one viewed by the left eye and one by the right eye. The circumference of each circle was defined by a high-contrast contour; the size of this circular region containing the rival RDCs varied across experiments. The presence of fusion contours flanking the rival targets in the two half-images made it possible to achieve stable binocular alignment by carefully adjusting the mirrors for each observer.

In some experiments observers pressed keys on the computer keyboard to track fluctuations in dominance and suppression between left- and right-eye RDCs. In other experiments, observers were instructed to depress a key when a given eye's stimulus achieved complete, exclusive dominance, an action that triggered a brief change in either the dominant RDC viewed by that eye or the suppressed RDC viewed by the other eye. The observer was then required to make a forced-choice judgment about the change in motion.

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Notes

1. This reasoning assumes that neural adaptation at a higher stage of processing will not influence processing at an earlier stage. However, the presence of feedback loops within cortical circuits complicates this reasoning. We discuss this point in great detail in the section dealing with the nonselectivity of rivalry suppression.
2. It is worth noting that at signal levels weaker than 30%, including 0% signal, motion was uncorrelated between the two eyes, and in principle, these dichoptic displays may have produced rivalry, too. However, both left- and right-eye RDCs appeared too incoherent for observers to judge motion direction and, hence, eye dominance.
3. Whether alternations in dominance affected the build-up of

adaptation was unimportant for our purposes, just so long as we could generate monocular MAEs of sufficient strength. As pointed out later in this paper, rivalry suppression has no effect on the build-up of this translational MAE.

REFERENCES

- Allman, J. M., Miezin, R., & McGuinness, E. (1985). Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT). *Perception, 14*, 105-126.
- Anstis, S. M., & Duncan, K. (1983). Separate motion after-effect from each eye and from both eyes. *Vision Research, 23*, 161-169.
- Anstis, S. M., & Moulden, B. P. (1970). Aftereffect of seen movement: Evidence for peripheral and central components. *Quarterly Journal of Experimental Psychology, 22*, 222-229.
- Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The oblique effect in man and animals. *Psychological Bulletin, 78*, 266-278.
- Barlow, H. B., & Brindley, G. S. (1963). Inter-ocular transfer of movement after-effects during pressure blinding of the stimulated eye. *Nature, 200*, 1346-1347.
- Bell, H. H., Lehmkuhle, S. W., & Westendorf, D. H. (1976). On the relation between visual surround and motion after-effect velocity. *Perception and Psychophysics, 20*, 13-16.
- Blake, R. (1988). Dichoptic reading: The role of meaning binocular rivalry. *Perception & Psychophysics, 44*, 133-141.
- Blake, R. (1995). Psychoanatomical strategies for studying human vision. In T. Papathomas, C. Chubb, E. Kowler, & A. Gorea (Eds.), *Early vision and beyond* (pp. 17-25). Cambridge, MA: MIT Press.
- Blake, R., & Boothroyd, K. (1985). The precedence of binocular fusion over binocular rivalry. *Perception & Psychophysics, 37*, 114-124.
- Blake, R., & Fox, R. (1974). Binocular rivalry suppression: Insensitive to spatial frequency and orientation change. *Vision Research, 14*, 687-692.
- Blake, R., & Hiris, E. (1993). Another means for measuring the motion aftereffect. *Vision Research, 33*, 1589-1592.
- Blake, R., O'Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Visual Neuroscience, 8*, 469-478.
- Blake, R., Zimba, L., & Williams, D. (1985). Visual motion, binocular correspondence, and binocular rivalry. *Biological Cybernetics, 52*, 391-397.
- Born, R. T., & Tootell, R. B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357*, 497-499.
- Breese, B. B. (1899). On inhibition. *Psychological Monographs, 3*, 1-65.
- Bressan, P. (1991). A context-dependent illusion in the perception of velocity. *Vision Research, 31*, 333-336.
- Britten, K. H., Shadlen, M. N., Newsome, W. T., & Movshon, J. A. (1993). Responses of neurons in macaque MT to stochastic motion signals. *Visual Neuroscience, 10*, 1157-1169.
- Crick, F. (1996). Visual perception: Rivalry and consciousness. *Nature, 379*, 485-46.
- de Weert, C. M. M., & Wade, N. J. (1984). Canceling of pattern motion: Dichoptic and monoptic observations. *Vision Research, 24*, 883-887.
- Emerson, R. C., Bergen, J. R., & Adelson, E. H. (1992). Directionally selective complex cells and the computation of motion energy in cat visual cortex. *Vision Research, 32*, 203-218.

- Felleman, D. J., & Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, *1*, 1-47.
- Fox, R. (1991). Binocular rivalry. In D. M. Regan (Ed.), *Binocular vision and psychophysics* (pp. 93-110). London: MacMillan Press, Ltd.
- Fox, R., & Check, R. (1968). Detection of motion during binocular rivalry suppression. *Journal of Experimental Psychology*, *78*, 388-395.
- Fox, R., Todd, S., & Bettinger, L. A. (1975). Optokinetic nystagmus as an objective indicator of binocular rivalry. *Vision Research*, *15*, 849-853.
- Graziano, M. S. A., Andersen, R. A., & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience*, *14*, 54-67.
- Hiris, E., & Blake, R. (1992). Another perspective on the visual motion aftereffect. *Proceedings of the National Academy of Science*, *89*, 9025-9028.
- Hiris, E., & Blake, R. (1995). Discrimination of coherent motion when local motion varies in speed and direction. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 308-317.
- Lack, L. C. (1978). *Selective attention and the control of binocular rivalry*. The Hague, Netherlands: Mouton.
- Lagae, L., Gulyas, B., Raiguel, S. E., & Orban, G. A. (1989). Laminar analysis of motion information processing in macaque V5. *Brain Research*, *496*, 361-367.
- Lehmkuhle, S. W., & Fox, R. (1975). Effect of binocular rivalry suppression on the motion after-effect. *Vision Research*, *15*, 855-859.
- Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*, *379*, 549-553.
- Liu, L., Tyler, C. W., & Schor, C. (1992). Failure of rivalry at low contrast: Evidence of a suprathreshold binocular summation process. *Vision Research*, *32*, 1471-1480.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature*, *380*, 621-624.
- Logothetis, N. K., & Schall, J. D. (1989). Neuronal correlates of subjective visual perception. *Science*, *245*, 761-763.
- Morrone, M. C., Burr, D. C., & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature*, *376*, 507-509.
- Movshon, J. A. (1990). Visual processing of moving images. In H. Barlow, C. Blakemore, & M. Weston-Smith (Eds.), *Images and understanding* (pp. 122-137). New York: Cambridge University Press.
- Movshon, J. A., & Lennie, P. (1979). Pattern-selective adaptation in visual cortical neurones. *Nature*, *278*, 850-852.
- Nawrot, M., & Sekuler, R. (1990). Assimilation and contrast in motion perception. *Vision Research*, *30*, 1439-1451.
- Ooi, T. L., & Loop, M. S. (1994). Visual suppression and its effect upon color and luminance sensitivity. *Vision Research*, *34*, 2997-3003.
- O'Shea, R. P., & Crassini, B. (1981). Interocular transfer of the motion aftereffect is not reduced by binocular rivalry. *Vision Research*, *21*, 801-804.
- O'Shea, R. P., & Williams, D. R. (1996). Binocular rivalry with isoluminant stimuli visible only via short-wavelength-sensitive cones. *Vision Research*, *36*, 1561-1571.
- Ramachandran, V. S. (1991). Form, motion, and binocular rivalry. *Science*, *251*, 950-951.
- Riggs, L. A., & Day, R. H. (1980). Visual aftereffects derived from inspection of orthogonally moving patterns. *Science*, *208*, 416-418.
- Sengpiel, F., Blakemore, C., & Harrad, R. (1995). Interocular suppression in the primary visual cortex: A possible neural basis of binocular rivalry. *Vision Research*, *35*, 179-196.
- Smith, E. L., Levi, D. M., Harwerth, R. S., & White, J. M. (1982). Color vision is altered during the suppression phase of binocular rivalry. *Science*, *218*, 802-804.
- Steiner, V., Blake, R., & Rose, D. (1994). Interocular transfer of expansion, rotation, and translation motion aftereffects. *Perception*, *23*, 1197-1202.
- Tootell, R. B. H., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., Brady, T. J., & Rosen, B. R. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature*, *375*, 139-141.
- Wade, N. J., de Weert, C. M. M., & Swanston, M. T. (1984). Binocular rivalry with moving patterns. *Perception and Psychophysics*, *35*, 111-122.
- Wales, R., & Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Perception & Psychophysics*, *8*, 90-94.
- Walker, P., & Powell, D. J. (1974). Lateral interaction between neural channels sensitive to velocity in the human visual system. *Nature*, *252*, 732-733.
- Walker, P., & Powell, D. J. (1979). The sensitivity of binocular rivalry to changes in the nondominant stimulus. *Vision Research*, *19*, 247-249.
- Wiesenfelder, H., & Blake, R. (1990). The neural site of binocular rivalry relative to the analysis of motion in the human visual system. *Journal of Neuroscience*, *10*, 3880-3888.
- Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, *24*, 55-62.