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Both monocular and binocular signals contribute to motion rivalry

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Abstract

There is an ongoing debate on whether binocular rivalry involves competition among monocular cells or binocular cells. We investigated this issue psychophysically with two specially designed test stimuli. One test stimulus contained monocular motion signals but greatly reduced binocular motion signals, while the other contained binocular motion signals but no monocular motion signals. For comparison, we also employed a normal rivalrous control containing both monocular and binocular motion signals, and a non-rivalrous flicker-noise control with neither monocular nor binocular motion signals. We found that binocular rivalry for the two test stimuli was significantly reduced compared with the normal rivalrous control, but not completely eliminated compared with the non-rivalrous control. Therefore, both monocular and binocular motion signals appear to contribute to motion rivalry, suggesting that motion rivalry must involve competition among both monocular and binocular cells.

Keywords: Binocular motion; Monocular motion; Interocular motion; Interocular pairing; Binocular rivalry

1. Introduction

When two very different stimuli are presented to the left and right eyes separately, our perception alternates between the two views, with one stimulus dominant and the other suppressed at a given time in each local area. This well-known phenomenon of binocular rivalry has been the subject of many studies since its discovery. However, the underlying mechanisms remain highly controversial to date (Blake & Logothetis, 2002). A central, unresolved issue is at which stage along the visual processing pathway binocular rivalry occurs. A closely related question is whether rivalry is a result of competition among monocular cells or competition among binocular cells.

Classical theories of binocular rivalry posit that rivalry results from competition between two pools of monocular cells, with one pool driven by the left eye and the other by the right eye (Blake, 1989; Lehky, 1988; Matsuoka, 1984; Mueller, 1990; Nguyen, Freeman, & Wenderoth, 2001). An implication is that rivalry should occur at a relatively early visual area where monocular cells can be found in abundance. The classical theories are supported by a variety of experimental evidence. For example, visually evoked potentials related to rivalry were found to start at a latency shorter than the usual binocular combination time (Valle-Inclan, Hackley, de Labra, & Alvarez, 1999). Magnetoencephalography reveals rivalry-related fluctuations in the occipital lobe (Srinivasan, Russell, Edelman, & Tononi, 1999), and functional magnetic resonance imaging (fMRI) studies found that neuronal events correlated with rivalry are expressed as early as V1 (Polonsky, Blake, Braun, & Heeger, 2000). Furthermore, Tong and Engel (2001) recorded rivalry-related fMRI signals in the monocular V1 region corresponding to the retinal blind-spot of the other eye, suggesting that rivalry may be fully resolved in monocular visual cortex.

On the other hand, there is also ample evidence supporting the view that rivalry may involve competition among binocular cells, or occur at relatively high visual cortical areas where nearly all cells are binocular (Bonneh, Sagi, & Karni, 2001; Kovacs, Papathomas, Yang, & Feher, 1996; Leopold & Logothetis, 1996; Logothetis & Schall, 1989; Sengpiel, Blakemore, & Harrad, 1995; van der Zwan & Wenderoth, 1994; van der Zwan, Wenderoth, & Alais, 1993). For instance, Sengpiel et al. (1995) reported that the majority of binocular cells in the

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primary visual cortex of cat were significantly suppressed by rivalry stimuli. Logothetis et al. reported that many binocular neurons in V1, V2 and particularly V4 had activities correlated with the perceptual dominance and suppression of a stimulus during rivalry (Logothetis & Schall, 1989), while almost all recorded monocular cells were unaffected by perceptual alterations (Leopold & Logothetis, 1996). In addition, the proportion of cells whose activities correlated with rivalry was highest in V4 and lowest in V1.

In his review on binocular rivalry, Blake (1989) analyzed the activation of monocular and binocular cells to different combinations of left-eye and right-eye stimulation (Fig. 1A–E). Among the five possibilities from A to E, observers can perceive binocular rivalry only when two different orientations are presented separately to each eye (Fig. 1E). In this case, both monocular and binocular cells tuned to the two different orientations are activated. To differentiate between the contributions of monocular and binocular competitions to rivalry in Fig. 1E, we need stimuli that could activate either the monocular cells alone (Fig. 1F) or binocular cells alone (Fig. 1G). Although it may be difficult to achieve the ideal conditions in Fig. 1F–G, we have managed to manipulate the strengths of monocular and binocular signals using two specially designed random-dot kinematograms (RDKs) in a motion-rivalry task. Motion rivalry was used instead of orientation rivalry because neuronal responses to motion can be reduced through a local pairing procedure in RDKs (Qian & Andersen, 1994). Previously, we reported that binocular rivalry was significantly reduced when the dots of different eyes had spatially overlapping trajectories through interocular pairing (Matthews, Geesaman, & Qian, 2000). Since monocular cells cannot be sensitive to interocular spatial relationship, we concluded that binocular cells must contribute to binocular rivalry. However, that study did not address the complementary issue of monocular contribution to rivalry, as we did not determine whether rivalry was eliminated or simply reduced with interocular pairing. In addition, the dots were moving horizontally, and the lack of rivalry under the interocular pairing condition might be explained by binocular fusion. Finally, as illustrated in Fig. 2, there are actually two possible binocular motion activities in the brain: (i) A binocular cell could inherit motion sensitivity from left and right monocular motion cells (BM2 in Fig. 2), or (ii) it could be sensitive to interocular motion (BM1 in Fig. 2) even when there is no monocular motion present (Lu & Sperling, 1995a; Shadlen & Carney, 1986). Our previous study did not distinguish between these two possibilities. We address all of these issues in this paper. Our findings suggest that *both* monocular and binocular motion signals contribute to motion rivalry. Preliminary results have been reported in abstract form (Meng, Chen, & Qian, 2002).

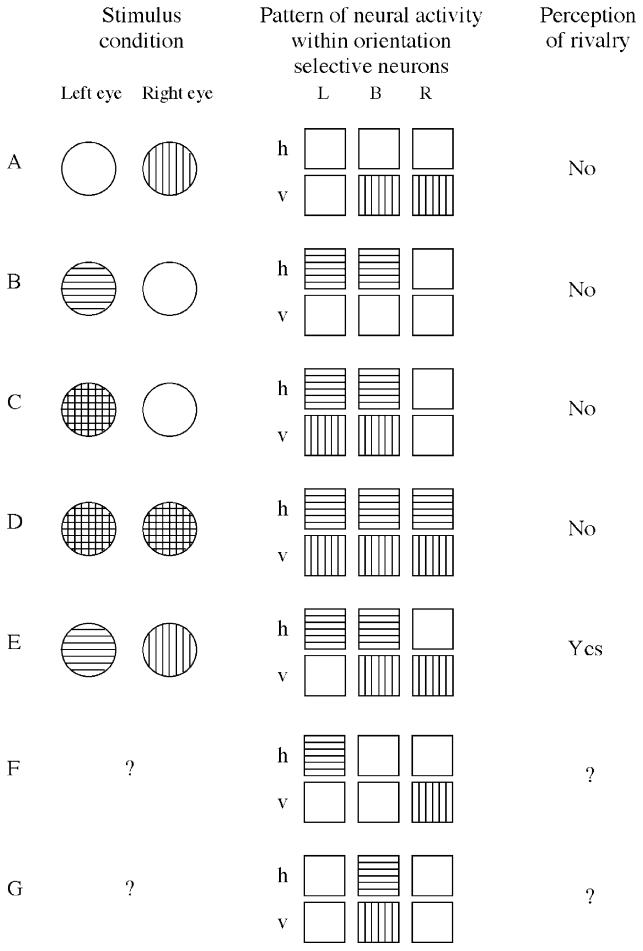

Fig. 1. Schematic representation of monocular and binocular cell activation under various stimulus conditions (A–E were redrawn from Blake (1989)). The left set of circles indicates the stimuli shown to the left eye and right eye respectively. The middle set of boxes represents pools of orientation selective neurons. Boxes in the rows labeled 'h' and 'v' represent neurons selective for horizontal and vertical orientations, respectively. The three columns of boxes represent pools of neurons innervated by the left eye (L) only, by both eyes (B), and by the right eye (R) only. The rightmost column indicates whether the observer perceives binocular rivalry. The stimuli A–D do not generate rivalry while E does. To differentiate the contributions of monocular and binocular competitions to rivalry in E, we need stimuli that could activate either the monocular neurons alone (F) or binocular neurons alone (G).

2. Experiment 1

In this experiment, we studied the effect of reducing binocular motion signals on motion rivalry.

2.1. Methods

2.1.1. Observers

The observers included two of the authors and two individuals who were naïve about the purpose of the study. All had normal or corrected-to-normal acuity.

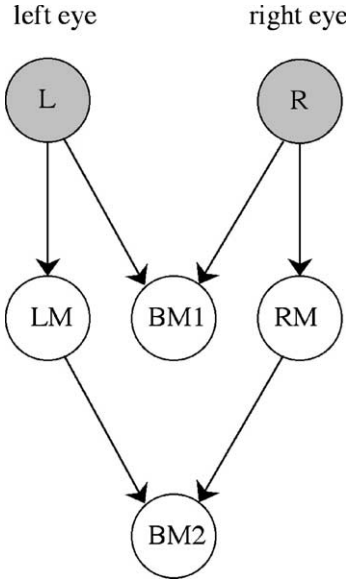

Fig. 2. A schematic illustration of the possible motion processing stages. Gray circles represent pools of non-direction selective neurons; open circles represent pools of direction selective neurons. L and R denote monocular cells for the left and right eyes that are not tuned to motion. The outputs of these non-direction selective cells can then be combined to form direction-selective cells. First, the combination could occur within each monocular pool, and this would lead to monocular direction selective cells; they are labeled as LM and RM in the figure. Second, there may be two kinds of binocular direction-selective cells, BM1 and BM2. BM1 cells become directionally sensitive by the proper combination of inputs from the non-motion cells of each eye. In other words, these cells are tuned to interocular motion. The second type of binocular motion cells (BM2) simply inherit motion tuning from both left and right direction selective cells.

The experiments were undertaken with the written consent of each observer.

2.1.2. Apparatus and stimuli

The experiment was conducted on a 21′ ViewSonic P817 monitor controlled by a Macintosh G4 computer. The vertical refresh rate was 120 Hz, and the spatial resolution was 1024 by 768 pixels. The stimulus for each eye was presented on the monitor side by side. In a well-lit room, observers foveally viewed the stimuli through a mirror stereoscope from a distance of 85 cm, using a chin rest to stabilize head position.

The screen had a constant veiling luminance of 21.6 cd/m^2. The stimuli were RDKs, seen as black (0.9 cd/m^2) dots moving or flickering within a white (98.4 cd/m^2) circular aperture that was 4° in diameter for each eye. There were 100 dots in each aperture, resulting in a dot density of 8 dots/deg^2. Each dot was a 2×2 pixel square (approximately 3.2′ on each side).

Three different types of stimuli were used: interocularly paired, interocularly unpaired, and flicker-noise. Each stimulus had a duration of 60 s. In the interocularly paired stimulus, each dot presented to the left eye was paired along the vertical axis with a dot presented to the right eye, with a separation of 16′ between them (Fig. 3B). In the first frame of the stimulus, 100 such interocular dot-pairs were randomly placed in the left and right apertures, with the right eye's dot above the corresponding left eye's dot in 50 randomly chosen pairs and the reverse for the remaining 50 pairs. All dots were updated every 92 ms. In the first update, the two dots in the first 50 pairs, in which the right eye's dot was *above* the left eyes dot, switched their spatial positions (but preserved their ocularity; Fig. 3B). This generated a downward apparent motion in the right eye, and an upward apparent motion in the left eye. The speed of both monocular motions was about 3°/s. There was no interocular motion, however, because the update did not change the superposition of the two eyes' views in any way. At the same time, the remaining dot pairs (in which the right eyes dot was *below* the left eye's dot previously) were replotted to new random locations, but now the right eye's dots was *above* the corresponding left eye's dots. In the next update, the dots in the second 50 pairs did the same exchange of positions to maintain the two monocular motion signals, while the first 50 pairs were replotted to new random locations again with the right

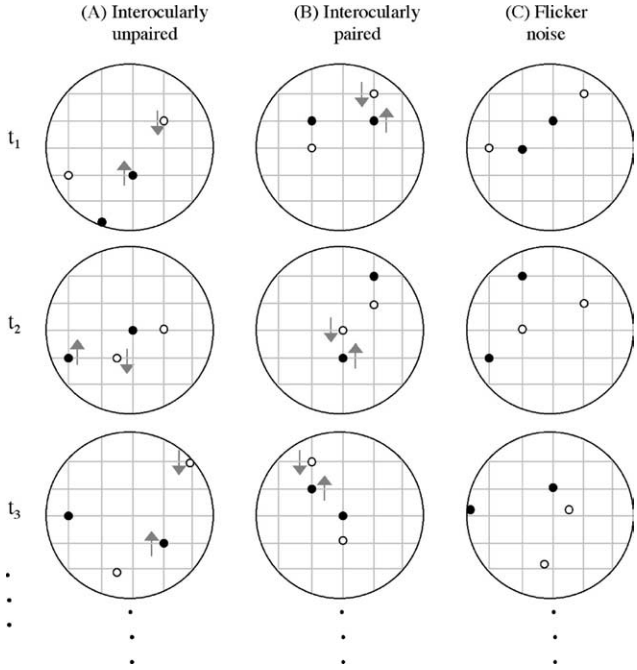

Fig. 3. Schematic representation of the stimuli used in Experiment 1. The filled and open dots represent the dots for the left and right eyes, respectively. During the experiment all dots were black on a white background without grids. At each update, half of the dots in the interocularly unpaired stimulus (A) and interocularly paired stimulus (B) moved in the vertical directions indicated by the arrows. The other half of dots were replotted at random positions. For the flicker-noise stimulus (C), all dots were randomly replotted every update. The interocularly unpaired and paired stimuli had identical monocular motion signals, but very different binocular motion signals. The flicker-noise stimulus had no motion signal. See text for further explanation.

eye's dot *above* the corresponding left eye's dot in each pair. This process was then repeated over the duration of the stimulus. The net effect was that at any given time, 50% of the dots were generating up and down monocular motion signals, and there was no interocular motion signal (BM1 in Fig. 2). The interocular pairing process employed here must also greatly reduce the binocular motion activities inherited from monocular motion cells (BM2 in Fig. 2) since MT cells and strongly direction-selective V1 cells show highly suppressed activation when opposite directions of motion are locally paired (Qian & Andersen, 1994). Therefore, the total binocular motion signal (BM1 plus BM2) in the interocularly paired stimulus is likely to be extremely weak. We chose vertical directions of motion here in order to eliminate possible depth perception from binocular fusion of the two dots in each interocular pair; vertical disparity is harder to fuse than horizontal disparity (Stevenson & Schor, 1997), and even if there were fusion, vertical disparity is much weaker in generating depth perception than horizontal disparity for the small displays used here (Howard & Rogers, 1995; Westheimer, 1978).

The interocularly unpaired stimulus was identical to the interocularly paired stimulus in all aspects except that there was no spatial pairing of dots across the eyes (Fig. 3A). At each update, half of the dots for the left (and right) eye were simply displaced up (and down) by $16'$ respectively. Therefore, this was a typical motion rivalry stimulus with a RDK of 50% coherence. Note that the interocularly paired and unpaired stimuli contained identical monocular motion signals. The only difference was that the paired stimulus had little binocular motion signals while the unpaired stimulus had normal binocular motion signals.

In order to have a baseline measure of rivalry, we included a third, flicker-noise stimulus type (Fig. 3C). Here the dots for the two eyes were independently positioned, and at each update, all dots were replotted to new, randomly chosen positions. All other parameters were identical to those for the interocularly paired and unpaired cases. Since there was no global motion signal present, whether monocular or binocular, in the flicker-noise stimulus, it should not generate real motion rivalry. Any reported motion rivalry could thus be attributed to subjects' response error or to random fluctuations of coincident motion signals.

The stimuli were generated in Matlab, using Psychophysics Toolbox extensions generously provided by Brainard (1997) and Pelli (1997).

2.1.3. Procedure

All stimuli were presented in random order, with 12 trials for each type. For the interocularly paired and unpaired stimuli, dots moved upward for the left eye, downward for the right eye in half of the trials, while dots moved downward for the left eye, upward for the right eye in the remaining trials. Since all stimuli were generated online, the 12 instances of the same stimulus type were only identical statistically but not in dot spatial locations. Each trial began with two white apertures for the two eyes, respectively. After having fused the apertures with the aid of the mirror stereoscope, observers pressed a key to initiate the presentation of a stimulus for 60 s. They were instructed to hold down the key whenever they perceived exclusive dominance of either upward or downward motion, and release the key otherwise. No monocular examples of the stimuli were given to adjust their subjective criteria. There was an inter-trial interval of at least 15 s during which the stimulus for next trial was computed. The total of 36 trials were randomly divided into three 12-trial blocks, with a 5-min break between blocks. In addition, the trials were self-paced and observers were encouraged to take breaks between trials if desired. Before data collection, all observers first completed several practice blocks.

During the experiment, the durations of the exclusive dominance periods were recorded. The data from each stimulus condition was analyzed and a gamma probability density function ($f(x) = \frac{1}{\Gamma(\gamma)\lambda^{\gamma}} x^{\gamma-1} e^{-x/\lambda}$, where $\Gamma(\gamma) = \int_0^{\infty} t^{\gamma-1} e^{-t}\, dt$) was applied to fit each distribution of exclusive dominance.

2.2. Results

The average duration of exclusive dominance across 12 trials for each observer and stimulus type is shown as a percentage of total presentation time in Fig. 4. For each subject and each stimulus type, the standard error was calculated from the 12 repeated trials. The three columns on the far right represent the mean values across all four observers, and the standard errors were calculated after removing the consistent individual differences (Loftus & Masson, 1994). A one-way-ANOVA between every two stimulus conditions revealed that the exclusive dominance duration in the interocularly unpaired condition (mean = 39.5%) is significantly larger than that in the interocularly paired condition (mean = 20.9%) ($p = 0.004$, $F(1,3) = 21.1$), which in turn is significantly larger than that in the flicker-noise condition (mean = 2.67%) ($p = 0.00004$, $F(1,3) = 51.6$). We also examined data from each observer individually by calculating the rivalry duration in each trial and then running a within-trials one-way-ANOVA between any two-stimulus conditions. For all but one observer (HT), the differences between any two conditions were significant at the 0.01 level. Observer HT failed to show significant difference between the interocularly paired condition and the flicker-noise condition.

As we discussed in Section 2.1, the interocularly unpaired stimulus was a normal motion-rivalry pattern

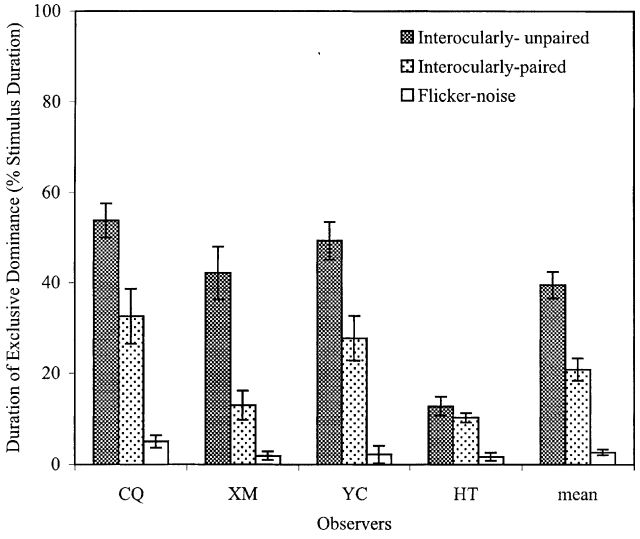

Fig. 4. Effect of interocular pairing on the duration of motion rivalry. The duration of the exclusive dominance is expressed as a percentage of the 60-s viewing duration. For each subject and each stimulus type, the standard error was calculated from the 12 repeated trials. The mean value across four observers for each condition is shown on the far right; standard errors were calculated after removing consistent individual differences (Loftus & Masson, 1994).

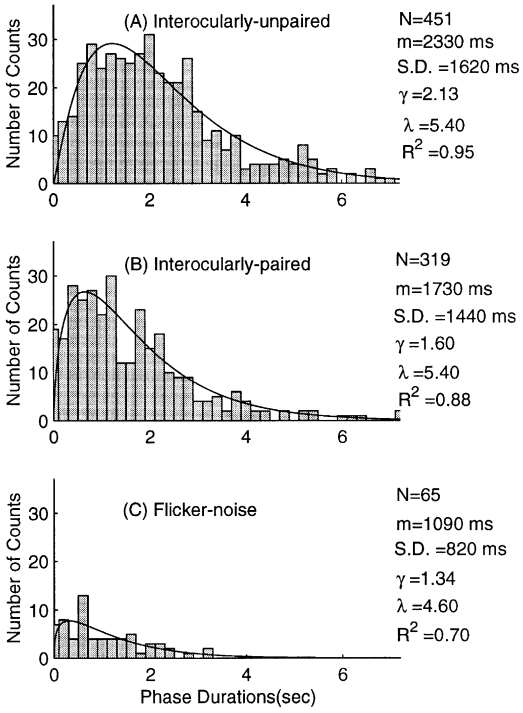

Fig. 5. Distributions of exclusive-dominance durations for the three stimulus conditions in Experiment 1: (A) interocularly unpaired, (B) interocularly paired, and (C) flicker-noise. Results are compiled from all four subjects. Data were fit by Gamma distribution (smooth solid curves). N denotes the number of durations recorded from all subjects; m is the mean duration in ms across all subjects and SD denotes standard deviation. The parameters of Gamma distribution are shown as γ and λ. R^2 is the coefficient of determination.

containing both monocular and binocular motion signals. In contrast, the flicker-noise stimulus contained no coherent motion at all, and should not generate any real motion rivalry; the small amount of reported rivalry under this condition in Fig. 4 must be due to subjects' response error or to random fluctuations of coincident motion signals in the noise. The interocularly paired stimulus contained the same monocular motion signals as the interocularly unpaired stimulus, but had nearly no binocular motion signals due to the pairing manipulation. Since the interocularly paired stimulus showed significantly less rivalry than the interocularly unpaired condition, we conclude that binocular motion signals are likely to contribute to motion rivalry. On the other hand, the rivalry in the interocularly paired stimulus was not completely eliminated, as judged by the baseline level of rivalry produced by the flicker-noise. This suggests that monocular motion signals also contribute to motion rivalry.

Fig. 5 shows the distribution of rivalry duration compiled from all observers for the three stimulus conditions. In the interocularly unpaired condition (Fig. 5A), the data were well fit by a gamma probability density function ($R^2 = 0.95$), consistent with previous studies of binocular rivalry (Blake, Fox, & Mcintyre, 1971; De Marco, Penengo, & Trabucco, 1977; Fox & Herrmann, 1967; Kalarickal & Marshall, 2000; Kovacs et al., 1996; Lehky, 1995; Leopold & Logothetis, 1996; Levelt, 1965; Logothetis, Leopold, & Sheinberg, 1996; Walker, 1975). The fit became progressively worse in the interocularly paired condition ($R^2 = 0.88$) and the flicker-noise condition ($R^2 = 0.70$). In addition to the different mean values of the three distributions, Fig. 5 shows that the number of counts (N) of the exclusive dominance periods differed greatly in the three conditions. In particular, subjects rarely indicated exclusive dominance for the flicker-noise stimulus, as expected.

An underlying assumption in this experiment is that if motion signals are reduced, then motion rivalry should also decrease. This is a reasonable assumption because the presence of motion signals is a necessary condition for motion rivalry. Indeed, when motion signals were eliminated as in our flicker-noise stimulus, motion rivalry was diminished. We also performed a control experiment with two of the authors (XM and YC) to verify this assumption independently. The stimuli were identical to the interocularly unpaired stimulus except that four different levels of motion coherence (100%, 60%, 30%, and 0% of the dots) were presented in random order. No other stimuli were used in this experiment. The experimental procedure was the same as that of the main experiment. The exclusive dominance duration decreased with the motion coherence level as shown in Fig. 6. For both observers, the differences between any two conditions were significant at the 0.05 level.

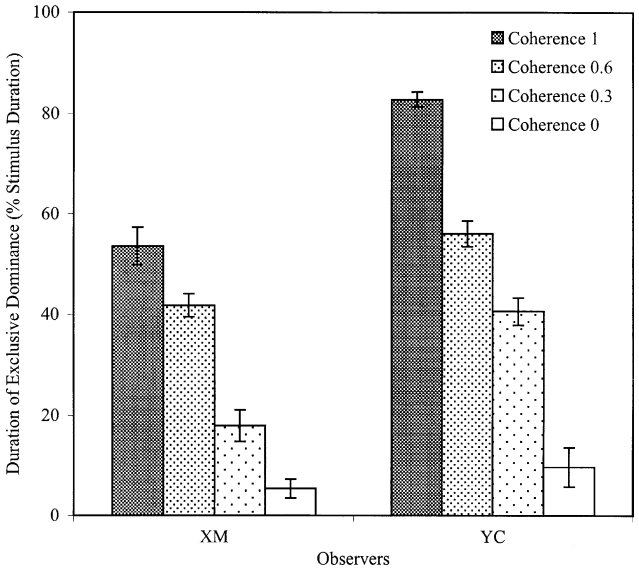

Fig. 6. Effect of coherence on the duration of motion rivalry. The duration of the exclusive dominance is expressed as a percentage of the 60-s viewing duration. For each subject and each stimulus type, the standard error was calculated from the 12 repeated trials.

The results in Fig. 4 might be confounded by eye movement. Specifically, different stimuli may elicit different amounts of eye movement, which could contribute to the different degrees of motion rivalry. To rule out this possibility, we modified the main experiment by introducing a binocular fixation cross (0.4° each dimension) and by placing the stimulus center 2.5° randomly to either side of the fixation. The gap between the fixation center and the nearest edge of the stimuli was 0.5°. Subjects were instructed to maintain central fixation while judging exclusive dominance of motion in the periphery. All other aspects of the experiment were identical to those of the original experiment. This arrangement should greatly reduce the amount of eye movement as confirmed by observers' subjective report. The results from two of the authors (XM and YC) were very similar to those in Figs. 4 and 5. For XM, the mean exclusive dominance durations as a percentage of the total duration were 36.8%, 12.2% and 1.1% for the interocularly unpaired, interocularly paired and flicker-noise conditions, respectively. For YC, these values were 69.8%, 44.2% and 12.7%. For both observers, the differences between any two conditions were significant at the 0.05 level.

3. Experiment 2

In this experiment, we examined how rivalry may be affected by removing monocular motion signals from a stimulus. Therefore, this experiment complements Experiment 1.

3.1. Methods

3.1.1. Observers

All the observers of the first experiment served as subjects in this experiment.

3.1.2. Apparatus and stimuli

The apparatus for this experiment was identical to that for Experiment 1. There were also three types of stimuli in this experiment. Two of them, the interocularly unpaired and flicker-noise stimuli, were generated in the same way as those in Experiment 1 (Fig. 3A and C). The remaining type was an interocular-motion stimulus, which contained interocular-motion signals but no monocular motion signals. Specifically, at each update, all dots for the left eye were randomly replotted, but half of the right eye's dots were displaced upward from the corresponding left eye's dot positions before the update (Fig. 7A). The spatial and temporal steps of updating were identical to those of Experiment 1 so that the manipulation generated an upward interocular motion of 3 deg/s. The other half of the right eye's dots were similarly displaced at each update to generate a downward interocular motion of 3 deg/s (Fig. 7A). It is important to note that there is no monocular motion signal for either eye. In fact, monocularly, the interocular-motion stimulus was identical to the flicker-noise stimulus. This version of the interocular-motion stimulus was asymmetric (Fig. 7A). We also generated stimuli in which the displacement of the dots was symmetric (Fig. 7B) and obtained the same results. In the symmetric version, there was a downward interocular motion from the right eye to the left eye, and an upward interocular motion from left eye to the right eye.

3.1.3. Procedure

The procedure was the same as in Experiment 1.

3.2. Results

Fig. 8 shows the percentage duration of exclusive dominance for each observer and stimulus condition. The format of the figure is identical to that of Fig. 4. Similar to Experiment 1, the results of one-way-ANOVA between every two conditions revealed that the rivalry duration in the interocularly unpaired condition (mean = 52.2%), is significantly larger than that in the interocular-motion condition (mean = 15.5%) ($p = 0.00003$, $F(1,3) = 56.4$), which in turn is significantly larger than that in the flicker-noise condition (mean = 5.66%) ($p = 0.03$, $F(1,3) = 8.13$). When each observer was considered individually, all observers except CQ showed a significant difference between any two conditions at the 0.01 level. Observer CQ failed to show a significant difference between the interocular-motion and flicker-noise conditions. The large reduction of ri-

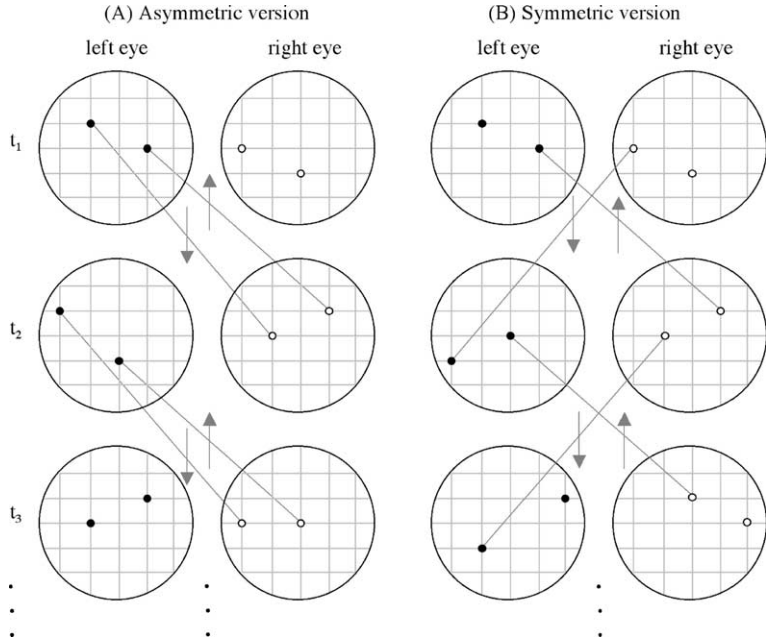

Fig. 7. Schematic representation of the interocular-motion stimuli used in Experiment 2. Interocular motion can be introduced either asymmetrically (A) or symmetrically (B). The filled and open dots represent the dots for the left and right eyes, respectively. During the experiment all dots were black on a white background without grids. Dots connected by a long gray line generate vertical interocular motion. The arrow on the line marks the direction of the interocular motion. In the asymmetric version (A), the dots for left eye were replotted randomly every update, while the dots for right eye depended on the dots for the left eye in the previous frame to create interocular motion. In the symmetric version (B), half of the dots in each eye were replaced randomly, while the remaining half generated interocular motion.

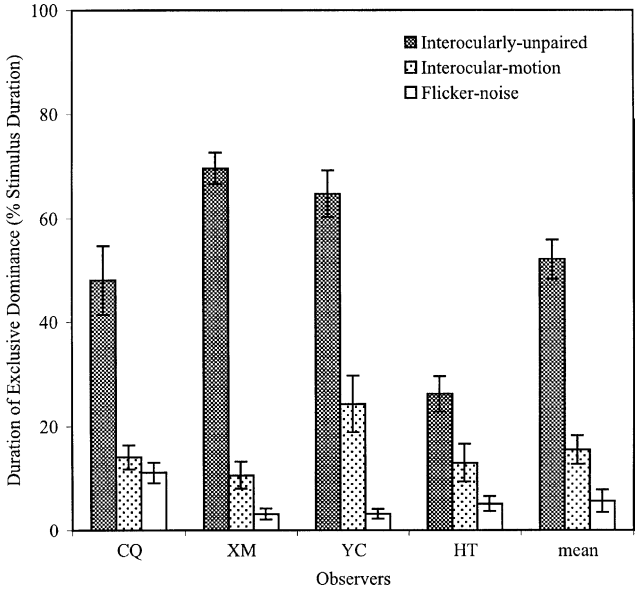

Fig. 8. Effect of interocular correlation on the duration of motion rivalry. The duration of the exclusive dominance is expressed as a percentage of the 60-s viewing duration. The format of this figure is identical to that of Fig. 4.

valry from the interocularly unpaired to interocular-motion conditions implies that the monocular motion signal and the binocular motion signal inherited from monocular activities (BM2 in Fig. 2) both determine motion rivalry to a large degree. On the other hand, the fact that rivalry in the interocular-motion condition did not decrease to the level of the flicker-noise condition suggests there is also a contribution of interocular-motion signal to motion rivalry. These results again demonstrate both monocular and binocular motion signals contribute to motion rivalry, consistent with the results in Experiment 1.

Note that observers reported more rivalry in the interocularly unpaired and the flicker-noise conditions in Experiment 2 than in Experiment 1, although the stimuli were identical in the two experiments. (The differences are not significant, however, with $p = 0.30$, $F(1,3) = 1.27$ and $p = 0.25$, $F(1,3) = 1.66$, respectively.) One possibility is that observers are usually much less sensitive to interocular motion than to the monocular motion (Lu & Sperling, 1995b). The observers might have lowered their criteria of motion detection in Experiment 2, and the corresponding duration of rivalry thus increased.

Similar to Fig. 5, we also show the distributions of rivalry duration and the fit curves in Fig. 9. Here we see again that the goodness of fit, the mean of distribution, and the number of occurrences of exclusive dominance all decreased from the interocularly unpaired condition to interocular-motion condition and to flicker-noise condition, indicating a progressive decrease of motion rivalry.

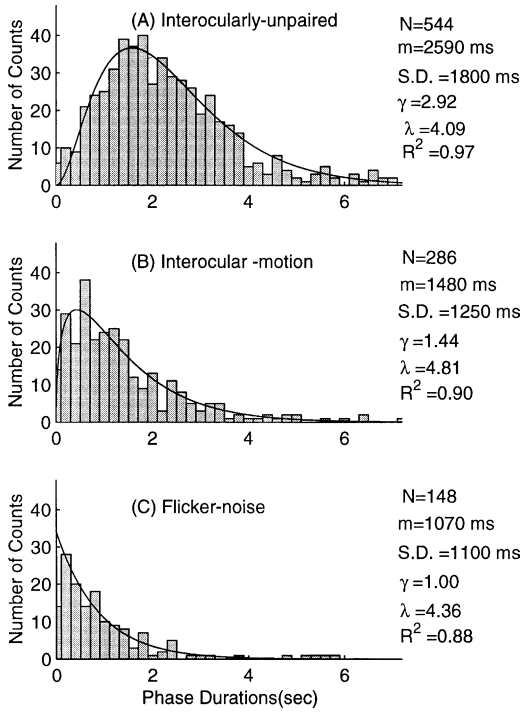

Fig. 9. Distributions of exclusive-dominance durations for the three stimuli in Experiment 2: (A) interocularly unpaired, (B) interocular-motion, and (C) flicker-noise. Results are compiled from all four subjects. The format of this figure is identical to that of Fig. 5.

In Experiment 2, we used an asymmetric version of the interocular-motion stimulus (Fig. 7A). This asymmetry might have affected our results. To rule out this possibility, we ran a control experiment for two of the authors (XM and YC) with the interocular-motion introduced symmetrically (Fig. 7B). The results from the symmetric and asymmetric version of the stimuli were very similar. For XM, the mean values for the symmetric and asymmetric version were 19.9% and 18.1% respectively. For YC, these values were 13.3% and 11.7% respectively. The differences were not significant ($p = 0.62$, $F(1,11) = 0.25$ for XM; $p = 0.72$, $F(1,11) = 0.13$ for YC), suggesting that symmetry is not important.

4. Discussion

In this paper, we used four specially designed RDKs to examine the contributions of monocular and binocular motion signals to motion rivalry. The interocularly unpaired RDK was a normal motion-rivalry stimulus that should activate both monocular and binocular motion sensitive cells. It sets the upper limit for rivalry among the four RDKs in our experiments. The flicker-noise RDK contained no coherent motion signal of any kind, and thus provided a baseline measure of no motion rivalry. The interocularly paired stimulus in Experiment 1 had the same amount of monocular motion signals as the interocularly unpaired stimulus; however, the two types of binocular motion signals (see Fig. 2) in this stimulus were diminished due to the pairing process. If motion rivalry were exclusively determined by competition between monocular motion cells, then the paired and the unpaired stimuli would show equal amount of rivalry (but see next paragraph for another possibility). If, on the other hand, motion rivalry were completely determined by competition among binocular cells, then the interocularly paired stimulus would behave like the flicker-noise stimulus with little rivalry. We found that the interocularly paired stimulus generated an intermediate level of rivalry, midway between the upper and lower limits set by the interocularly unpaired and the flicker-noise stimuli. This is consistent with the contributions of both monocular and binocular motion signals to motion rivalry.

However, the above argument did not consider the possibility that even though the paired and unpaired stimuli contain essentially identical monocular motion signals, the *competition* between the monocular signals may be different in the two cases. Specifically, the competition may depend on the interocular distance between the two eyes' motion vectors, and this distance was smaller for the paired than for the unpaired stimulus on average. Should the degree of competition, and thus rivalry, increase or decrease with interocular distance? We think it should decrease because interocular competition is believed to operate over a local region (Blake, 1989). In addition, if the two eyes' features are widely separated without overlap, there will be no competition or rivalry. Therefore, the proximity consideration alone should predict a stronger rivalry in the paired condition than in the unpaired condition. Since our observation was precisely the opposite, we conclude that the diminished binocular motion signals in the paired stimulus is the dominant factor that is responsible for the observed rivalry reduction. Our conclusion that binocular motion signals are likely to contribute to motion rivalry is thus still valid. The residual rivalry in the paired stimulus (compared with the flicker stimulus) may be due to either monocular contributions or enhanced competition between the monocular signals or both.

There is evidence indicating that monocular cells in LGN and V1 input layer exhibit interocular inhibition (Sengpiel et al., 1995). If this inhibition is stronger at smaller interocular distance, it may contribute to the different degrees of rivalry of the paired and unpaired stimuli, and raises the possibility that the observed difference may not be due to binocular contributions. However, this inhibitory interaction was found to be independent of interocular differences in orientation, and thus unlikely to be involved in orientation rivalry

(Sengpiel et al., 1995; see also Lehky & Maunsell, 1996). Likewise, these cells are also not tuned to motion, and thus unlikely to be responsible for the motion rivalry reported here. In addition, when a monocular cell is strongly inhibited by inputs through the other eye, one has to reconsider the definition of monocular and binocular cells and the related definition of monocular and binocular contributions to rivalry. Another question is: does a stronger inhibitory interaction between opposing motion directions imply a stronger or weaker rivalry? On the one hand, interocular inhibition between monocular cells may be the basis of competition (Blake, 1989), and a stronger inhibition should thus imply a stronger rivalry. On the other hand, inhibition among (binocular) V1 and MT cells tuned to opposite directions greatly reduces their motion responses (Qian & Andersen, 1994; Snowden, Treue, Erickson, & Andersen, 1991), and should therefore reduce motion rivalry. Perhaps these two different types of inhibition play different roles. Obviously, a combined physiological and psychophysical study would be needed to settle the issue.

In our second experiment, the interocular-motion stimulus contained no monocular motion signals just like the flicker-noise stimulus. Unlike the noise, however, it had upward and downward interocular-motion signals that must be detected by binocular cells tuned to interocular motion. We found that similar to the interocularly paired stimulus in Experiment 1, the rivalry for the interocular-motion stimulus was above the baseline level of the noise stimulus but below the level of the interocularly unpaired stimulus. This suggests that interocular motion by itself, which is a type of binocular motion signal (BM1 in Fig. 2), can contribute to motion rivalry. [1]

It is well known that interocular motion is much weaker than monocular motion. Recent psychophysical evidence also indicates that interocular motion is strongly influenced by attention (Blaser, Sperling, & Lu, 1999; Lu & Sperling, 1995a). Therefore, the weak upward and downward motion signals in the interocular-motion stimulus of Experiment 2 may need an attentional boost to become dominant, and the rivalry observed in this stimulus may reflect, at least partially, subjects' attentional alternations between the two motion directions. Also note that each of the two opposite motion directions in the interocular-motion stimulus was carried by dots in both eyes. If one eye's input were completely suppressed, there would be no interocular motion. Thus, the rivalry must be between the two motion directions instead of between the two eyes in this case. This type of stimulus rivalry (as versus eye rivalry) was first demonstrated by Logothetis et al. (1996) with flickering gratings of orthogonal orientations constantly exchanged between the two eyes. Lee and Blake (1999) later pointed out that stimulus rivalry with gratings can only be seen under limited conditions (relatively low contrast gratings within a narrow range of spatial and temporal frequencies, rapid flickering rate, and abrupt interocular exchange); otherwise, eye rivalry dominates. In contrast, we used high-contrast RDK motion stimuli and a different paradigm in our experiments, and we did not have to fine tune any parameters to observe stimulus rivalry (as long as there were clear interocular-motion signals). This difference is perhaps not surprising given the known independence between motion and form rivalry (Carney, Shadlen, & Switkes, 1987; Andrews & Blackmore, 2002). On the other hand, consistent with Lee and Blake's grating study, stimulus rivalry under our interocular-motion condition is relative weak compared with normal binocular rivalry (Fig. 8), and is observed under the condition where monocular motion signals for eye rivalry is eliminated.

It should be emphasized that Fig. 2 with different types of motion cells is only meant to illustrate the logic of the experiments and the implication of the data; it does not provide a theory or even an explanation of binocular rivalry. A related point is that although the figure only depicts monocular and binocular cells, real cells in V1 form a continuum with various degrees of ocular balance (Hubel & Wiesel, 1962). (Cells before and after V1 are largely monocular and binocular, respectively.) How a V1 cell should respond to our interocularly paired and interocular-motion stimuli must depend on the degree of its ocular dominance. Our conclusions are still valid to the extent that these responses reflect cells' degrees of ocular dominance, and thus the relative contributions of the monocular and binocular components.

The results reported here confirm and extend a previous study from this lab (Matthews et al., 2000). In the previous work, we used an interocular pairing procedure to show that binocular motion cells must contribute to rivalry. However, since we did not interleave a flicker-noise stimulus, we did not have a baseline measure of no-rivalry, and therefore could not establish the monocular contributions to rivalry. In addition, we previously used horizontal motion directions, and the reduced rivalry in the interocularly paired condition might be due to binocular fusion. This problem was avoided in this paper with vertical motion directions. Furthermore, the motion trajectory of each dot spanned several consecutive positions in the previous study. Here we used two-frame apparent motion to allow better control over interocular motion. In particular, the

[1] One should not expect that the degrees of rivalry exhibited by the interocularly paired stimulus in Experiment 1 and the interocular-motion stimulus in Experiment 2 to sum up to the normal degree of rivalry of the interocularly unpaired stimulus because the second type of binocular motion signal (BM2 in Fig. 2) is largely missing in the sum, and the contributions of different types of motion signals may not sum linearly.

two-frame interocularly paired stimulus generates no interocular motion; this is not true for the paired stimulus in the previous study. Finally, the interocular-motion stimulus in Experiment 2 of this study was not used previously.

In summary, our data suggest important roles for both monocular and binocular neurons in motion rivalry. Competition among either type of cells could generate rivalry, but strong rivalry may require the participation of both cell types.

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