Motion dominance in binocular rivalry depends on extraretinal motions

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In binocular rivalry, moving stimulus is dominant over stationary stimulus. This is called motion dominance. The motion here is usually a motion defined on the retina (retinal motion). However, motion can be defined in several different coordinates. It can be defined with respect to objects in the background (object-based motion) or to observers' head or body (spatiotopic motion), as well as to the retinal coordinate. In this study, we examined the role of motions defined by these three coordinates. A dichoptic pair of gratings was presented to create a binocular rivalry, one of which was moving and the other stationary. A fixation point and a reference background were either moving with the grating or stationary, depending on the condition. Different combinations of the three types of motions were created by having the observer track the fixation point or the background when they are moving. It was found that the retinal motion does not necessarily yield motion dominance, and that the motion dominance is determined by the combination of motions defined by different coordinate systems.

Introduction

Perceptual dominance during binocular rivalry is a function of various aspects of stimuli, including intensity, spatial configuration, meaningfulness, and so on. Motion is known as one of the most powerful factors among them (Blake, Zimba, & Williams, 1985; Breese, 1899). A moving stimulus presented to one eye strongly suppresses the conscious perception of a stationary stimulus presented to the other eye, and the opposite never happens. This motion dominance is commonly observed in several different "invisible" phenomena such as Troxler effect (Troxler, 1804), motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001), and adaptation-induced blindness (Motoyoshi & Hayakawa, 2010). These results suggest that motion is a particularly salient visual feature, and plays a critical role in the visibility of stimulus.

In studies of motion itself and its role in visual awareness, motion has usually been defined as positional change over time on the retina, or retinal motion. However, motion can be defined in several different spatial coordinates in addition to the retinal coordinate. There are three most notable motions based on three different coordinate systems. They are retinal, object-based, and spatiotopic motions. Retinal motion is the motion on the retina, that is, the motion defined in the retinal coordinate. Object-based motion is the motion with respect to other objects or the background scene. Spatiotopic motion is the motion with respect to the observer's body or head. These three types of motions are involved in motion perception in the ordinary scene; however, in experimental settings, we can control the contribution of each component by manipulating the motion of the object and the motion of eyes or body. For example, an object moves and observers are asked to fixate on a stationary fixation point, the object moves in all three coordinates. However, when the observer is asked to fixate on a moving object and track it by eye movements, the object is moving relative to the background and to the body of observers, but it is stationary on the retina. The processing of retinal motion can be conducted by using only retinal input, but the processing of motion in nonretinal coordinates needs to integrate retinal input with the information of eye and body movements
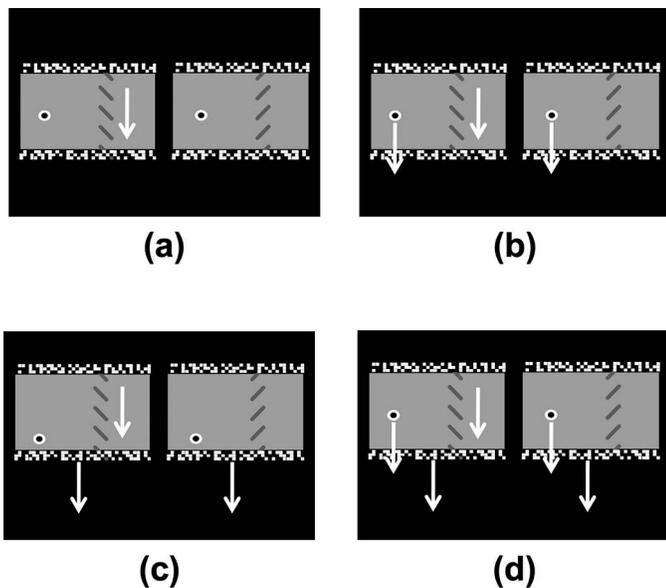
Figure 1. Schematic of the stimulus display used in the experiment. The observers viewed the display dichoptically. White arrows indicate motion of each stimulus component. (a) Grating drifts in the left eye when the fixation point and the background reference are stationary (stationary fixation/reference, SFR condition). (b) Grating drifts in the left eye when the observer tracks the fixation point moving together with the grating (moving fixation, MF condition). In contrast to (a), the grating drifts retinally in the right eye, but not in the left eye. (c) The reference moves together with the grating drifting in the left eye while the fixation point stays stationary (moving reference, MR condition). In contrast to (a), the right grating contains object-based motion relative to the background reference. (d) Both the fixation point and the reference move together with the drifting grating in the left eye, and the observer tracked the fixation point (moving fixation/reference, MFR condition). The retinal and object-based motions are reversed from case (a).

provided by efferent signals or proprioceptive feedback (Wurtz, 2008).

The visual system is known to have neural mechanisms that compute motions in nonretinal coordinates. Psychophysical and electrophysiological evidence suggests the existence of neural mechanisms that detect object-based or relative motions (Allman, Miezin, & McGuinness, 1985; Born & Tootell, 1992). Several classical studies have demonstrated the effects of eye and body movement on motion perception, which suggests the existence of mechanisms that detect spatiotopic motions (e.g., Aubert-Fleischl phenomenon, Filehne illusion; Filehne, 1922). Recent psychophysical studies investigate mechanisms of spatiotopic motion processing by analyzing the motion or pattern perception during smooth pursuit eye movement (Schütz, Braun, Kerzel, & Gegenfurtner, 2008; Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007;

Terao & Murakami, 2011). Electrophysiological studies also show evidence for cells that specifically respond to spatiotopic motions in cortical areas such as V3A (Galletti, Battaglini, & Fattori, 1990), MST (Chukoskie & Movshon, 2009; Erickson & Thier, 1991), and 7a (Sakata, Shibutani, Kawano, & Harrington, 1985). In view of these findings, it is plausible that the perceptual dominance in binocular rivalry is affected by object-based and spatiotopic motions that involve higher-order motion processing as well as retinal motion. The purpose of the present study, therefore, is to reanalyze the motion dominance in binocular rivalry from the viewpoint of separate coordinate systems. The main focus is to examine the true contribution of retinal motion in the motion dominance.

We introduced a simple stimulus display (Figure 1) that enables us to examine the effects of three types of motion: retinal, object-based, and spatiotopic. The stimulus is a dichoptic pair of displays each consisted of a grating, a fixation point, and a gray rectangular background (reference). Each of the three components was stationary or moved independently. The fixation point and the gray background stayed stationary or moved vertically depending on the condition, and the stationary/moving parameter was constant between the two eyes. The grating was stationary or moving, and the stationary/moving parameter was varied independently between the two eyes. There were four possible combinations in the movement of three components. The first condition was that only the grating in one eye drifted and the others all were stationary (Figure 1a: stationary fixation/reference, SFR condition). In this case, the drifting grating involved all types of motion: retinal, object-based, and spatiotopic. In the second condition, the observer tracked the fixation point that moved together with the drifting grating while the reference background was stationary (Figure 1b: moving fixation, MF condition). In this case, the drifting grating was stationary in retinal coordinate but drifted in both object-based and spatiotopic coordinates. In the third condition, the reference moved together with the drifting grating while the fixation point stayed stationary (Figure 1c: moving reference, MR condition). In this case, the grating was stationary relative to the reference but moved on the retina and relative to the observer. In the fourth condition, both fixation point and reference moved together with the drifting grating (Figure 1d: moving fixation/reference, MFR condition). In this condition, the grating was stationary on the retina and relative to the reference, but drifted relative to the observer. Using these displays, we tried to dissociate the three coordinates of target motion and quantitatively estimate their relative contributions of motions in different coordinate systems to the perceptual dominance in binocular rivalry. In this study, we focused on the dominance for

dichoptic stimuli presented for 2 s. It has been known that the binocular rivalry during the earlier phase of presentation (initial phase) and the long-term dynamics of dominance are different (Mitchell, Stoner, & Reynolds, 2004). Therefore, in this sense, what we examined in this study is the modulation of dominance in the initial phase of rivalry.

Methods

Observers

Four naive participants (HS, MF, MW, TK) and one of the authors (RN), with corrected-to-normal vision, participated in the experiment.

Apparatus

Images were generated by a personal computer using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) and MATLAB (MathWorks, Inc., Natick, MA), and displayed on a gamma-corrected 21-inch CRT (Mitsubishi Diamondtron M2 RDF223G; 1024×768 pixel) through a video attenuator (Bits++; Cambridge Research Systems, Ltd., Rochester, UK) with a frame rate of 60 Hz. The pixel resolution of the CRT was 1.88 min/pixel at the viewing distance of 57 cm. For dichoptic presentations, we employed a mirror haploscope with a septum dividing the screen into two sides. Throughout the experiment, movements of both eyes were monitored by means of Viewpoint Eye Tracker (220 Hz; Arrington Research, Inc., Scottsdale, AZ), which was located behind the cold mirrors in the haploscope that filtered infrared light. The front screen of the CRT together with the frame of display was covered by a neutral-density (ND) film of 23% transmittance so that the dark part of the CRT screen was kept as dark as possible.

Stimuli

Visual stimulus was a dichoptic pair of images, each of which consisted of three components (Figure 1): a rectangle-wave grating (duty ratio = 0.2), a fixation point (0.52° in diameter), and a gray reference background (H13 × V8.7°; 10.5 cd/m^2). The fixation point was superimposed on the reference, which spatially windowed the grating to keep it visible only within the reference. The grating pattern was composed of lines (1.5 × 0.22°; length × width) with a separation of 0.87°. Moving grating pattern drifted within a virtual window of 1.1° × 8.7° (length × width); that is, the

leading edge of the pattern disappeared when it reached the end of this window and new pattern was supplied at the other end of the window. The grating was orthogonally oriented between the eyes (45° and 135°), and located at 5.7° to the right of the fixation point. In order to aid binocular fusion, the reference background was framed by random dot patterns. The edge of the CRT was almost completely invisible due to the ND film.

Each of the components was either stationary or moving depending on the experimental condition. The grating presented to one eye drifted with the speed of 6°/s on the CRT screen. The direction of motion was either upward or downward. This moving grating is hereafter called *MOVING grating*, since it physically moved on the CRT screen although it may be stationary with respect to one or two coordinates due to experimental manipulation. The grating presented to the other eye was stationary on the CRT, and is called *STATIONARY grating*. The eye to which the MOVING grating was presented and the motion direction were randomized between trials. The fixation point and the reference were either stationary or moving. When they moved, they moved with the same velocity and in the same direction as the MOVING grating. The motion of fixation point and reference, when they moved, were synchronous between the two eyes.

There were four combinations of the stationary/moving parameters for the fixation point and reference. The first was the stationary fixation/reference (SFR) condition (Figure 1a), in which both the fixation point and the reference were stationary, the observer fixated the fixation point, and the MOVING grating had all three types of motion: retinal, object-based, and spatiotopic. This condition was created to test classical motion dominance. The second combination was the moving fixation (MF) condition (Figure 1b), in which the fixation point moved in the same direction and with the same velocity as the MOVING grating. In this condition, the MOVING grating became stationary in the retinal coordinate as a result of tracking eye movement, but was moving in object-based and spatiotopic coordinates. The third combination was the moving reference (MR) condition (Figure 1c), in which the reference moved in the same direction and with the same velocity as the MOVING grating, while the fixation point remained stationary. In this condition, the MOVING grating moved in retinal and spatiotopic coordinates but was stationary in object-based coordinate. The last combination was the moving fixation/reference (MFR) condition (Figure 1d), in which both the fixation point and the reference moved and the observer tracked the moving fixation point. In this condition, the MOVING grating had spatiotopic motion alone, since retinal and object-based motions were cancelled by tracking eye movement and motion

	MOVING grating			STATIONARY grating		
Spatial coordinates of motion	R	O	S	R	O	S
Stationary fixation/reference	♦	♦	♦	—	—	—
Moving fixation	—	♦	♦	♦	—	—
Moving reference	♦	—	♦	—	♦	—
Moving fixation/reference	—	—	♦	♦	♦	—

Table 1. Three types of motion observed for each experimental condition: *R* represents the retinal coordinate, *O* represents the object-based (relative) coordinate, and *S* represents the spatiotopic coordinate. Yellow diamonds denote the presence of the corresponding type of motion involved, respectively, in the MOVING grating and the STATIONARY grating.

of the reference. The type of motion involved in both MOVING and STATIONARY gratings are graphically represented in Table 1 for each experimental condition. In addition to the experimental conditions, there was a control condition in which all the components were stationary, including gratings.

To quantify the perceptual dominance between the MOVING and STATIONARY gratings, we varied the contrast ratio between the two gratings and estimated the point at which judged dominance during the 2-s trial period was equally likely to be reported to be either of the two rival gratings. The total contrast of the grating pair was also varied across experimental blocks over three levels (0.1, 0.2, and 0.8).

Procedure

The experiment was conducted in a dark room. Each condition was tested in separated random-ordered blocks. In each trial, all stimuli remained still for 1 s, and the designated components started to move for 2 s. The contrast ratio of the two gratings was randomly varied between 0.05 and 0.95. The observer was required to fixate at the fixation point, or track it as accurately as possible. After each trial, observers were asked to indicate the orientation (left or right tilted) of the grating that appeared dominant by pressing a button.

The accuracy of tracking the fixation point was checked in every trial. The analysis was done for the period from 0.5 to 1.5 s after stimulus onset during the total stimulus duration of 2 s. The trajectory of the fixation point was first estimated by fitting a linear function to the eye position data regarding each eye. A root mean square error (RMSE) in X-Y position was calculated between the gaze and the estimated fixation point. This error was taken as a measure of the accuracy of fixation and tracking. We discarded trials in which the RMSE deviated beyond the 99% confidence interval of average RMSE for the control condition, in which observers viewed only totally static stimuli, for all four conditions (SFR, MF, MR, and MFR). As a result, 73% of trials were used for SFR, 74% were used for MF, 76% were used for MR, and 74% were used for MFR condition. In all, 74% (9,985/13,496) trials were used in the subsequent analysis.

Results

The results of a typical observer (MW) are shown in Figure 2. In these graphs, the visibility (proportion of "dominance" response) of the MOVING grating is plotted as a function of its contrast ratio. Each symbol represents the data for five different motion conditions: stationary fixation/reference (SFR, red), moving fixation (MF, blue), moving reference (MR, orange), moving fixation/reference (MFR, green), and control (black). The curves are fitted by logistic functions. Each panel shows the results for different total contrasts (0.1, 0.2, and 0.8). Since all stimuli were stationary in the control condition, one of the gratings was randomly designated as the MOVING grating and the other one as the STATIONARY grating.

Two-way ANOVA reveals the main effect of motion type, $F(4, 16) = 13.04$, $p = 0.0001$, and the interaction between total contrast and motion condition, $F(8, 32) = 5.35$, $p = 0.0003$, but the main effect of total contrast is not significant, $F(2, 8) = 1.433$, $p = 0.29$.

In Figure 2, open circles show the results of binocular rivalry between stationary gratings. In this control condition, dominance should balance at a contrast of 0.5; that is, the curve should intersect with the horizontal line that represents the dominance of 0.5 since there was no motion involved in either stimulus, and the actual data shows this is the case. A shift to the left of the curve indicates the dominance of the MOVING grating, because it means that the MOVING grating with a lower contrast balanced the STATIONARY grating with a higher contrast.

The red filled circles in the left panel of Figure 2 show the results of binocular rivalry between the moving and stationary gratings for a total contrast of 0.1 (SFR condition). The red curve is clearly shifted to the left relative to the control condition, and intersects with the horizontal line at the contrast ratio of 0.3. That is, the MOVING grating, with a contrast of 0.03, and the STATIONARY grating, with a contrast of 0.07, balanced perceptually. Thus, these results indicate clear motion dominance, and similar results were obtained for all of the total contrast values. These
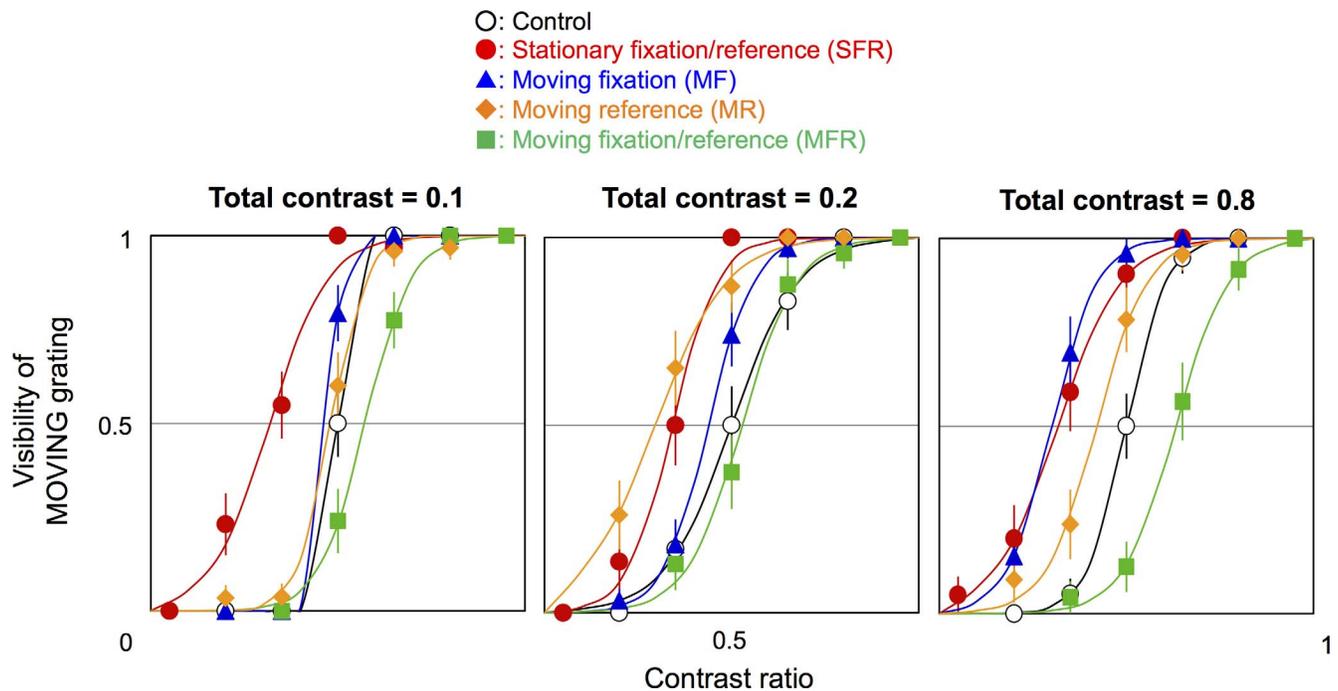
Figure 2. Psychometric functions for the visibility of the MOVING grating (observer MW). The proportion of "dominant" response of the MOVING grating is plotted as a function of the contrast ratio relative to the total contrast across both eyes. Each panel shows the results for total contrasts of 0.1, 0.2, and 0.8, respectively. Red circles represent the results for the stationary fixation/reference (SFR) condition, blue triangles the results for the moving fixation (MF) condition, orange diamonds the results for the moving reference (MR) condition, and green squares the results for the moving fixation/reference (MFR) condition. Open circles show the results for the control (totally stationary) condition. Error bars represent ±1 *SE*.

results are consistent with classical motion dominance (Blake et al., 1985).

In the MF condition (blue triangle), observers were asked to track the fixation point that moved along with the MOVING grating. Because of this tracking, the retinal motion for the grating that was moving when there was no tracking (the stimulus moving relative to the reference) disappeared and the grating that was stationary relative to the reference started to have retinal motion. If the motion dominance in binocular rivalry is determined by retinal motion, the dominance in rivalry should be reversed with respect to the SFR condition, and the blue curve should be shifted to the other side of the curve for the control condition. However, the results indicate that this does not happen. Instead, the curves intersected with the 0.5 line at around a total contrast of 0.5, or even stayed on the left side for a total contrast of 0.8. These results clearly show that motion dominance in binocular rivalry is not determined by retinal motion alone.

In the MR condition (orange diamond), the reference moved along with the MOVING grating while observers were asked to fixate on a stationary fixation point. In this case, the object-based motion was extinguished for the grating originally moving (MOVING) grating, and a new object-based motion was generated on the other eye, but the retinal and

spatiotopic motions were the same as the SFR condition. If retinal motion determines dominance, the result should be the same as, or at least similar to that for, the SFR condition. However, the orange curve approaches the control condition except for a total contrast of 0.2. Again, this shows that motion dominance is not determined by retinal motion alone.

Finally, in the MFR condition (green square), the fixation point and the reference moved along with the MOVING grating and observers were asked to track the fixation point. In this case, retinal and object-based motions disappeared, and only spatiotopic motion remained for the originally moving (MOVING) grating. The other eye had retinal and object-based motions generated by tracking, but the grating was spatiotopically stationary. Finally, however, in this case, we could obtain reversed results from the SFR condition. The green curve shifts rightward relative to the control condition, and comes to the opposite side of the control condition. These results indicate that the existence of retinal motion alone is not enough to generate motion dominance. Object-based motion has to be present together with retinal motion, but the existence of spatiotopic motion is not required.

To quantify the perceptual dominance of the gratings, we estimated contrast ratios that yield the response proportion of 0.5 (balance contrast) by fitting a logistic
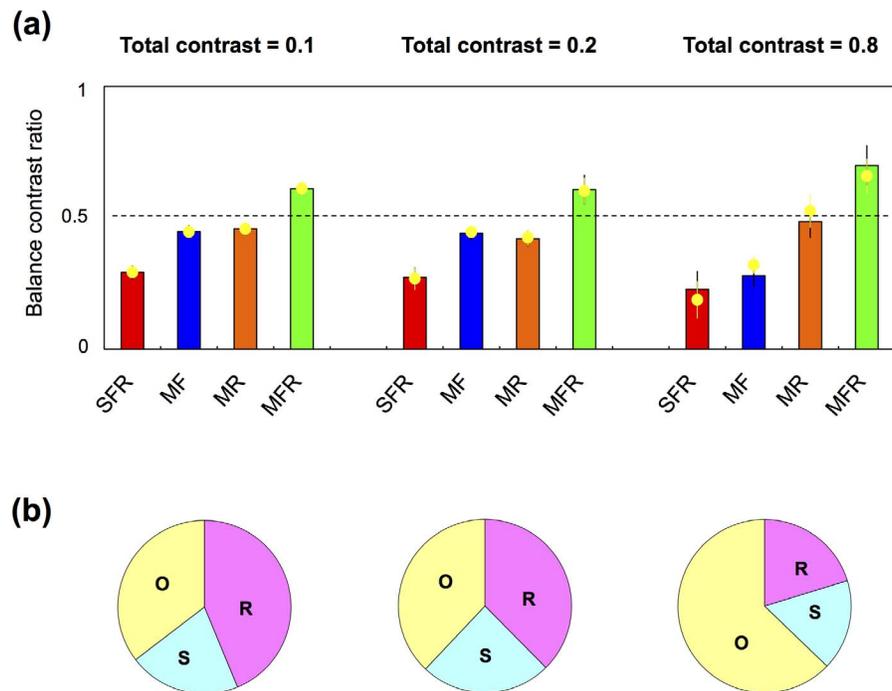
Figure 3. (a) Contrast ratio that balanced the visibility of gratings between eyes. Each bar shows the results for four different motion conditions and three different total contrasts. Yellow circles represent the average of the balance point as estimated by the weighted-sum model. Error bars represent ±1 *SE* across observers. (b) The relative weights of retinal (*R*), object-based (*O*), and spatiotopic (*S*) motions as estimated by the weighted-sum model. Each pie chart shows the results for different total contrasts.

function to the response functions. Figure 3a shows the estimated balance contrast ratio averaged across observers. Values below 0.5 (measured balance contrast ratio of the control condition) indicate dominance of the MOVING grating, and values above 0.5 indicate dominance of the STATIONARY grating. For the SFR condition, the red bar in the left panel of Figure 3a, for example, shows the balance point of 0.25, which is significantly smaller than 0.5; this tendency is the same for all total contrast values, $t(8) = 6.76$, $p = 0.002$, $t(8) = 6.76$, $p = 0.002$, $t(8) = 5.22$, $p = 0.006$ in 0.1, 0.2, 0.8 total contrast, respectively. These results indicate, as has been widely acknowledged (Blake et al., 1985), that a moving stimulus is perceptually dominant over a stationary stimulus. As for the MF condition (blue bar), the balance contrast ratio was significantly lower than 0.5 for all the total contrasts, $t(8) = 3.69$, $p = 0.021$, $t(8) = 4.96$, $p = 0.007$, $t(8) = 6.54$, $p = 0.003$, in 0.1, 0.2, 0.8 total contrast, respectively. Although the difference was small for the total contrast of 0.1, it was still statistically significant. These results show that the dominance of binocular rivalry is not determined by retinal motion alone.

In contrast to the results obtained for the MF condition that has just been summarized, the results obtained for the MR condition are quite the opposite. The balance point of the MR condition (orange bar) is not different from that of the control condition, $t(8) = 2.69$, $p = 0.055$, $t(8) = 2.57$, $p = 0.062$, $t(8) = 1.35$, $p =$

0.249, in 0.1, 0.2, 0.8 total contrast, respectively. This demonstrates that motion dominance is determined neither by retinal or objected-based motion alone. The balance point of the MFR condition (green bar) is significantly higher than 0.5 for all the total contrasts, $t(8) = 4.55$, $p = 0.010$, $t(8) = 3.10$, $p = 0.036$, $t(8) = 3.39$, $p = 0.028$, in 0.1, 0.2, 0.8 total contrast, respectively. This indicates that the results here were reversed with respect to those of the SFR condition. In the MFR condition, retinal and object-based motions are generated for the originally stationary (STATIONARY) gating. Therefore, these results strongly suggest that coexistence of retinal and object-based motions is necessary for motion dominance in binocular rivalry.

An additional experiment on the effects of attention

It is known that spatial attention involves high-level processes rather than low-level processes, and is mainly concerned with object-based or spatiotopic positions rather than retinal positions (Crespi et al., 2011; Mitchell et al., 2004). Attention has also been noted to have considerable effect on binocular rivalry (Ooi & He, 1999; Watanabe et al., 2011). These findings indicate the possibility that a large part of the contribution of object-
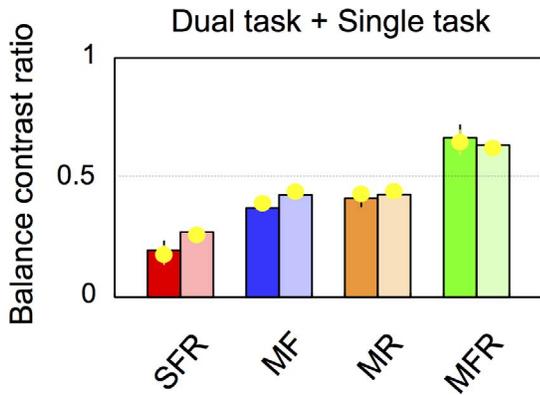
Figure 4. Balance contrast ratio for dual task. Bars with deep color show the average of the measured contrast ratio for dual task. Bars with light color are for single task. Yellow plots show the average of the balance contrast ratio estimated by the weighted-sum model. Error bars represent ±1 *SE*. Total contrast is 0.2.

based or spatiotopic motion in binocular rivalry is simply a product of spatial attention. To separate the effects of attention, we repeated the experiment for one contrast level (0.2) while employing a dual task to manipulate attention. On each trial, the white fixation point changed its color to red, green, or blue for 200 ms. The color change occurred 1–3 times with intervals of more than 600 ms during 100–1900 ms within the stimulus motion period of 2 s. The observer reported the last color of the fixation point, then judged the dominance of the competing gratings. The total contrast was fixed at 0.2, and the other procedure was identical with the main experiment.

Figure 4 shows the results. The bars with deep colors show the balance contrast ratios measured in the dual task. The bars with light colors are replots of the data in the main experiment (single task). Yellow circles show the contrast ratios estimated by the weighted-sum model. The data are very similar between the single and dual task modes, ANOVA: $F(1, 4) = 4.30$, $p = 0.11$, indicating that object-based and spatiotopic motions have a significant contribution even under the general reduction of one's attentional resources by the dual task. This means that the results of the main experiment were unlikely to be the result of accidental effects of attention itself.

Discussion

The present results indicate that perceptual dominance of moving stimuli during binocular rivalry is not determined by retinal motion alone; motions defined by object-based and spatiotopic coordinates make a significant contribution. The results demonstrated a clear

dominance when both retinal and object-based motions were presented to the same eye (SFR and MFR condition in Figure 3a). However, when the stimulus presented to one eye moved in a retinal coordinate and the other in an object-based coordinate, the result was not consistent. The dominance shifted toward the side of the object-based motion in the MF condition, and in the MR condition, dominance displayed a balanced or almost significant ($p < 0.07$) shift toward the side of retinal motion for total contrasts of 0.1 and 0.2. It is possible that this inconsistency could be caused by the contribution of spatiotopic motion.

Relative contribution of different motion coordinates

To analyze the apparent inconsistency found in the dominance results, we tried to calculate the relative contributions of the three types of motions in perceptual dominance by using a weighted linear summation model, which is analogous to those used for investigating the effect of different cues for depth perception (Clark & Yuille, 1990; Johnston, Cumming, & Landy, 1994; Landy, Maloney, Johnston, & Young, 1995).

The model is based on an assumption that the balance contrast ratio is determined by a difference between eyes in the weighted sum of motion defined by three different coordinates:

$$
\begin{aligned}
C_{\text{balance}} = 0.5 \\
+ (W_R \times R_M + W_O \times O_M + W_S \times S_M) \\
- (W_R \times R_S + W_O \times O_S + W_S \times S_S),
\end{aligned}
\tag{1}
$$

where R_M, O_M, and S_M are binaries that indicate the presence (1) or absence (0) of motion in a given coordinate (retinal, object-based, and spatiotopic, respectively) in a MOVING stimulus; R_S, O_S, and S_S are binaries for a STATIONARY stimulus; and W_R, W_O, and W_S are free parameters that specify the weight for each motion coordinate. We estimated these weights that gave the best fit between the prediction of the model and actual data for each observer. The estimates were separately calculated for each total contrast level.

Yellow circles in Figure 3a show the C_{balance} estimated by the model. It is found that the model provides extremely good predictions of the observed data. The estimated weights are W_R, W_O, $W_S = 0.08$, 0.07, 0.04; $SEM = 0.02$, 0.01, 0.01 across observers for 0.1 total contrast; W_R, W_O, $W_S = 0.09$, 0.09, 0.06; $SEM = 0.02$, 0.03, 0.01 for 0.2 total contrast; and W_R, W_O, $W_S = 0.06$, 0.19, 0.05; $SEM = 0.03$, 0.05, 0.03 for 0.8 total contrast, respectively. These weights, except for W_R and W_S for 0.8 total contrast, are significantly

larger than zero, $t(8) > 3.41$, $p < 0.03$. Pie charts in Figure 3b show the relative amounts of weight for motions defined by retinal (R), object-based (O), and spatiotopic (S) coordinates for each contrast level.

These results quantitatively show that object-based and spatiotopic motions contribute as significantly to perceptual dominance of the target grating as retinal motion. Further, as the total contrast increases, the contribution of object-based motion tends to increase, and the contribution of retinal motion tends to decrease. This is consistent with past findings that the response of relative-motion detectors in high-level areas such as MT increases proportionally with the luminance contrast of stimuli (Levitt & Lund, 1997; Pack, Hunter, & Born, 2005). On the other hand, the contribution of spatiotopic motion appears constant across a wide range of total contrasts. This degree of contribution well explains the inconsistency mentioned above. The sum of the relative weights is different between MF and MR conditions since the weight of object-based motion is as much as, or becomes clearly larger than (for a total contrast of 0.8) that of retinal motion. In other words, spatiotopic motion works as a determinant of dominance in cases where retinal and object-based motions are almost equally effective, as in the MF condition, or it will add a slight shift to balance the rivalry of gratings in cases where retinal and object-based motions are not too different, as in the MR condition. This implies a possibility that the visual process involved in spatiotopic motion is independent of the processing of retinal and object-based (relative) motions.

Relation to past spatiotopic adaptation results

Several authors have suggested the existence of neural channels tuned to spatiotopic location of stimuli (Andersen, Essick, & Siegel, 1985; Burr & Morrone, 2011). In particular, in the context of binocular rivalry, van Boxtel, Alais, & van Ee (2008) demonstrated that the effect of prior adaptation on the perceptual dominance is tuned to spatiotopic position. They showed that when observers were adapted to a pattern and shifted their gaze, the perception of the adapted pattern was less dominant when it was presented at a position spatiotopically identical to the adapted position than when presented at other irrelevant positions. That is, the effect of adaptation occurs at spatiotopically identical positions although the effect is smaller compared to retinally identical positions. Thus, these results indicate the relevance of a spatiotopic coordinate system in binocular rivalry, and in this regard, the present results, especially those with spatiotopic motion, might be related to their results. However, van Boxtel et al. (2008) used fairly high-level stimuli such as human face, and the motion stimuli used in the present study involve

several different levels of motion processing. The motion in coordinate systems other than retinal coordinate probably involves higher level processing (Galletti & Fattori, 2003). This point needs further examination.

Effects of sensitivity modulation

Schütz et al. (2007) reported that the temporal contrast sensitivity function for a retinally drifting grating is significantly modulated by smooth pursuit. This may appear to indicate a sensitivity change of early visual sensors contingent on eye movement. However, in psychophysics, it is known that contrast detection is determined not only by early sensory level, but also by many higher-order factors including attention (Carrasco, 2006; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Motoyoshi, 2011). In fact, Schütz et al. (2007) attributed their results to sensitivity modulation caused by movement of focal attention during pursuit. The present results may also be interpreted in part by feature-based attention on the grating that drifted in the same direction as the fixation point, but our control experiment showed, as described later, that manipulation of attentive tracking did not affect the pattern of the results. Considering physiological findings that cells sensitive to spatiotopic motion were mainly found in V3A, MST, and 7a, but less so in V1 (Erickson & Thier, 1991; Galletti & Fattori, 2003; Ilg & Thier, 1996), and that perisaccadic remapping of visual receptive fields was reported in neurons in LIP, FEF, MT, and MST (Duhamel, Colby, & Goldberg, 1992; Nakamura & Colby, 2002; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997), the contribution of spatiotopic motion we observed would most likely emerge at relatively higher levels of visual, or multimodal, mechanisms.

Effects of attention and eccentricity

In this study, the stimulus period (2 s) was long enough to cause rivalry, but it was within the temporal range for putative initial phase. In binocular rivalry, initial dominance is known to be modulated by observer's attention to visual targets (Mitchell et al., 2004), but the results of our additional experiment to examine the effect of attention by using dual task contradicted this notion and demonstrated that there was little influence of attentional factors at least for the experimental conditions of the present study (Figure 4). There is still a possibility that the remaining part of the reduced attention may affect these results, but in light of the similarity to the main results, it seems that the mechanisms of motion processing and visual awareness play a key role in the contributions of object-based and spatiotopic motions.

The retinal eccentricity of target grating is different according to the experimental conditions. In binocular rivalry, exclusive visibility increases in peripheral (Blake, O'Shea, & Mueller, 1992). In our experiments, the eccentricity changes in the conditions in which eye movements or motions of stimulus as a whole were involved. However, even in these conditions, eccentricity changes synchronously along the vertical axis between the two eyes, and the eccentricity of the two stimuli was the same. It could be a problematic when the results from conditions involving these motions and the results from conditions where there was no such motion were compared. However, even in these conditions, the average eccentricity was the same between the different conditions. Therefore, we believe that the changes in eccentricity do not cause strong effects on the present results. However, it is possible that there are interactions between eccentricity and the degree of dominance enhancement by each type of motion. This point still needs to be clarified.

Keywords: binocular rivalry, coordinate system, motion dominance, nonretinotopic motion, smooth pursuit eye movement

Acknowledgments

Commercial relationships: none.
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References

Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience, 8,* 407–430.

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. *Science, 230*(4724), 456–458. doi:10.1126/science.4048942.

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. doi:10.1017/S0952523800004971.

Blake, R., Zimba, L., & Williams, D. (1985). Visual motion, binocular correspondence and binocular rivalry. *Biological Cybernetics, 52,* 391–397.

Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature, 411*(6839), 798–801. doi:10.1038/35081073.

Born, R. T., & Tootell, R. B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357*(6378), 497–499. doi:10.1038/357497a0.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Breese, B. B. (1899) *On inhibition.* In J. M. Baldwin & J. M. Cattell (Eds.), *The psychological review: monograph supplements* (Vol. 3, pp. 1–65). Lancaster, PA, New York, & London: The Macmillan Company.

Burr, D. C., & Morrone, M. C. (2011). Spatiotopic coding and remapping in humans. *Philosophical Transactions of the Royal Society B, Biological Sciences, 366*(1564), 504–515. doi:10.1098/rstb.2010.0244.

Carrasco, M. (2006). Covert attention increases contrast sensitivity: Psychophysical, neurophysiological and neuroimaging studies. *Progress in Brain Research, 154,* 33–70.

Carrasco, M., Penpeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF: Support for signal enhancement. *Vision Research, 40,* 1203–1215. doi:10.1016/S0042-6989(00)00024-9.

Chukoskie, L., & Movshon, J. A. (2009). Modulation of visual signals in macaque MT and MST neurons during pursuit eye movement. *Journal of Neurophysiology, 102,* 3225–3233. doi:10.1152/jn.90692.2008.

Clark, J. J., & Yuille, A. L. (1990). *Data fusion for sensory information processing systems.* Kluwer International Series in Engineering and Computer Science. Boston, MA: Kluwer Academic Publishers.

Crespi, S., Biagi, L., D'Avossa, G., Burr, D. C., Tosetti, M., & Morrone, M. C. (2011). Spatiotopic coding of BOLD signal in human visual cortex depends on spatial attention. *PLoS One, 6*(7),

e21661 doi:ARTN e21661 DOI 10.1371/journal. pone.0021661.

Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, 255(5040), 90–92.

Erickson, R. G., & Thier, P. (1991). A neuronal correlate of spatial stability during periods of self-induced visual motion. *Experimental Brain Research*, 86, 608–616.

Filehne, W. (1922). Uber das optische Wahrnehmen von Bewegungen. *Zeitschr Sinnephysiol*, 53, 134–145.

Galletti, C., Battaglini, P. P., & Fattori, P. (1990). "Real-motion" cells in area V3A of macaque visual cortex. *Experimental Brain Research*, 82, 67–76.

Galletti, C., & Fattori, P. (2003). Neuronal mechanisms for detection of motion in the field of view. *Neuropsychologia*, 41, 1717–1727.

Ilg, U. J., & Thier, P. (1996). Inability of rhesus monkey area V1 to discriminate between self-induced and externally induced retinal image slip. *European Journal of Neuroscience*, 8, 1156–1166.

Johnston, E. B., Cumming, B. G., & Landy, M. S. (1994). Integration of stereopsis and motion shape cues. *Vision Research*, 34, 2259–2275.

Landy, M. S., Maloney, L. T., Johnston, E. B., & Young, M. (1995). Measurement and modeling of depth cue combination: In defense of weak fusion. *Vision Research*, 35, 389–412. doi:10.1016/0042-6989(94)00176-M.

Levitt, J. B., & Lund, J. S. (1997). Contrast dependence of contextual effects in primate visual cortex. *Nature*, 387(6628), 73–76. doi:10.1038/387073a0.

Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, 429(6990), 410–413. doi:10.1038/nature02584.

Motoyoshi, I. (2011). Attentional modulation of temporal contrast sensitivity in human vision. *PLoS One*, 6, e19303. doi:10.1371/journal.pone.0019303.

Motoyoshi, I., & Hayakawa, S. (2010). Adaptation-induced blindness to sluggish stimuli. *Journal of Vision*, 10(2):16, 1–8, doi:10.1167/10.2.16. [PubMed] [Article]

Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences, USA*, 99, 4026–4031. doi:10.1073/pnas.052379899.

Ooi, T. L., & He, Z. J. J. (1999). Binocular rivalry and visual awareness: The role of attention. *Perception*, 28, 551–574. doi:10.1068/P2923.

Pack, C. C., Hunter, J. N., & Born, R. T. (2005). Contrast dependence of suppressive influences in cortical area MT of alert macaque. *Journal of Neurophysiology*, 93, 1809–1815. doi:10.1152/jn.00629.2004.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442. doi:10.1163/156856897x00366.

Sakata, H., Shibutani, H., Kawano, K., & Harrington, T. L. (1985). Neural mechanisms of space vision in the parietal association cortex of the monkey. *Vision Research*, 25, 453–463.

Schütz, A. C., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2008). Improved visual sensitivity during smooth pursuit eye movements. *Nature Neuroscience*, 11, 1211–1216. doi:10.1038/nn.2194.

Schütz, A. C., Delipetkos, E., Braun, D. I., Kerzel, D., & Gegenfurtner, K. R. (2007). Temporal contrast sensitivity during smooth pursuit eye movements. *Journal of Vision*, 7(13):3, 1–15, doi:10.1167/7.13.3. [PubMed] [Article]

Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, 444(7117), 374–377. doi:10.1038/nature05279.

Terao, M., & Murakami, I. (2011). Compensation for equiluminant color motion during smooth pursuit eye movement. *Journal of Vision*, 11(6):12, 1–12, doi:10.1167/11.6.12. [PubMed] [Article]

Troxler, D. (1804). Ueber das Verschwinden gegebener Gegenstande innerhalb unseres Gesichtskreises. In K. Himly & J. A. Schmidt (Eds.), *Ophthalmologisches Bibliothek* (Vol. 2, pp. 1–53). Jena, Thüringen: Frommann.

Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, 78, 1373–1383.

van Boxtel, J. J., Alais, D., & van Ee, R. (2008). Retinotopic and non-retinotopic stimulus encoding in binocular rivalry and the involvement of feedback. *Journal of Vision*, 8(5):17, 1–10, doi:10.1167/8.5.17. [PubMed] [Article]

Watanabe, M., Cheng, K., Murayama, Y., Ueno, K., Asamizuya, T., Tanaka, K., & Logothetis, N. (2011). Attention but not awareness modulates the BOLD signal in the human V1 during binocular suppression. *Science*, 334(6057), 829–831. doi:10.1126/science.1203161.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, 48, 2070–2089. doi:10.1016/j.visres.2008.03.021.