Distinct Contributions of the Magnocellular and Parvocellular Visual Streams to Perceptual Selection

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Abstract

■ During binocular rivalry, conflicting images presented to the two eyes compete for perceptual dominance, but the neural basis of this competition is disputed. In interocular switch rivalry, rival images periodically exchanged between the two eyes generate one of two types of perceptual alternation: (1) a fast, regular alternation between the images that is time-locked to the stimulus switches and has been proposed to arise from competition at lower levels of the visual processing hierarchy or (2) a slow, irregular alternation spanning multiple stimulus switches that has been associated with higher levels of the visual system. The existence of these two types of perceptual alternation has been influential in establishing the view that rivalry may be resolved at multiple hierarchical levels of the visual system.

We varied the spatial, temporal, and luminance properties of interocular switch rivalry gratings and found, instead, an association between fast, regular perceptual alternations and processing by the magnocellular stream and between slow, irregular alternations and processing by the parvocellular stream. The magnocellular and parvocellular streams are two early visual pathways that are specialized for the processing of motion and form, respectively. These results provide a new framework for understanding the neural substrates of binocular rivalry that emphasizes the importance of parallel visual processing streams, and not only hierarchical organization, in the perceptual resolution of ambiguities in the visual environment. ■

INTRODUCTION

Ambiguous visual displays, in which multiple perceptual interpretations of a single display are possible, dissociate visual percept from visual stimulus, thereby providing an opportunity to study the neural selection processes that lead to visual awareness (Blake & Logothetis, 2002). Binocular rivalry is a powerful example of an ambiguous visual display (Alais & Blake, 2005). During binocular rivalry, conflicting images presented to the two eyes result in a visual percept that alternates between the two images, although the visual stimuli remain constant. Because stimulus-related visual information is represented in multiple brain regions and at multiple levels of the visual processing hierarchy, an important goal for visual neuroscience is the identification of the neural substrates of perceptual selection.

In the case of binocular rivalry, studies have provided evidence for perceptual selection both at the level of monocular representations (the "eye level") and at higher levels of the visual hierarchy that contain binocular representations of visual stimuli (the "stimulus level"). In support of perceptual selection at the eye level, psychophysical studies have shown that the detection of a probe stimulus is impaired if it is presented to the eye containing the currently suppressed stimulus (Blake, Yu, Lokey, & Norman, 1998; Blake & Fox, 1974; Wales & Fox, 1970; Fox & Check, 1966, 1968) and that a single interocular exchange of rivalrous stimuli causes the previously dominant eye to remain dominant, leading to the sudden dominance of the previously suppressed stimulus (Blake, Westendorf, & Overton, 1980).

Brain imaging studies using fMRI in humans have likewise shown fluctuations in eye-specific activity that are time-locked to perceptual alternations during binocular rivalry, both in the monocular blind spot in V1 (Tong & Engel, 2001) and in regions of the LGN showing strong eye preference (Haynes, Deichmann, & Rees, 2005; Wunderlich, Schneider, & Kastner, 2005). Interestingly, electrophysiological recordings from monocular cells of macaque V1 during binocular rivalry have revealed very little modulation of spike rate as a function of perceptual alternation (Leopold & Logothetis, 1996), although such modulations are more common in higher-order areas in both the ventral (area V4, Leopold & Logothetis, 1996; inferotemporal cortex, Sheinberg & Logothetis, 1997) and dorsal (area MT, Logothetis & Schall, 1989) cortical processing streams.

In support of perceptual selection at the stimulus level, various binocular rivalry paradigms result in visual percepts that require integration of information from the two eyes. For example, when parts of two meaningful images are distributed between the eyes, subjects may perceive alternation between the coherent images instead of between the monocular inputs (Kovács, Papathomas, Yang, & Fehér, 1996 [see also Lee & Blake, 2004, for an eye rivalry-based interpretation of these results]; Diaz-Caneja, 1928 [translated into English in Alais, O'Shea, Mesana-Alais, & Wilson,

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2000]). Logothetis, Leopold, and Sheinberg (1996) introduced the interocular switch (IOS) rivalry paradigm, in which conflicting stimuli are exchanged between the two eyes about three times per second (Figure 1) and contain on–off flicker at a higher frequency (Logothetis et al., 1996). IOS rivalry can elicit two types of percepts. The first is a fast, regular perceptual alternation that is time-locked to the stimulus switches. Because this alternation corresponds to the sequence of stimuli presented to one eye, it has been proposed to arise from interocular competition, or "eye rivalry" (Lee & Blake, 1999). We will call this type of percept *fast, regular alternation (FRA) rivalry*. The second possible percept is a slow, irregular alternation, in which perception of a single stimulus can persist over several interocular stimulus switches. Because both stimuli are presented to each eye during a period of stable perception of just one of the stimuli, this alternation has been considered to result from competition between binocular stimulus representations in the brain, or "stimulus rivalry" (Logothetis et al., 1996). We will call this type of percept *slow, irregular alternation (SIA) rivalry*.

Given the compelling evidence for perceptual selection at both eye and stimulus levels, a consensus view has emerged in which perceptual selection may occur at multiple levels in the visual hierarchy, perhaps simultaneously (Pearson, Tadin, & Blake, 2007; Tong, Meng, & Blake, 2006; Freeman, 2005; Nguyen, Freeman, & Alais, 2003; Blake & Logothetis, 2002). However, this synthesis offers little explanation as to why perceptual selection may occur at different levels and currently does not specify the factors that determine the level(s) at which perceptual selection is resolved for a given visual display.

In the IOS rivalry paradigm, the prevalence of FRA and SIA rivalry is highly dependent on the properties of the visual stimuli that are shown (Kang & Blake, 2008; van Boxtel, Knapen, Erkelens, & van Ee, 2008; Silver & Logothetis, 2007; Bonneh, Sagi, & Karni, 2001; Lee & Blake, 1999). This makes it an attractive paradigm for the study of how perceptual selection is governed by the specific visual information present in a display. To better understand the influence of spatial, temporal, and luminance factors on perceptual selection, we measured the proportions of FRA and SIA rivalry for IOS rivalry gratings over a range of spatial frequencies, flicker frequencies, and luminance conditions. Our findings suggest a new framework for understanding perceptual selection during IOS rivalry, in which the type of perceptual alternation depends on distinct contributions from the magnocellular (M) and parvocellular (P) visual streams.

In Experiment 1, we found a strong spatio-temporal interaction between stimulus factors that affected the type of perceptual alternation in IOS rivalry, with different effects of flicker frequency for high and low spatial frequency stimuli. The pattern of this interaction correlates with the well-studied physiological response properties of the M and P streams. Specifically, it is consistent with the M stream being important for FRA rivalry and the P stream being preferentially associated with SIA rivalry. In Experiment 2, we tested this hypothesis by using isoluminant red–green gratings in IOS rivalry to reduce the M stream response to the stimuli. We observed more SIA rivalry when subjects viewed isoluminant IOS rivalry gratings compared with monochromatic black–white gratings, as predicted by the M/P framework. In Experiment 3, we probed the specific M stream mechanisms that could account for the effects of flicker frequency by varying the flicker frequency as well as the duration of a preswitch blank period for nonflickering stimuli. We found similar effects of flicker frequency and preswitch blank duration, suggesting that if M responses to successive presentations of orthogonal gratings are sufficiently separated in time, SIA rivalry is more likely to occur. These results suggest that transient M stream neuronal responses are a critical determinant of the type of perceptual alternation that occurs in IOS rivalry.

The M/P framework suggested by our findings provides a novel conceptual model for perceptual selection during binocular rivalry, incorporating distinct contributions from the M and P streams. This framework accounts for a number of stimulus dependencies either previously described in the IOS rivalry literature or investigated here for the first time, including spatial frequency, temporal frequency, luminance contrast, and color contrast. Unlike the distinction between lower and higher levels of the visual processing hierarchy, which is consistent with a variety of neural substrates, the M/P framework is based on fundamental physiological and anatomical subdivisions of the visual system. It is therefore amenable to further testing using a variety of neurophysiological methods and suggests new approaches for the investigation of the neural mechanisms of perceptual selection.
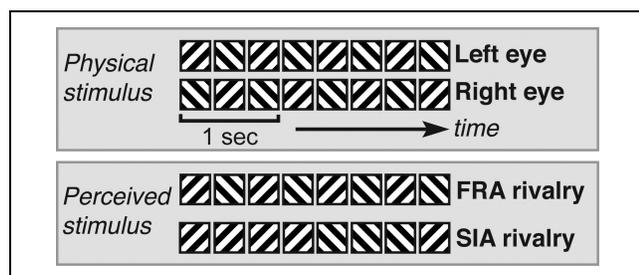
Figure 1. IOS rivalry stimuli and percepts. Orthogonal gratings are exchanged between the eyes three times per second. These stimuli give rise to two types of visual percepts: fast, regular alternations in perceived orientation that are time-locked to the stimulus exchanges (FRA rivalry) or slow, irregular orientation alternations that span multiple IOSs (SIA rivalry).

METHODS

Subjects

Twenty-three subjects participated in the experiments. Five of these subjects participated in two of the experiments,

and two participated in all three (one was an author). Seven subject data sets from individual experiments were excluded from analysis (see Subject Exclusion section below). This left a total of 17 subjects (aged 19–32 years, 10 women), 6 of whom participated in Experiment 1, 8 in Experiment 2, and 11 in Experiment 3. All subjects provided informed consent, and all experimental protocols were approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley.

Visual Stimuli

IOS rivalry displays were generated on a Macintosh PowerPC computer using Matlab and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and were displayed on two halves of a gamma-corrected NEC MultiSync FE992 CRT monitor with a refresh rate of 60 or 90 Hz at a viewing distance of 100 cm. Subjects viewed the rivalrous stimuli through a mirror stereoscope with their heads stabilized by a chin rest. Rivalry stimuli were circular grating patches 1.8° in diameter. Each grating was surrounded by a black annulus with a diameter of 2.6° and a thickness of 0.2°. Binocular presentation of this annulus allowed it to serve as a vergence cue to stabilize eye position.

In Experiments 1 and 3, IOS rivalry stimuli were sinusoidal gratings with 4 or 7 cycles per degree (cpd), presented at 25% contrast on a neutral gray background (luminance of 59 cd/m^2). The two gratings were orthogonally oriented with ±45° tilts and were simultaneously flickered on and off, with a 50% duty cycle, at different frequencies on different trials. Gratings had the same mean luminance as the background. Flicker frequencies were 0 (no flicker), 6, 9, 15, 22.5, and 30 Hz in Experiment 1 and 6, 9, 15, and 22.5 Hz in Experiment 3. The two grating orientations were exchanged between the eyes three times per second (except in the 22.5 Hz flicker frequency condition, in which the orientations were exchanged at 2.8 Hz to have an integral number of flicker cycles in each IOS period, given a 90-Hz monitor refresh rate).

In Experiment 2, IOS rivalry gratings were presented on a 23% gray background (luminance of 27 cd/m^2), which was selected based on pilot testing as a luminance level that could be perceptually matched to both red and green without saturating either color. Rivalry stimuli were circular patches of 4 cpd square-wave gratings and were either black–white monochrome or red–green isoluminant. Flicker frequencies were 0 (no flicker), 3, 6, 9, 15, 22.5, and 30 Hz. Monochrome gratings varied from dark to bright around the background gray level, with 46% contrast and the same mean luminance as the background. Red and green luminance values for the isoluminant gratings were psychophysically matched to the background gray level individually for each subject using flicker photometry (see below).

In Experiment 3, trials were either *continuous-flicker* (identical to those in Experiment 1) or *blank-only*. In blank-only trials, rivalry gratings were always on except for a brief off period (replaced with gray background luminance) just before each IOS. The duration of this blank period was matched to the duration of the final off period in a corresponding continuous-flicker trial. For example, in a continuous-flicker trial with 15 Hz flicker frequency, a full flicker cycle has a duration of 67 msec, so each on and off portion of the flicker lasts 33 msec. Therefore, in the corresponding blank-only trial, the 333-msec IOS period consisted of a 300-msec on interval followed by a 33-msec off interval, followed immediately by the IOS.

Task

In all experiments, subjects viewed rivalry displays for 1 min per trial. They continuously indicated their percept by holding down one of three keys: (1) fast, regular switching of perceived grating orientation, (2) slow, irregular switching (grating tilted left), or (3) slow, irregular switching (grating tilted right). Subjects were instructed to press a key continuously for as long as the corresponding percept was predominant and not to press any key for ambiguous percepts that were not one of the three response categories. Subjects completed three trials in each condition, with trials from all conditions randomly intermixed. In Experiment 2, two subjects viewed the rivalry displays for 30 sec per trial. Excluding these subjects did not qualitatively change any of the results, so we included them in the analyses presented here.

Flicker Photometry

Before completing the rivalry task of Experiment 2, subjects performed flicker photometry to determine their psychophysical red and green isoluminant values for use in the rivalry task. Subjects completed two flicker photometry sessions consisting of three runs each. The first session served as practice to acclimate participants to the task. The results of the second session were used to determine the isoluminant red and green intensity values that were then used in Experiment 2.

During each run, two disk colors flickered back and forth at a rate of 20 Hz while participants used key presses to increase or decrease the luminance value of the variable-luminance disk until it matched the constant-luminance disk in perceived luminance. In the first run of each session, subjects matched a green disk to the gray background. In the second run, subjects matched a red disk to the green disk, using the green luminance value determined in the first run. Finally, subjects matched a red disk to the gray background. This allowed us to estimate the consistency of the red–green isoluminant match. All disks were surrounded by black annuli, were the same dimensions as the grating stimuli used in the rivalry task, and were viewed through the stereoscope using the same setup as in the rivalry task.

Each flicker photometry run contained four trials: In two of these, the variable-luminance disk started at a high luminance value, whereas in the other two, the variable-luminance disk started at a low luminance value. The mean red and green color values selected for the variable-luminance disk across all trials were used as the isoluminant red and green values for an individual subject in the rivalry task.

Data Analysis

IOS Rivalry Index

The "IOS rivalry index" is defined as the difference between the total time in which subjects reported SIA rivalry (sum of tilted left and tilted right response durations) and the total time they reported FRA rivalry, normalized by the sum of these values:

$$\text{IOS rivalry index}_{(\text{subject,condition})}$$
$$= \frac{\text{time(``SIA rivalry'')} - \text{time(``FRA rivalry'')}}{\text{time(``SIA rivalry'')} + \text{time(``FRA rivalry'')}}$$

Normalization and Statistical Testing

Because we were interested in within-subject differences across the experimental conditions, we normalized each subject's IOS rivalry index values using the group mean. To do this, we first calculated the group mean IOS rivalry index across all conditions from the raw data and then added a constant to the mean of each individual subject's data across conditions so that it was equal to the group mean. This procedure does not change the mean values of the group data or the relationships among data points for single subjects, but it corrects for overall differences between subjects that would affect responses in all conditions, such as a general tendency toward experiencing SIA or FRA rivalry. All statistics and error bars were calculated using normalized data and between-subject variance.

Statistical testing in Experiments 1 and 2 did not include the no flicker data (all trials in Experiment 3 had flicker). This is because it was not clear where to place nonflickering stimuli on a flicker frequency continuum: Although they have a flicker frequency of zero, they are perceptually more similar to the 30-Hz flicker frequency stimuli (which appeared as nonflickering, lower contrast stimuli as a result of flicker fusion) than to the 6-Hz flicker frequency stimuli (for which the slow flicker with long blank durations was easily perceived).

Flicker versus Blank-only Comparison

In Experiment 1, high flicker frequencies were associated with reduced SIA rivalry for low spatial frequency stimuli, with a roughly inverse linear relationship between flicker frequency and IOS rivalry index values. In Experiment 3, we tested whether this effect held for blank-only stimuli. To do this, we fit linear functions to the continuous-flicker and blank-only data. These linear functions were generated in each condition for each subject, and we tested whether, across subjects, the slopes of these lines were different from zero using a two-tailed t test on the individual subject slopes.

Subject Exclusion

A total of seven subjects were excluded from the analysis (one subject from Experiment 2 and six subjects from Experiment 3). In Experiment 2, the subject was excluded because of inconsistent flicker photometry performance. Both when matching green to the background gray level and when matching red to gray and to green, the variance of this subject's flicker photometry values was greater than two standard deviations above the mean variance of all subjects. It is therefore likely that the isoluminant values for this subject were inaccurate; however, the results do not qualitatively change if this subject is included in the analysis.

In Experiment 3, five subjects were excluded because their IOS rivalry index was at floor or ceiling in one or more of the flicker type–spatial frequency conditions. Therefore, it was not possible to test the effects of flicker frequency for these subjects with accuracy. A subject's data were considered to be at floor or ceiling when the mean IOS rivalry index value across flicker frequencies for any flicker type–spatial frequency combination was below −0.95 or above 0.95 (the index ranges from −1 to 1). One additional subject was excluded from Experiment 3 because in the 4 cpd, blank-only condition, this subject's fitted slope was greater than 2.5 standard deviations from the group mean. However, all reported effects do not change if this subject is included in the analysis.

RESULTS

Spatio-temporal Interactions in IOS Rivalry

Previous studies have examined the influence of spatial and temporal stimulus factors on the type of perceptual alternation during IOS rivalry. These factors include the spatial frequency of the stimuli (Lee & Blake, 1999), the temporal frequency of the IOSs (Lee & Blake, 1999), and the duty cycle of the stimulus flicker (van Boxtel et al., 2008). However, there is currently no unified physiological explanation for these dependencies. Furthermore, flicker of the IOS rivalry stimuli facilitates SIA rivalry (Lee & Blake, 1999; Logothetis et al., 1996), but the neural basis of this phenomenon remains unclear. Flicker has been proposed to disrupt the normal processes underlying conventional binocular rivalry (Lee & Blake, 1999) and plays a key role in a computational model of IOS rivalry (Wilson, 2003). In this model, stimulus flicker prevents the build-up of inhibition between monocular neurons,

allowing perceptual competition to bypass the eye level and to be resolved instead at the stimulus level. However, van Boxtel et al. (2008) found that a short blank period immediately preceding the interocular stimulus switch was sufficient to cause SIA rivalry and that flickering the stimuli was not required.

To investigate the spatio-temporal properties of IOS rivalry and to better understand the role of flicker in facilitating SIA rivalry, we varied the spatial frequency and flicker frequency of IOS rivalry gratings and measured the proportions of FRA and SIA rivalry. Six subjects viewed IOS rivalry gratings for periods of 1 min and held down keys to continuously report their percept: (1) fast, regular switching of perceived grating orientation, (2) slow, irregular switching (grating tilted left), or (3) slow, irregular switching (grating tilted right). Subjects withheld their response for ambiguous percepts that did not correspond to any of the three response categories.

We calculated an IOS rivalry index for each subject and each experimental condition, defined as the difference between the average amount of time per trial in which subjects reported SIA rivalry and the average amount of time they reported FRA rivalry, divided by the average amount of time they reported either SIA or FRA rivalry. This index ranges from 1 to −1, with 1 indicating *only SIA rivalry*, −1 indicating *only FRA rivalry*, and 0 indicating *equal amounts of SIA and FRA rivalry*.

The IOS rivalry index was calculated from the total time subjects reported the SIA rivalry or FRA rivalry percept, but there was also a certain amount of time in each trial during which subjects made no response at all, indicating that their percept did not match any of the response categories. We found no significant effects on the average amount of "no response" time for any of the experimental manipulations we report here. Thus, all changes in the IOS rivalry index resulted from trade-offs between SIA rivalry and FRA rivalry (Supplementary Figures S1–S3 show SIA and FRA total response durations plotted separately for each experiment).

Flicker frequency affected the proportions of FRA and SIA rivalry for IOS rivalry gratings at both spatial frequencies tested (4 and 7 cpd; Figure 2; see also Supplementary Figure S1). In accordance with previous findings (Lee & Blake, 1999; Logothetis et al., 1996), we observed more SIA rivalry with flicker than without it. At high spatial frequencies without flicker, we observed more SIA rivalry than reported in previous studies (Lee & Blake, 1999), perhaps because of our longer trial duration and our method of continuous response collection. We also observed more SIA rivalry for high spatial frequency than for low spatial frequency stimuli, consistent with previous reports (Lee & Blake, 1999).

Importantly, we found a strong interaction between flicker frequency and spatial frequency (two-way ANOVA, $F_{(4, 50)} = 8.71$, $p < .0001$). As flicker frequency increased, SIA rivalry increased for high spatial frequency gratings, but FRA rivalry increased for low spatial fre-
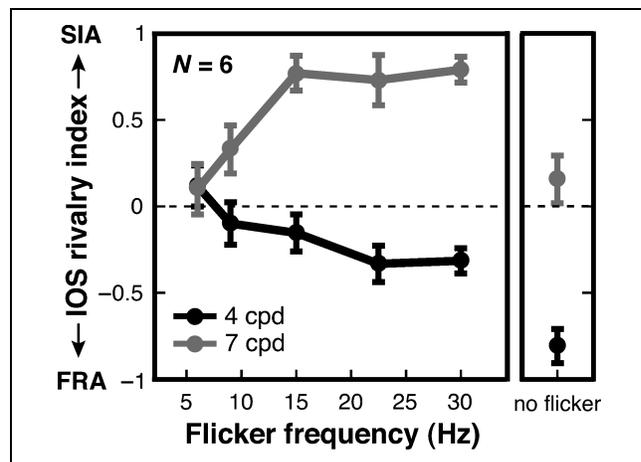
Figure 2. Results of Experiment 1. Spatio-temporal interaction in IOS rivalry. IOS rivalry gratings with high or low spatial frequencies and different on–off flicker frequencies were presented on a gray background. As flicker frequency increased, the predominance of SIA rivalry increased for high spatial frequency gratings (7 cpd, gray line) but decreased for low spatial frequency gratings (4 cpd, black line). Error bars are *SEM*.

quency gratings (Figure 2). We first consider the flicker frequency effect for high spatial frequency gratings. This effect could reflect changes in effective stimulus contrast, because effective contrast decreases with increasing flicker rate (Robson, 1966) and stimuli with lower physical contrast have been reported to enhance SIA rivalry (Lee & Blake, 1999). If effective contrast acts like physical contrast in IOS rivalry, the reduced effective contrast at higher flicker frequencies could lead to more SIA rivalry, as we observed. Indeed, we found qualitative support for this account in separate experiments in which we psychophysically measured the effective contrast of flickering high spatial frequency gratings for individual observers and then repeated the IOS rivalry experiment using (1) nonflickering gratings with physical contrasts set to the measured effective contrasts for each subject and (2) flickering gratings with physical contrasts set to equate effective contrast across flicker frequencies (Supplementary Figure S4 and Supplementary Data).

Effective contrast differences may also contribute to the relatively higher proportion of FRA rivalry observed for zero-flicker stimuli, which have higher effective contrast than their flickering counterparts. To emphasize this difference between flickering and nonflickering stimuli, as well as the perceptual similarity of nonflickering to fast flickering stimuli (which can appear as nonflickering because of flicker fusion), we place no-flicker data points to the right of the flicker data points in all figures (except Supplementary Figure S4, which shows data from experiments in which we explicitly manipulated contrast).

Although effective contrast could explain the effect of flicker frequency on IOS rivalry for high spatial frequency gratings, the increase in FRA rivalry with increased flicker

frequency for low spatial frequency gratings (Figure 2) is *inconsistent* with (and, in fact, is in the opposite direction of) the effect expected from changes in effective contrast alone. Likewise, an increase in FRA rivalry with increased flicker frequency would not be predicted by a model in which flicker allows a monocular competition stage to be bypassed (Wilson, 2003), because in this model, high flicker rates are proposed to reduce inhibitory interactions among monocular neurons, leading to increased SIA rivalry.

The spatio-temporal interaction in IOS rivalry observed here cannot be explained by existing models of rivalry. What physiological mechanisms could account for these results? The P and M visual streams have spatial and temporal frequency selectivities that correlate with the stimulus parameters that promote SIA and FRA rivalry, respectively. In our data, high spatial frequencies were preferentially associated with SIA rivalry, whereas low spatial frequencies led to relatively more FRA rivalry. In the LGN of the thalamus, P neurons have smaller receptive fields (Derrington & Lennie, 1984) and higher spatial resolution (Kaplan & Shapley, 1982) compared with M neurons, consistent with an association of P neurons with high spatial frequencies and M neurons with low spatial frequencies. Although both spatial frequencies tested here (4 and 7 cpd) are likely to evoke some response from neurons in the P stream, neurophysiological results suggest that the M stream would respond more weakly to the 7-cpd rivalry stimuli than to the 4-cpd stimuli (Derrington & Lennie, 1984). Therefore, processing of 4-cpd stimuli is likely to be biased toward the M stream, relative to processing of 7-cpd stimuli. For these low spatial frequency stimuli, higher temporal frequencies promoted FRA rivalry. This pattern of results correlates with the temporal properties of the M stream, where higher temporal frequencies evoke larger responses in M neurons in the LGN, up to about 20 Hz (Derrington & Lennie, 1984). The association of SIA rivalry with the P stream and FRA rivalry with the M stream is also generally consistent with the canonical functions of these two visual streams, with slow, sustained processing of visual form occurring in the P stream and rapid processing of transient, moving stimuli occurring in the M stream (Livingstone & Hubel, 1988).

Effects of Isoluminance on IOS Rivalry

To test the hypothesis that the M stream promotes FRA rivalry and the P stream is associated with SIA rivalry using a different type of stimulus manipulation, we conducted Experiment 2, in which we used red–green isoluminant stimuli to reduce responses of M stream neurons. Single-cell recordings from macaque LGN have shown that P neurons have color-opponent center–surround receptive fields, whereas the center and surround portions of M neuron receptive fields are not as selective for color (Schiller & Malpeli, 1978). In addition, the magnitude of the reduction in response to red–green isoluminant

stimuli compared with luminance-defined stimuli is greater for M than for P LGN neurons in the macaque (Hubel & Livingstone, 1990), although this has not always been found (Logothetis, Schiller, Charles, & Hurlbert, 1990). Finally, lesions of the P layers of the LGN cause severe deficits in perception of heterochromatic red–green flicker, whereas M lesions have no effect on performance of this task (Schiller, Logothetis, & Charles, 1990). Isoluminant stimuli containing only color contrast are, therefore, commonly used to decrease the contribution of the M stream in psychophysical tasks (e.g., Livingstone & Hubel, 1987, 1988).

We used flicker photometry to determine each subject's isoluminant red and green values with respect to a standard gray background. We compared IOS rivalry for 4-cpd monochrome gratings, like those used in Experiment 1, to red–green isoluminant gratings with the same spatial frequency. This spatial frequency should activate both the M and P streams, leading to a bias in favor of the P stream in the isoluminant condition, relative to the monochrome condition.

As predicted by our M/P model of perceptual selection in IOS rivalry, reducing the contribution of the M stream using isoluminant stimuli increased SIA rivalry. A two-factor ANOVA with flicker frequency and isoluminance as factors showed a main effect of isoluminance on the IOS rivalry index ($F(1, 84) = 9.14$, $p < .005$), with subjects reporting more SIA rivalry in the isoluminant condition (Figure 3; see also Supplementary Figure S5).

Because there was less SIA rivalry at higher flicker frequencies for both the monochrome and isoluminant conditions, the interaction between flicker frequency and isoluminance condition did not reach significance in this group of subjects. However, those subjects who showed
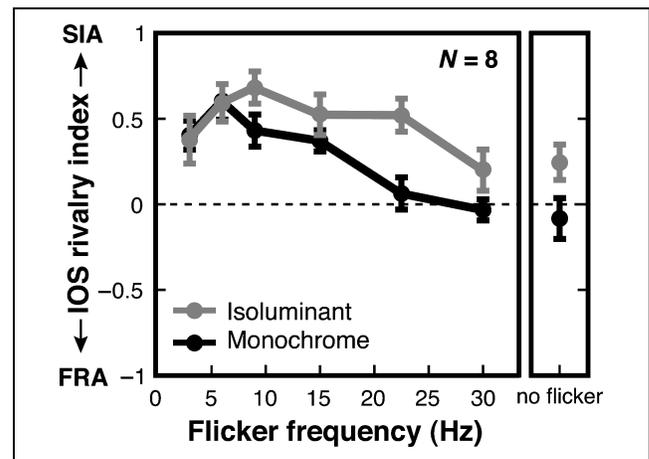
Figure 3. Results of Experiment 2. Isoluminance increases the amount of SIA rivalry in IOS rivalry. Monochrome (black–white) or isoluminant (red–green) gratings with different flicker frequencies were presented on a gray background. Subjects perceived more SIA rivalry for isoluminant gratings (gray line) than for monochrome gratings (black line). Error bars are *SEM*.

a strong flicker frequency effect for isoluminant stimuli were also those who had a negligible main effect of isoluminance. It is possible that luminance contrast was not sufficiently minimized in the red–green stimuli presented to these subjects, possibly because of error in the flicker photometry measurements. Therefore, we selected a subset of subjects for further analysis who showed a significant effect of isoluminance at one or more flicker frequencies, as measured by paired t tests of total time per trial reporting SIA or FRA rivalry in the monochrome compared with the isoluminant condition. Like the full sample of eight subjects, the group of six subjects who met this criterion exhibited a main effect of isoluminance ($F(1, 60) = 13.74$, $p < .001$), with more SIA rivalry for isoluminant stimuli. In addition, this subset of subjects exhibited an interaction between flicker frequency and isoluminance condition ($F(5, 60) = 2.79$, $p < .05$), with higher flicker frequency leading to more FRA rivalry in the monochrome condition but not in the isoluminant condition (Supplementary Figure S5). This interaction is analogous to the spatio-temporal interaction observed in Experiment 1 and is again consistent with the M/P framework.

The results from Experiment 2 corroborate those from Experiment 1 by using isoluminance, a manipulation of the relative contributions of the M and P streams that is wholly orthogonal to the spatial and temporal frequency manipulations employed in Experiment 1. In both experiments, a reduction in the ability of the IOS rivalry gratings to engage the M stream, through the use of high spatial frequency, low temporal frequency (for low spatial frequency stimuli) or isoluminant stimuli resulted in an increase in SIA rivalry.

M Stream Temporal Properties and the Flicker Frequency Effect

Experiment 1 showed that the prevalence of FRA rivalry increases with increasing flicker frequency only for low spatial frequency gratings (Figure 2), suggesting that the M stream contributes to this flicker frequency effect. In Experiment 2, we replicated this effect and found it to be weaker when the stimuli were isoluminant (Figure 3 and Supplementary Figure S5), again pointing to a role for the M stream in mediating the perception—and specifically the temporal frequency dependence—of FRA rivalry. In Experiment 3, we tested which temporal properties of the M stream might account for the observed flicker frequency dependence of the IOS rivalry percept. We considered two hypotheses, both based on the known temporal properties of M neurons. M neurons in the LGN exhibit larger responses to higher temporal frequencies, up to about 20 Hz (Derrington & Lennie, 1984). Therefore, in Experiments 1 and 2, the increase in FRA rivalry with increasing flicker frequency could have been because of greater activation of the M stream by higher flicker frequencies. We will call this the *temporal frequency*

hypothesis. Second, neurons in the M layers of the LGN have more transient responses, in contrast to the more sustained responses of P stream neurons (Schiller & Malpeli, 1978). Extracellular recordings from the LGN show that the duration of the majority of M responses is less than 50 msec, whereas P responses are sustained for more than 200 msec (Maunsell et al., 1999). If interactions between M stream responses to successive stimuli (i.e., at the time of the IOS) are required to generate a switch in perceived grating orientation in IOS rivalry, then orthogonal gratings presented closer together in time may result in more FRA rivalry. In this case, higher flicker rates contain shorter blank intervals between successive stimulus presentations at the time of the IOS, facilitating interactions between successive M responses to these stimuli and leading to more FRA rivalry. We will call this the *response transiency hypothesis*.

Experiment 3 tests whether the temporal frequency tuning of the M stream or its response transiency is more likely to explain the flicker frequency effect on IOS rivalry observed in Experiments 1 and 2. Two flicker conditions were employed. One of these conditions (the *continuous-flicker condition*) replicated the continuous, 50% duty cycle on–off flicker used in Experiments 1 and 2. In the other condition (the *blank-only condition*), the rivalry gratings were presented for the entire IOS period without flicker but were removed from both eyes just before each switch, creating a short preswitch blank period (van Boxtel et al., 2008). The duration of this blank period was matched to the duration of the flicker off period (i.e., one half of the flicker cycle) for each of the frequencies in the continuous-flicker condition (Figure 4A). Thus, continuous-flicker trials and their corresponding blank-only trials were identical during the off period just before the IOS. However, they differed with respect to the presence or absence of flicker before this off period. If the temporal frequency hypothesis is correct, the proportions of FRA and SIA rivalry should be independent of the duration of the preswitch blank period in the blank-only trials, as these trials do not contain any flicker. On the other hand, if the response transiency hypothesis is correct, the variation in the duration of the preswitch blank period should produce a pattern of results similar to that caused by changes in flicker frequency in Experiments 1 and 2.

We tested rivalry gratings with spatial frequencies of 4 and 7 cpd in the continuous-flicker and blank-only conditions (Figure 4B; see also Supplementary Figure S3). In the continuous-flicker condition, we replicated the spatio-temporal interaction between spatial frequency and flicker frequency found in Experiment 1 (two-way ANOVA, $F(3, 80) = 7.50$, $p < .0005$). We also observed a significant main effect of flicker condition, with more SIA rivalry for continuous-flicker trials than for blank-only trials (three-way ANOVA, $F(1, 160) = 88.8$, $p < .0001$). This effect of flicker condition may have been because of lower effective contrast for continuous-flicker trials compared with blank-only trials (Robson, 1966).

Figure 4. Stimulus design and results for Experiment 3. Short preswitch blanks promote FRA rivalry for low spatial frequency IOS rivalry gratings. (A) Two types of stimuli were constructed. The stimulus sequence is shown for only one of the eyes. Continuous-flicker stimuli flickered on and off with a 50% duty cycle at one of four flicker frequencies in different trials. For each flicker frequency, a corresponding blank-only stimulus was constructed in which gratings were always on except during a short blank period immediately preceding the IOS. The duration of this blank period was the same as the duration of the preswitch off period in the corresponding continuous-flicker condition. In the example shown here, the flicker frequency is 9 Hz, and the corresponding blank duration is 56 msec. (B) Two spatial frequencies and four flicker frequencies were tested for both the continuous-flicker (solid lines) and blank-only (dotted lines) conditions. For low spatial frequency stimuli (4 cpd, left, black lines), increases in flicker frequency and decreases in blank duration both resulted in increased FRA rivalry. High spatial frequency stimuli (7 cpd, right, gray lines) showed no effect of either flicker frequency or blank duration on

the IOS rivalry index. (C) Linear functions were fit to individual subject data for each spatial frequency–flicker condition. Means of the fitted slopes for each condition are plotted as bars (dark = low spatial frequency; light = high spatial frequency). Error bars are *SEM*. Fitted slopes for individual subjects are shown as white circles.
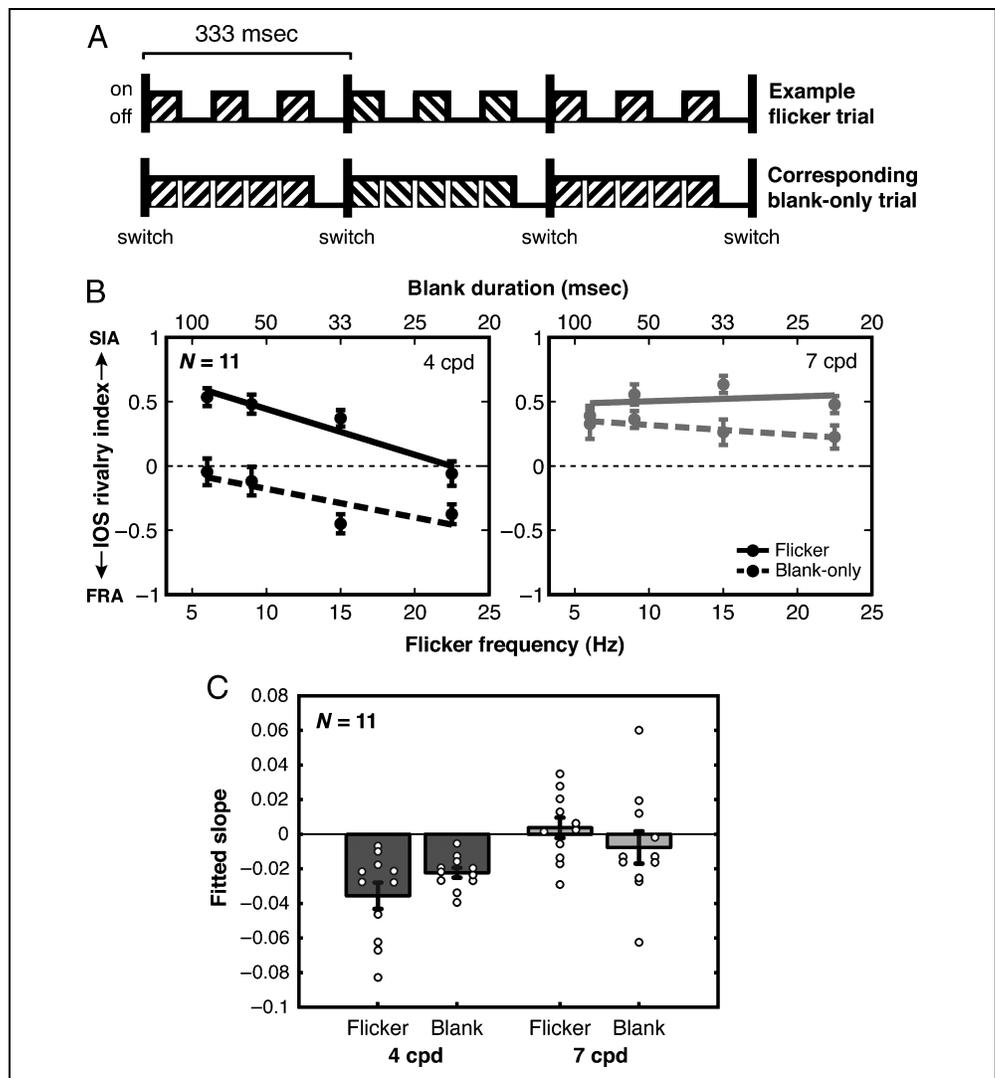
To test the temporal frequency and response transiency hypotheses, we fit linear functions to individual subject data from continuous-flicker and blank-only trials (Figure 4C). For low spatial frequency stimuli, the slopes of the linear fits were significantly different from zero for both the continuous-flicker and blank-only conditions (*t* test, continuous-flicker, $t(10) = 4.67, p < .001$; blank-only, $t(10) = 7.74, p < .0001$). In both cases, increased flicker frequency (or reduced blank duration) resulted in more FRA rivalry. We also fit linear functions to the high spatial frequency data and found that neither the continuous-flicker nor the blank-only trials had slopes that were significantly different from zero (*t* test, continuous-flicker, $t(10) = 0.63$, *ns*; blank-only, $t(10) = 0.82$, *ns*). Thus, for high spatial frequency gratings that preferentially activate the P stream, there was no detectable effect of either flicker frequency or blank duration on perception during

IOS rivalry. On the other hand, clear and similar effects of flicker frequency and blank duration were observed specifically for the low spatial frequency gratings that are biased toward M stream processing.

These findings support the response transiency hypothesis—that interactions between responses to successive orthogonal stimuli in the M stream are important for the perception of FRA rivalry. They also counter the notion that flicker per se is required to generate SIA rivalry (Wilson, 2003; Lee & Blake, 1999), because changes in the duration of the preswitch blank period for nonflickering stimuli were sufficient to influence the proportion of SIA rivalry. A similar point was made by van Boxtel et al. (2008), who observed increased levels of SIA rivalry when a blank was inserted before IOSs in nonflickering IOS rivalry stimuli. Our results confirm this finding and further show that the dependence of this effect on blank

duration is only present for the spatial frequency that is relatively biased toward M stream processing. Lastly, the effect of blank duration is similar in size to the flicker frequency effect in the same subjects.

DISCUSSION

The neural sites at which binocular rivalry is resolved is a fundamental question in the study of visual awareness and has been the topic of much debate (Tong et al., 2006; Blake & Logothetis, 2002). A centerpiece of this debate has been the demonstration of "stimulus rivalry" during IOS rivalry: a pair of rivalrous stimuli that are periodically exchanged between the two eyes can generate slow, irregular alternations of percepts that require visual information to be combined across the two eyes over multiple interocular stimulus switches (SIA rivalry; Logothetis et al., 1996). This observation has been used to argue that high-level stimulus representations, as opposed to low-level, eye-specific ones, compete for perceptual selection during rivalry (Logothetis, 1998; Sengpiel, 1997; Logothetis et al., 1996). It has also influenced models in which binocular rivalry is resolved at multiple hierarchical levels in the visual system (Pearson et al., 2007; Tong et al., 2006; Freeman, 2005; Bonneh et al., 2001; Ooi & He, 1999; Dayan, 1998; Logothetis et al., 1996).

Although the existence of SIA rivalry has been interpreted as evidence for high-level perceptual selection, it has also been shown that these alternations occur only under specific stimulation conditions (Lee & Blake, 1999). Computational models in which rivalry may either occur at the "eye level" or at a higher "stimulus level" can account for some of these dependencies, such as the increase in SIA rivalry for flickering stimuli (Wilson, 2003). However, no existing model provides a unified account of the various documented stimulus factors that promote FRA or SIA rivalry.

Our findings provide new evidence regarding the stimulus properties that govern perception during IOS rivalry and suggest a physiologically grounded framework that accounts for many of the findings in the IOS rivalry literature. The M/P framework provides an alternative to the eye level–stimulus level dichotomy in that it does not require the FRA percept to result from selection at a lower level in the visual hierarchy than the SIA percept. Rather, the type of perceptual alternation is determined by the preferential processing of IOS rivalry stimuli in either the M or P stream. Combined with previous findings from physiological and lesion studies in the LGN, our results demonstrate an association between the temporal and spatial frequencies that generate FRA rivalry and activate the M stream and between those that generate SIA rivalry and activate the P stream (Table 1). Although we consider human IOS rivalry data alongside physiology and lesion results from macaque monkeys, a number of studies have shown that humans and macaques have very similar flicker detection thresholds (De Valois, Morgan, Polson, Mead, & Hull, 1974), CSFs (De Valois, Morgan, & Snodderly, 1974), and perceptual alternations during binocular rivalry (Leopold & Logothetis, 1996).

The M/P framework not only accounts for effects of spatial frequency, temporal frequency, and color contrast on IOS rivalry, but it may account for the effects of luminance contrast as well. Lee and Blake (1999) showed that lower contrast stimuli are more likely to generate SIA rivalry than higher contrast stimuli (see also Logothetis et al., 1996; Supplementary Figure S4). In the M/P framework, these findings would be consistent with an association between the P stream and low contrast vision. However, the physiology and lesion data diverge on the question of whether the processing of low contrast stimuli relies more on the P or the M stream (Table 1). Individual P cells exhibit weak contrast sensitivity, whereas individual M cells are highly sensitive to contrast (Derrington & Lennie, 1984; Kaplan & Shapley, 1982). However, P layer lesions result in reductions in contrast sensitivity, as measured behaviorally, whereas M layer lesions do not (except at high temporal frequencies), suggesting that the P stream supports processing of low-contrast stimuli (Merigan, Katz, & Maunsell, 1991; Schiller et al., 1990). This discrepancy between the physiological and lesion data for luminance contrast may be explained by the fact that there are many more retinal inputs to the P than to the M layers of the LGN (Perry, Oehler, & Cowey, 1984), and behavioral detection of low-contrast stimuli near threshold results from significant averaging across neurons. Therefore, both physiological and lesion results from the M and P pathways are in correspondence with the stimulus conditions favoring FRA and SIA rivalry in all cases where data are available, with the partial exception of luminance contrast—where the physiology and lesion data disagree and the M/P framework is consistent with results from lesion studies, which assess contrast sensitivity of the entire visual system.

In Experiment 2, we used isoluminant stimuli to decrease the relative contribution of M stream processing (Livingstone & Hubel, 1987, 1988) and found more SIA rivalry for isoluminant gratings, consistent with the M/P framework. However, it should be noted that red–green gratings have both lower luminance contrast and higher red–green color contrast than monochromatic gratings. It is therefore possible that the results from Experiment 2 could be because of differences in luminance contrast (see also Lee & Blake, 1999; Supplementary Figure S4) that are not related to differential contributions of the M and P streams. However, color stimuli with minimal luminance contrast are strongly biased toward P stream processing, and importantly, contrast effects alone cannot account for all of the results we report. Specifically, they cannot explain the decrease in SIA rivalry with increasing flicker frequency for 4 cpd, luminance-defined stimuli (Figures 2–4), while these results are predicted by the M/P framework.

Table 1. Relationships between Perception during IOS Rivalry and Properties of the P and M Processing Streams

Stimulus Attribute	Parallels between P Stream Properties and Stimulus Properties Leading to More SIA Rivalry			Parallels between M Stream Properties and Stimulus Properties Leading to More FRA Rivalry		
	P LGN Physiology (Macaques)	Effects of P LGN Lesions (Macaques)	SIA Rivalry (Humans)	M LGN Physiology (Macaques)	Effects of M LGN Lesions (Macaques)	FRA Rivalry (Humans)
Spatial frequency	Small receptive fields [1], high spatial resolution [1,2]	Decrease in visual acuity [3], reduction in contrast sensitivity especially for spatial frequencies >2 cpd [4]	Higher spatial frequency [5, present study]	Large receptive fields [1], low spatial resolution [1,2]	No effect on visual acuity [4]	Lower spatial frequency [5, present study]
Temporal frequency	Optimal temporal frequency ~10 Hz [1,6]	No effect on flicker detection [4]	Lower flicker rates [present study]	Optimal temporal frequency ~20 Hz [1,6]	Impairment of flicker detection [12], especially >15 Hz [4]	Higher flicker rates [present study]
Transience	Sustained responses [7,8]	N/A	Longer blank between successive orthogonal stimuli [9, present study]	Transient responses [7,8]	N/A	Shorter blank between successive orthogonal stimuli [9, present study]
Color contrast	Color-opponent receptive fields [7], strong responses to colored gratings [10]	Reduction in color contrast sensitivity [3] and heterochromatic flicker sensitivity [4]	Isoluminant red–green stimuli [present study]	No color-opponent receptive fields [7], poor responses to chromatic gratings [10]	No effect on color contrast sensitivity [3] or heterochromatic flicker sensitivity [4]	Monochrome black–white stimuli [present study]
Luminance contrast	Weak contrast sensitivity [1,2]	Reduction in contrast sensitivity [3,4]	Lower contrast [5,11, present study]	Strong contrast sensitivity [1,2]	No effect on contrast sensitivity [4] except at high temporal frequencies [3]	Higher contrast [5,11, present study]

Both physiological and lesion results from the M and P pathways are in correspondence with the stimulus conditions favoring FRA and SIA rivalry in all cases where data are available, with the partial exception of luminance contrast (see Discussion). References cited in the table are as follows: 1. Derrington & Lennie, 1984; 2. Kaplan & Shapley, 1982; 3. Merigan et al., 1991; 4. Schiller et al., 1990; 5. Lee & Blake, 1999; 6. Hicks, Lee, & Vidyasagar, 1983; 7. Schiller & Malpeli, 1978; 8. Maunsell et al., 1999; 9. van Boxtel et al., 2008; 10. Hubel & Livingstone, 1990; 11. Logothetis et al., 1996; 12. Merigan & Maunsell, 1990.

Our results suggest that stimuli that are more likely to elicit M stream responses lead to the perception of fast, regular alternations, whereas stimuli that are preferentially processed by the P stream result in slow, irregular alternations of sustained form percepts, with rivalry dynamics similar to conventional, static binocular rivalry. These changing and sustained form percepts are consistent with the general roles of the dorsal and ventral cortical processing streams in the perception of transient events and stimulus motion and the perception of sustained form information, respectively. The dorsal and ventral cortical streams, in turn, have been proposed to depend on the functions of the M and P systems (Livingstone & Hubel, 1988; Ungerleider & Mishkin, 1982).

Although the M/P framework is based on correlations between stimulus factors that produce either FRA or SIA rivalry and the results of physiological and lesion studies in the M and P layers of the LGN, the framework does not require that binocular rivalry be resolved in the LGN. In fact, orthogonal rivalrous stimuli and congruent grating pairs produce identical responses in LGN neurons of awake macaque monkeys performing a visual fixation task (Lehky & Maunsell, 1996). The amount of segregation of the M and P streams in visual cortex is controversial (Livingston & Hubel, 1988; Merigan & Maunsell, 1993; see Nassi & Callaway, 2009, for a recent review), but the complementary effects of lesions of the M and P layers of the LGN on visual perception suggest significant functional segregation of the two systems (Schiller et al., 1990). We propose that processing of visual stimuli in IOS rivalry is preferentially routed into distinct cortical circuits based on the relative responses of M and P LGN neurons and that the resulting perceptual alternations take place in these cortical circuits. Physiological studies will be required to assess this possibility directly.

Studies that compare motion to color and form during conventional binocular rivalry viewing are also consistent with the M/P framework. Rivalry between face stimuli strongly reduces sensitivity to the appearance of face probes presented to the suppressed eye but has no effect on the detection of probes containing visual motion (Alais & Parker, 2006). Analogous results have been obtained for motion rivalry and face probes (Alais & Parker, 2006), suggesting a high level of independence of rivalry for motion (associated with the M and dorsal cortical streams) and visual form rivalry (associated with the P and ventral cortical streams). Other studies have shown that rivalrous stimuli containing incongruent motion signals and incongruent form or color simultaneously generate a perception of binocular integration of motion and perceptual alternations of form or color (Andrews & Blakemore, 1999, 2002; Carlson & He, 2000; Carney, Shadlen, & Switkes, 1987). These findings have led to the suggestion that rivalry may be primarily a product of the P pathway (He, Carlson, & Chen, 2005; Carlson & He, 2000).

On the other hand, Livingstone and Hubel (1988) have suggested that binocular rivalry, like stereopsis, depends on the M stream, because it breaks down at high spatial frequencies (>10 cpd) and at isoluminance. In line with this view, rivalry can be generated by interocular differences in motion direction for stimuli that are otherwise identical (Logothetis & Schall, 1990; Enoksson, 1963). Our results suggest a possible reconciliation of these views, namely that rivalry may occur within either the M or P stream, depending on the relationship between stimulus properties and the selectivities of the two streams. This view is supported by the findings that large interocular differences in spatial (Yang, Rose, & Blake, 1992) or temporal (van de Grind, van Hof, van der Smagt, & Verstraten, 2001) stimulus properties do not produce binocular rivalry but instead result in a percept of transparency. Likewise, in random-dot stereograms, stereopsis may be mediated by one spatial frequency channel while rivalry simultaneously occurs in another (Julesz & Miller, 1975). One possibility is that two stimuli that are separately processed by the M and P streams cannot engage in rivalry and that rivalry can only occur within either the M or P stream.

Our third experiment suggests that the transient nature of M stream neuronal responses may underlie the relative predominance of FRA rivalry at high flicker frequencies for low spatial frequency gratings. We observed that successive, orthogonally oriented gratings presented closer together in time were more likely to lead to FRA rivalry than orthogonal gratings presented further apart in time. This effect was present only for low spatial frequency stimuli, implicating the M stream. This finding can also be viewed in the context of the role of the M stream in motion perception. One perceptual interpretation of FRA rivalry is that of a single grating apparently moving between left- and right-tilted orientations, either alternating between the two orientations or rotating clockwise or counterclockwise. Previous studies have found that perception of apparent motion is strongly dependent on the duration of the blank interval between successive stimulus presentations. Specifically, apparent motion perception is most sensitive to small changes in temporal interval in the range of 20–100 msec, with stronger apparent motion for shorter intervals and weaker apparent motion for longer intervals (Bours, Stuur, & Lankheet, 2007; Baker & Braddick, 1985). This interval range is similar to that of the preswitch blank durations in our Experiment 3, where we observed a similar pattern of sensitivity to temporal interval between successive stimulus presentations, with shorter intervals leading to increased perception of FRA rivalry (for low spatial frequency stimuli only). Therefore, one interpretation of the results from Experiment 3 is that the ISI-dependent mechanisms responsible for motion perception also contribute to the perception of FRA rivalry.

Previous studies have shown increases in SIA rivalry in the presence of on–off flicker in IOS rivalry (van Boxtel et al., 2008; Knapen, Paffen, Kanai, & van Ee, 2007; Lee & Blake, 1999; Logothetis et al., 1996). One prominent explanation of this effect has been that flicker reduces

interocular inhibition between monocular neuronal populations, resulting in perceptual selection at a higher, binocular level in the visual hierarchy. This explanation has been applied to the finding that stimulus flicker increases both SIA rivalry in IOS rivalry (van Boxtel et al., 2008) and interocular grouping of Diaz–Caneja-type "horseshoe" stimuli (Knapen et al., 2007). Wilson (2003) explicitly modeled this hypothesis using a two-level neural network, in which stimulus flicker prevents the build-up of inhibition between left eye and right eye neurons at the lower, monocular level, resulting in competition between incompatible stimulus representations at the higher, binocular level. Our data are not consistent with this model in three ways. First, we found that varying flicker frequency had different effects for high and low spatial frequency stimuli, a result that would not be predicted by a general model of this type. Second, we showed, in agreement with van Boxtel et al. (2008), that flicker is not required to increase the prevalence of SIA rivalry: a short blank before each orientation switch is sufficient. Third, we observed a substantial amount of SIA rivalry for high spatial frequency stimuli, even with no flicker and no blanks. Therefore, even when there is ample time for the build-up of monocular inhibition to occur, SIA rivalry can still take place.

One appealing aspect of the M/P framework is that it is amenable to physiological testing. Electrophysiology, brain imaging, lesion, and patient studies could all help to confirm or refute the validity of this framework. In addition, future physiological as well as psychophysical investigations could potentially refine the framework by testing specific mechanisms by which M stream activity might lead to FRA rivalry and P stream activity to SIA rivalry. Finally, the M pathway is selectively impaired in dyslexia (Demb, Boynton, Best, & Heeger, 1998) and schizophrenia (Butler & Javitt, 2005). A better understanding of the contributions of the M and P systems to perceptual selection will be useful for characterizing the consequences of M stream dysfunction in these diseases.

The M/P framework for interpreting experimental results from IOS rivalry brings together psychophysical and physiological results to shed light on the neural basis of perceptual selection. As an alternative to the eye level–stimulus level dichotomy, this framework raises important questions regarding how parallel visual processing pathways and the hierarchical organization of the visual system interact to generate perception. With its sensitivity to multiple physiologically relevant stimulus dimensions, IOS rivalry offers a powerful paradigm for continued exploration of these questions.

Acknowledgments

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