Published in final edited form as:

J Cogn Neurosci. 2012 January ; 24(1): 246–259. doi:10.1162/jocn_a_00121.

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

Rachel N. Denison¹ and Michael A. Silver^{1,2}

¹Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA, USA

²School of Optometry, University of California, Berkeley, Berkeley, CA, USA

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 (IOS) 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 IOS 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, even though the visual stimuli remain constant. Since 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 & Fox, 1974; Blake, Yu, Lokey, & Norman, 1998; Fox & Check, 1966, 1968; Wales & Fox, 1970) 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 cortical processing streams (area MT, Logothetis & Schall, 1989).

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 (Diaz-Caneja, 1928 (translated into English in Alais, O'Shea, Mesana-Alais, & Wilson, 2000); Kovács, Papathomas, Yang, & Fehér, 1996; see also Lee & Blake, 2004 for an eye-based rivalry interpretation of these results). Logothetis et al. (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, Leopold, & Sheinberg, 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 rivalry*, or *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 rivalry*, or *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 (Blake & Logothetis, 2002; Freeman, 2005; Nguyen, Freeman, & Alais, 2003; Pearson, Tadin, & Blake, 2007; Tong, Meng, & Blake, 2006). 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 (Bonneh, Sagi, & Karni, 2001; Kang & Blake, 2008; Lee & Blake, 1999; Silver & Logothetis, 2007; van Boxtel, Knapen, Erkelens, & van Ee, 2008). This makes it an attractive paradigm for the study of how perceptual selection is governed by the specific visual information present in a display. In order 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 spatiotemporal 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 in order to reduce the M stream response to the stimuli. We observed more SIA rivalry when subjects viewed isoluminant IOS rivalry gratings compared to 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 pre-switch blank period for non-flickering stimuli. We found similar effects of flicker frequency and pre-switch 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.

EXPERIMENTAL 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 seventeen subjects (aged 19-32 years, 10 female), six of whom participated in Experiment 1, eight in Experiment 2, and eleven 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 $\pm 45^\circ$ 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 in order 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 interocular switch. 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 ms, so each on and off portion of the flicker lasts 33 ms. Therefore, in the corresponding blank-only trial, the 333 ms IOS period consisted of a 300 ms on interval followed by a 33 ms off interval, followed immediately by the interocular switch.

Task

In all experiments, subjects viewed rivalry displays for one minute 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 continuously press a key for as long as the corresponding percept was predominant and to not 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 s 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 in order 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, while 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:

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

Normalization and statistical testing—Since 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 using between-subjects 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 “no flicker” 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 non-flickering, 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 vs. 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 was 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

Spatiotemporal 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 interocular switches (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. Further, 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 spatiotemporal 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 one minute 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.

(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 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 (2-way ANOVA, $F(4,50) = 8.71$, $p < 0.0001$). As flicker frequency increased, SIA rivalry increased for high spatial frequency gratings, but FRA rivalry increased for low spatial frequency gratings (Figure 2). We first consider the flicker frequency effect for high spatial frequency gratings. This effect could reflect changes in effective stimulus contrast, since 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) non-flickering 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 (Figure S4, Supplemental Text).

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 non-flickering stimuli, as well as the perceptual similarity of non-flickering to fast-flickering stimuli (which can appear as non-flickering due to flicker fusion), we place no-flicker data points to the right of the flicker data points in all figures (except 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), since in this model, high flicker rates are proposed to reduce inhibitory interactions among monocular neurons, leading to increased SIA rivalry.

The spatiotemporal 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, while low spatial frequencies led to relatively more FRA rivalry. In the lateral geniculate nucleus (LGN) of the thalamus, P neurons have smaller receptive fields (Derrington & Lennie, 1984) and higher spatial resolution (Kaplan & Shapley, 1982) compared to M neurons, consistent with an association of P neurons with high spatial frequencies and M neurons with low spatial frequencies. While 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, while 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 to 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, while 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 analysis of variance with flicker frequency and isoluminance as factors showed a main effect of isoluminance on the IOS rivalry index ($F(1,84) = 9.14$, $p < 0.005$), with subjects reporting more SIA rivalry in the isoluminant condition (Figure 3, see also 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 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 due to error in the flicker photometry measurements. Therefore, we selected a subset of subjects for further analysis that 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 to 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 ($F(1,60) = 13.74$, $p < 0.001$), with more SIA rivalry for isoluminant stimuli. In addition, this subset of subjects exhibited an interaction between flicker frequency and isoluminance condition ($F(5,60) = 2.79$, $p < 0.05$), with higher flicker frequency leading to more FRA rivalry in the monochrome condition but not in the isoluminant condition (Figure S5). This interaction is analogous to the spatiotemporal 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 (Figures 3 and 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 test which temporal properties of the M stream might account for the observed flicker frequency dependence of the IOS rivalry percept. We consider two hypotheses, both based on the known temporal properties of M neurons. Magnocellular 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 due to 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 ms, while P responses are sustained for more than 200 ms (Maunsell et al., 1999). If interactions between M stream responses to successive stimuli (i.e., at the time of the interocular stimulus switch) 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 interocular switch, 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 interocular switch period without flicker but were removed from both eyes just before each switch, creating a short pre-switch 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 one of the frequencies in the continuous-flicker conditions (Figure 4A). Thus, continuous-flicker trials and their corresponding blank-only trials were identical during the off period just before the interocular switch. However, they differed with respect to the presence or absence of flicker prior to 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 pre-switch 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 pre-switch 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 Figure S3). In the continuous-flicker condition, we replicated the spatiotemporal interaction between spatial frequency and flicker frequency found in Experiment 1 (2-way ANOVA, $F(3,80) = 7.50$, $p < 0.0005$). We also observed a significant main effect of flicker condition, with more SIA rivalry for continuous-flicker trials than for blank-only trials (3-way ANOVA, $F(1,160) = 88.8$, $p < 0.0001$). This effect of flicker condition may have been due to lower effective contrast for continuous-flicker trials compared to blank-only trials (Robson, 1966).

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, the slopes of the linear fits were significantly different from zero for both the continuous-flicker and blank-only conditions (t-test, continuous-flicker, $t(10) = 4.67$, $p < 0.001$; blank-only, $t(10) = 7.74$, $p < 0.0001$). 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, $t(10) = 0.63$, $p > 0.5$; blank-only, $t(10) = 0.82$, $p > 0.1$). 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 (Lee & Blake, 1999; Wilson, 2003), since changes in the duration of the pre-switch blank period for non-flickering 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 interocular switches in non-flickering 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 are resolved is a fundamental question in the study of visual awareness and has been the topic of much debate (Blake & Logothetis, 2002; Tong et al., 2006). 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; Logothetis et al., 1996; Sengpiel, 1997). It has also influenced models in which binocular rivalry is resolved at multiple hierarchical levels in the visual system (Bonneh et al., 2001; Dayan, 1998; Freeman, 2005; Logothetis et al., 1996; Ooi & He, 1999; Pearson et al., 2007; Tong et al., 2006).

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), contrast sensitivity functions (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 and 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, while 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, while 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 due to differences in luminance contrast (see also Lee and Blake (1999) and 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 towards 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.

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, 1998; 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 (Carlson & He, 2000; He, Carlson, & Chen, 2005).

On the other hand, Livingstone and Hubel (1988) have suggested that binocular rivalry, like stereopsis, depends on the M stream, since 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 (Enoksson, 1963; Logothetis & Schall, 1990). 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 ms, with stronger apparent motion for shorter intervals and weaker apparent motion for longer intervals (Baker & Braddick, 1985; Bours, Stuur, & Lankheet, 2007). This interval range is similar to that of the pre-switch 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 inter-stimulus interval-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 (Knapen, Paffen, Kanai, & van Ee, 2007; Lee & Blake, 1999; Logothetis et al., 1996; van Boxtel et al., 2008). 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We thank David Egert for contributions to the stimulus presentation code and Sarah Hillenbrand for assistance with data collection. This work was supported by a National Science Foundation Graduate Research Fellowship awarded to R.N.D. and NEI Core grant EY003176.

REFERENCES

- Alais, D.; Blake, R., editors. *Binocular Rivalry*. MIT Press; Cambridge, MA: 2005.
- Alais D, O'Shea RP, Mesana-Alais C, Wilson IG. On binocular alternation. *Perception*. 2000; 29:1437–1445. [PubMed: 11257967]
- Alais D, Parker A. Independent binocular rivalry processes for motion and form. *Neuron*. 2006; 52:911–920. [PubMed: 17145510]
- Andrews TJ, Blakemore C. Form and motion have independent access to consciousness. *Nature Neuroscience*. 1999; 2:405–406.
- Andrews TJ, Blakemore C. Integration of motion information during binocular rivalry. *Vision Research*. 2002; 42:301–309. [PubMed: 11809483]
- Baker CL Jr, Braddick OJ. Temporal properties of the short-range process in apparent motion. *Perception*. 1985; 14:181–192. [PubMed: 4069948]
- Blake R, Fox R. Binocular rivalry suppression: insensitive to spatial frequency and orientation change. *Vision Research*. 1974; 14:687–692. [PubMed: 4418766]
- Blake R, Logothetis NK. Visual competition. *Nature Reviews: Neuroscience*. 2002; 3:13–21.

- Blake R, Westendorf DH, Overton R. What is suppressed during binocular rivalry? *Perception*. 1980; 9:223–231. [PubMed: 7375329]
- Blake R, Yu K, Lokey M, Norman H. Binocular rivalry and motion perception. *Journal of Cognitive Neuroscience*. 1998; 10:46–60. [PubMed: 9526082]
- Bonneh Y, Sagi D, Karni A. A transition between eye and object rivalry determined by stimulus coherence. *Vision Research*. 2001; 41:981–989. [PubMed: 11301073]
- Bours RJ, Stuur S, Lankheet MJ. Tuning for temporal interval in human apparent motion detection. *Journal of Vision*. 2007; 7:2. [PubMed: 17461670]
- Brainard DH. The Psychophysics Toolbox. *Spatial Vision*. 1997; 10:433–436. [PubMed: 9176952]
- Butler PD, Javitt DC. Early-stage visual processing deficits in schizophrenia. *Current Opinion in Psychiatry*. 2005; 18:151–157. [PubMed: 16639168]
- Carlson TA, He S. Visible binocular beats from invisible monocular stimuli during binocular rivalry. *Current Biology*. 2000; 10:1055–1058. [PubMed: 10996073]
- Carney T, Shadlen M, Switkes E. Parallel processing of motion and colour information. *Nature*. 1987; 328:647–649. [PubMed: 3614368]
- Dayan P. A hierarchical model of binocular rivalry. *Neural Computation*. 1998; 10:1119–1135. [PubMed: 9654769]
- De Valois RL, Morgan H, Snodderly DM. Psychophysical studies of monkey vision. 3. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision Research*. 1974; 14:75–81. [PubMed: 4204839]
- De Valois RL, Morgan HC, Polson MC, Mead WR, Hull EM. Psychophysical studies of monkey vision. I. Macaque luminosity and color vision tests. *Vision Research*. 1974; 14:53–67. [PubMed: 4204837]
- Demb JB, Boynton GM, Best M, Heeger DJ. Psychophysical evidence for a magnocellular pathway deficit in dyslexia. *Vision Research*. 1998; 38:1555–1559. [PubMed: 9747491]
- Derrington AM, Lennie P. Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *The Journal of Physiology*. 1984; 357:219–240. [PubMed: 6512690]
- Díaz-Caneja E. Sur l'alternance binoculaire [On binocular alternation]. *Annales d'Oculistique*. 1928; 165:721–731.
- Enoksson P. Binocular rivalry and monocular dominance studied with optokinetic nystagmus. *Acta Ophthalmologica (Copenhagen)*. 1963; 41:544–563.
- Fox R, Check R. Forced-choice form recognition during binocular rivalry. *Psychonomic Science*. 1966; 6:471–472.
- Fox R, Check R. Detection of motion during binocular rivalry suppression. *Journal of Experimental Psychology*. 1968; 78:388–395. [PubMed: 5705853]
- Freeman AW. Multistage model for binocular rivalry. *Journal of Neurophysiology*. 2005; 94:4412–4420. [PubMed: 16148271]
- Haynes J-D, Deichmann R, Rees G. Eye-specific effects of binocular rivalry in the human lateral geniculate nucleus. *Nature*. 2005; 438:496–499. [PubMed: 16244649]
- He, S.; Carlson, T.; Chen, X. Parallel pathways and temporal dynamics in binocular rivalry.. In: Alais, D.; Blake, R., editors. *Binocular Rivalry*. MIT Press; Cambridge, MA: 2005. p. 81-100.
- Hicks TP, Lee BB, Vidyasagar TR. The responses of cells in macaque lateral geniculate nucleus to sinusoidal gratings. *The Journal of Physiology*. 1983; 337:183–200. [PubMed: 6875927]
- Hubel DH, Livingstone MS. Color and contrast sensitivity in the lateral geniculate body and primary visual cortex of the macaque monkey. *Journal of Neuroscience*. 1990; 10:2223–2237. [PubMed: 2198331]
- Julesz B, Miller JE. Independent spatial-frequency-tuned channels in binocular fusion and rivalry. *Perception*. 1975; 4:125–143.
- Kang M-S, Blake R. Enhancement of bistable perception associated with visual stimulus rivalry. *Psychonomic Bulletin & Review*. 2008; 15:586–591. [PubMed: 18567259]
- Kaplan E, Shapley RM. X and Y cells in the lateral geniculate nucleus of macaque monkeys. *The Journal of Physiology*. 1982; 330:125–143. [PubMed: 7175738]

- Knapen T, Paffen C, Kanai R, van Ee R. Stimulus flicker alters interocular grouping during binocular rivalry. *Vision Research*. 2007; 47:1–7. [PubMed: 17083956]
- Kovács I, Papathomas TV, Yang M, Fehér A. When the brain changes its mind: interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences, USA*. 1996; 93:15508–15511.
- Lee SH, Blake R. Rival ideas about binocular rivalry. *Vision Research*. 1999; 39:1447–1454. [PubMed: 10343813]
- Lee SH, Blake R. A fresh look at interocular grouping during binocular rivalry. *Vision Research*. 2004; 44:983–991. [PubMed: 15031091]
- Lehky SR, Maunsell JH. No binocular rivalry in the LGN of alert macaque monkeys. *Vision Research*. 1996; 36:1225–1234. [PubMed: 8711902]
- Leopold DA, Logothetis NK. Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature*. 1996; 379:549–553. [PubMed: 8596635]
- Livingstone MS, Hubel DH. Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *Journal of Neuroscience*. 1987; 7:3416–3468. [PubMed: 3316524]
- Livingstone MS, Hubel DH. Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*. 1988; 240:740–749. [PubMed: 3283936]
- Logothetis NK. Single units and conscious vision. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*. 1998; 353:1801–1818.
- Logothetis NK, Leopold DA, Sheinberg DL. What is rivalling during binocular rivalry? *Nature*. 1996; 380:621–624. [PubMed: 8602261]
- Logothetis NK, Schall JD. Neuronal correlates of subjective visual perception. *Science*. 1989; 245:761–763. [PubMed: 2772635]
- Logothetis NK, Schall JD. Binocular motion rivalry in macaque monkeys: eye dominance and tracking eye movements. *Vision Research*. 1990; 30:1409–1419. [PubMed: 2247951]
- Logothetis NK, Schiller PH, Charles ER, Hurlbert AC. Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance. *Science*. 1990; 247:214–217. [PubMed: 2294602]
- Maunsell JH, Ghose GM, Assad JA, McAdams CJ, Boudreau CE, Noerager BD. Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience*. 1999; 16:1–14. [PubMed: 10022474]
- Merigan WH, Katz LM, Maunsell JH. The effects of parvocellular lateral geniculate lesions on the acuity and contrast sensitivity of macaque monkeys. *Journal of Neuroscience*. 1991; 11:994–1001. [PubMed: 2010820]
- Merigan WH, Maunsell JH. Macaque vision after magnocellular lateral geniculate lesions. *Visual Neuroscience*. 1990; 5:347–352. [PubMed: 2265149]
- Merigan WH, Maunsell JH. How parallel are the primate visual pathways? *Annual Review of Neuroscience*. 1993; 16:369–402.
- Nassi JJ, Callaway EM. Parallel processing strategies of the primate visual system. *Nature Reviews: Neuroscience*. 2009; 10:360–372.
- Nguyen VA, Freeman AW, Alais D. Increasing depth of binocular rivalry suppression along two visual pathways. *Vision Research*. 2003; 43:2003–2008. [PubMed: 12842153]
- Ooi TL, He ZJ. Binocular rivalry and visual awareness: the role of attention. *Perception*. 1999; 28:551–574. [PubMed: 10664754]
- Pearson J, Tadin D, Blake R. The effects of transcranial magnetic stimulation on visual rivalry. *Journal of Vision*. 2007; 7:2, 1–11. [PubMed: 17685798]
- Pelli DG. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*. 1997; 10:437–442. [PubMed: 9176953]
- Perry VH, Oehler R, Cowey A. Retinal ganglion cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. *Neuroscience*. 1984; 12:1101–1123. [PubMed: 6483193]
- Robson JG. Spatial and temporal contrast-sensitivity functions of the visual system. *Journal of the Optical Society of America*. 1966; 56:1141–1142.

- Schiller PH, Logothetis NK, Charles ER. Functions of the colour-opponent and broad-band channels of the visual system. *Nature*. 1990; 343:68–70. [PubMed: 2296292]
- Schiller PH, Malpeli JG. Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*. 1978; 41:788–797. [PubMed: 96227]
- Sengpiel F. Binocular rivalry: ambiguities resolved. *Current Biology*. 1997; 7:R447–450. [PubMed: 9210367]
- Sheinberg DL, Logothetis NK. The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences, USA*. 1997; 94:3408–3413.
- Silver M, Logothetis N. Temporal frequency and contrast tagging bias the type of competition in interocular switch rivalry. *Vision Research*. 2007; 47:532–543. [PubMed: 17182075]
- Tong F, Engel SA. Interocular rivalry revealed in the human cortical blind-spot representation. *Nature*. 2001; 411:195–199. [PubMed: 11346796]
- Tong F, Meng M, Blake R. Neural bases of binocular rivalry. *Trends in Cognitive Sciences*. 2006; 10:502–511. [PubMed: 16997612]
- Ungerleider, LG.; Mishkin, M. Two cortical visual systems.. In: Ingle, DJ.; Goodale, M.; Mansfield, RJW., editors. *Analysis of Visual Behaviour*. MIT Press; Cambridge, MA: 1982. p. 549-586.
- van Boxtel JJA, Knapen T, Erkelens CJ, van Ee R. Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries. *Journal of Vision*. 2008; 8:13.11–17. [PubMed: 19146297]
- van de Grind WA, van Hof P, van der Smagt MJ, Verstraten FA. Slow and fast visual motion channels have independent binocular-rivalry stages. *Proceedings of the Royal Society B: Biological Sciences*. 2001; 268:437–443.
- Wales R, Fox R. Increment detection thresholds during binocular rivalry suppression. *Perception and Psychophysics*. 1970; 8:90–94.
- Wilson HR. Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences, USA*. 2003; 100:14499–14503.
- Wunderlich K, Schneider KA, Kastner S. Neural correlates of binocular rivalry in the human lateral geniculate nucleus. *Nature Neuroscience*. 2005; 8:1595–1602.
- Yang Y, Rose D, Blake R. On the variety of percepts associated with dichoptic viewing of dissimilar monocular stimuli. *Perception*. 1992; 21:47–62. [PubMed: 1528703]

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 interocular switches (SIA rivalry).

Figure 2.

Results of Experiment 1: Spatiotemporal 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 s.e.m.

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 s.e.m.

Figure 4.

Stimulus design and results for Experiment 3: Short pre-switch 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 interocular switch. The duration of this blank period was the same as the duration of the

pre-switch 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 ms. (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 s.e.m. Fitted slopes for individual subjects are shown as white circles.

Table 1

Relationships between perception during IOS rivalry and properties of the P and M processing streams. *Top*, properties of P pathway and stimulus conditions leading to SIA rivalry. *Bottom*, properties of M pathway and stimulus conditions leading to FRA rivalry. 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 and Blake, 1999; 6. Hicks et al., 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.

Parallels between P stream properties and stimulus properties leading to more SIA rivalry			
Stimulus attribute	Parvocellular LGN physiology (macaques)	Effects of parvocellular LGN lesions (macaques)	SIA 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]
Temporal frequency	Optimal temporal frequency ~10 Hz [1,6]	No effect on flicker detection [4]	Lower flicker rates [present study]
Transience	Sustained responses [7,8]	N/A	Longer 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]
Luminance contrast	Weak contrast sensitivity [1,2]	Reduction in contrast sensitivity [3,4]	Lower contrast [5,11, present study]

Parallels between M stream properties and stimulus properties leading to more FRA rivalry			
Stimulus attribute	Magnocellular LGN physiology (macaques)	Effects of magnocellular LGN lesions (macaques)	FRA rivalry (humans)
Spatial frequency	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 ~20 Hz [1,6]	Impairment of flicker detection [12], especially >15 Hz [4]	Higher flicker rates [present study]
Transience	Transient responses [7,8]	N/A	Shorter blank between successive orthogonal stimuli [9, present study]
Color contrast	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	Strong contrast sensitivity [1,2]	No effect on contrast sensitivity [4] except at high temporal frequencies [3]	Higher contrast [5,11, present study]