Available online at www.sciencedirect.com
ScienceDirect
Vision Research 47 (2007) 532–543
Vision Research
www.elsevier.com/locate/visres

Temporal frequency and contrast tagging bias the type of competition in interocular switch rivalry

Michael A. Silver [a,b,*], Nikos K. Logothetis [a]

[a] *Max Planck Institute for Biological Cybernetics, Spemannstrasse 38, D 72076 Tübingen, Germany*
[b] *School of Optometry and Helen Wills Neuroscience Institute, University of California, Berkeley, CA 94720, USA*

Received 11 July 2006; received in revised form 6 October 2006

Abstract

The nature of competition underlying perceptual alternations in binocular rivalry remains controversial. Interocular swapping of rivalrous stimuli can result in either slow irregular perceptual alternations that bridge multiple interocular switches or fast regular alternations that are time locked to the stimulus exchanges. We labeled either the inputs to the eyes or the individual rivalrous stimuli using temporal frequency and contrast tagging. Tagging of eye-of-origin signals enhanced the fast regular perceptual alternations associated with eye rivalry, while stimulus tagging shifted perception towards slow irregular alternations characteristic of stimulus rivalry. Thus, the type of competition in binocular rivalry can be biased based on additional cues in the visual inputs. The results are consistent with a model in which the brain combines information across multiple visual features to resolve ambiguities in visual inputs.

Keywords: Binocular rivalry; Binocular vision; Flicker; Visual perception; Perceptual selection

1. Introduction

When two incompatible visual stimuli are presented to the two eyes, a perceptual alternation between the two stimuli typically occurs, a phenomenon known as binocular rivalry. Binocular rivalry is extremely useful for studying neural correlates of visual perception, because perceptual alternations occur in the absence of any changes in visual stimulation. However, binocular rivalry can also be used to investigate how the visual system resolves ambiguity in sensory inputs. While the alternating percepts in binocular rivalry often correspond to the individual monocular stimuli, interocular grouping of the two stimuli that results in an alternation between two coherent patterns has also been described (Diaz-Caneja, 1928 (translated into English in Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Kovács, Papathomas, Yang, & Fehér, 1996). While there is substantial evidence for competition in binocular rivalry between signals based on eye-of-origin (Blake & Fox, 1974; Blake, Westendorf, & Overton, 1980; Tong & Engel, 2001) and between stimulus representations (Diaz-Caneja, 1928; Kovács et al., 1996; Logothetis, 1998), there is a growing consensus that both forms of competition can occur (Blake & Logothetis, 2002; Bonneh, Sagi, & Karni, 2001; Haynes & Rees, 2005; Ooi & He, 2003; Wilson, 2003). However, the factors that influence the likelihood of eye-based versus stimulus-based rivalry are not well understood.

Interocular switching (IOS) of orthogonal gratings at a rate of 3 Hz (Fig. 1A) can result in perceptual alternations between the two orientations that persist over multiple stimulus switches (Logothetis, Leopold, & Sheinberg, 1996). That is, subjects experience a perception of a particular stimulus and phenomenal suppression of the other stimulus, even though both stimuli are presented to both eyes during this period of stable perception. In addition, the durations of these stable percepts are variable and exhibit sequential independence, resulting in a slow irregular

---

[*] Corresponding author. Present address: School of Optometry, 360 Minor Hall, #2020, University of California, Berkeley, CA 94720-2020, USA. Fax: +1 510 643 5109.
E-mail address: masilver@berkeley.edu (M.A. Silver).

0042-6989/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2006.10.011

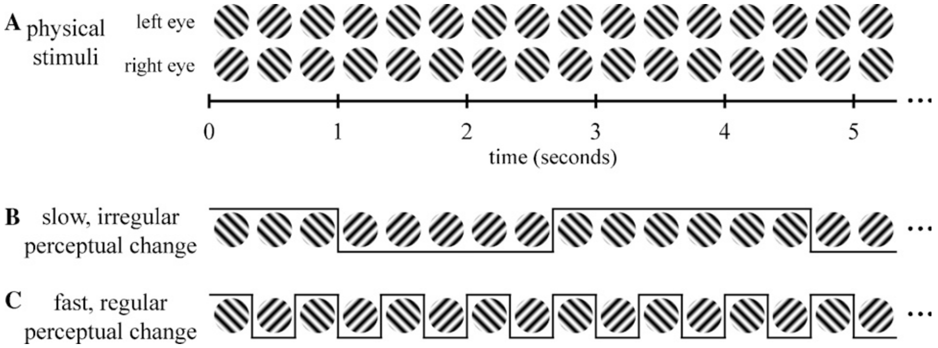

Fig. 1. Visual stimuli and two possible percepts in interocular switch (IOS) rivalry. (A) Physical stimuli: the two eyes always view an orthogonal pair of gratings, but the gratings are swapped between the eyes at a frequency of 3 Hz. (B) Example of slow irregular perceptual alternation. Periods of stable perception of one orientation or the other persist over multiple stimulus exchanges, and the durations of these stable percepts are variable and sequentially independent. (C) Example of fast regular perceptual alternation. Switching of perception between one orientation and the other is time-locked to the physical stimulus exchanges. This example shows a sequence of percepts corresponding to the left eye's inputs, but it is unknown whether the fast regular perceptual change is a stable percept associated with one eye or whether there are alternations between the two monocular percepts.

alternation between stimulus orientations (Fig. 1B; Logothetis et al., 1996). Under optimal stimulus conditions, this result argues strongly against competition based on eye-of-origin signals for IOS rivalry. However, changes to low-level stimulus features such as contrast, spatial frequency, and/or interocular switch rates in IOS rivalry can generate a very different percept in which the perceived orientation changes with every stimulus switch (Fig. 1C; Lee & Blake, 1999). Because this fast regular alternation is identical to the stimulus sequence presented to a single eye, the underlying competition has been postulated to be between the two monocular pathways (Lee & Blake, 1999).

We have employed temporal frequency and contrast tagging to label either eye-of-origin or stimulus orientation in IOS rivalry between orthogonal gratings. Tagging of eye-of-origin enhanced fast regular switching (characteristic of eye rivalry), while orientation tagging enhanced slow irregular switching (characteristic of stimulus rivalry). These results suggest that when the visual system is presented with two different perceptual ambiguities (interocular and orientation incompatibility), additional information in the stimuli biases the perceptual alternation. Importantly, the differences in temporal frequency (O'Shea & Blake, 1986) and contrast (Levelt, 1968) used to tag the stimuli or eyes do not generate rivalrous perceptual alternations on their own.

2. Experiment 1

Before examining the factors that influence the predominance of either fast regular or slow irregular perceptual switching in IOS rivalry, it was important to more completely characterize the two types of perceptual alternations. The interpretation of slow irregular switching is relatively straightforward—subjects report alternations between the two stimulus orientations that are independent of the ocular configuration of the stimuli (Logothetis et al., 1996), strongly suggesting that competition can occur between the two stimulus representations. However, the fast regular perceptual alternation is much more difficult to study using psychophysical methods. In this case, the percept changes with every stimulus swap (typically at a rate of a few Hz), and subjects are unable to generate real-time reports of their percepts at this alternation rate. The fast switching perceptual alternation has been attributed to eye rivalry, primarily because the percept is similar to monocular viewing of the IOS display (Lee & Blake, 1999). However, in IOS rivalry, both eyes are presented with the same sequence of alternating gratings, and this sequence is 180 deg out of phase in the two eyes (Fig. 1A). Therefore, even if the fast regular switching is indeed a monocular percept, it is unclear whether the perception corresponds to the left eye's inputs, the right eye's inputs, or some alternation between the two.

Another interpretation of the fast regular perceptual switching in IOS rivalry is that every stimulus swap causes the previously suppressed stimulus to become dominant. It is known that abrupt changes in a suppressed stimulus during conventional (non-switching) binocular rivalry can cause the stimulus to immediately become dominant (Blake, Westendorf, & Fox, 1990; Walker & Powell, 1979). If there is short-term adaptation (on the time scale of a few hundred milliseconds) in visual neurons responsive to the dominant stimulus, it is possible that they would be at a competitive disadvantage following a stimulus swap. The result would be a fast regular perceptual alternation that would be time-locked to the stimulus swaps, but this alternation would not necessarily be attributable to interocular competition. This hypothesis predicts that introduction of additional changes in stimulus orientation during IOS rivalry would increase the rate of perceptual alternation, while the eye rivalry account predicts little or no effect of additional stimulus orientation changes that are not accompanied by interocular stimulus exchanges.

2.1. Methods

A total of four paid volunteers participated in this study. All had normal or corrected-to-normal vision and were screened for deficits in stereoscopic or color vision. None of them had knowledge about the experimental hypotheses or about binocular rivalry in general. Subjects viewed stimuli through a custom-built stereoscope that allowed independent viewing of two gamma-corrected CRT monitors with a pixel resolution of 1280 × 800 pixels and a frame refresh rate of 90 Hz. The viewing distance was 123 cm.

Stimuli were selected to produce maximal amounts of fast regular perceptual alternations in IOS rivalry. Lee & Blake (1999) reported that gratings of high contrast and low spatial frequency were more likely to result in fast regular than slow irregular switching. In the present experiment, subjects viewed pairs of orthogonal monochromatic sinusoidal gratings with spatial frequency of 2 cyc/deg and Michelson contrast of 0.5. The gratings were presented within a circular aperture with diameter 1.8 deg and on a gray background with mean luminance equal to 19.4 cd/m^2. Vergence cues were provided by a binocular black circular annulus with inner diameter 3.51 and outer diameter 3.65 deg that surrounded the gratings.

The orientations of the gratings were 45 and 135 deg, and they were swapped between the two eyes every 400 (Fig. 2D) or 800 ms (Fig. 2E and F). In addition, global orientation transients were introduced every 400 (Fig. 2D and F) or 800 ms (Fig. 2E). These consisted of brief presentation of vertical/horizontal dichoptic grating pairs for 1, 3, or 5 monitor refresh frames, corresponding to 11, 33, or 55 ms. Two orientation transients were possible: vertical in left eye/horizontal in right eye and horizontal in left eye/vertical in right eye. Each of these was presented randomly with a 50% probability for each configuration of orientation transient. The orientation transients and interocular stimulus switches occurred simultaneously, except for the condition in which transients occurred every 400 ms and stimulus switches every 800 ms. In this case, every other transient occurred at the time of a stimulus switch.

Subjects reported with a button press whether the rate of perceptual alternation was slow (corresponding to one switch every 800 ms) or fast (one switch every 400 ms). Before data collection, subjects viewed training examples consisting of oblique congruent gratings (same orientation

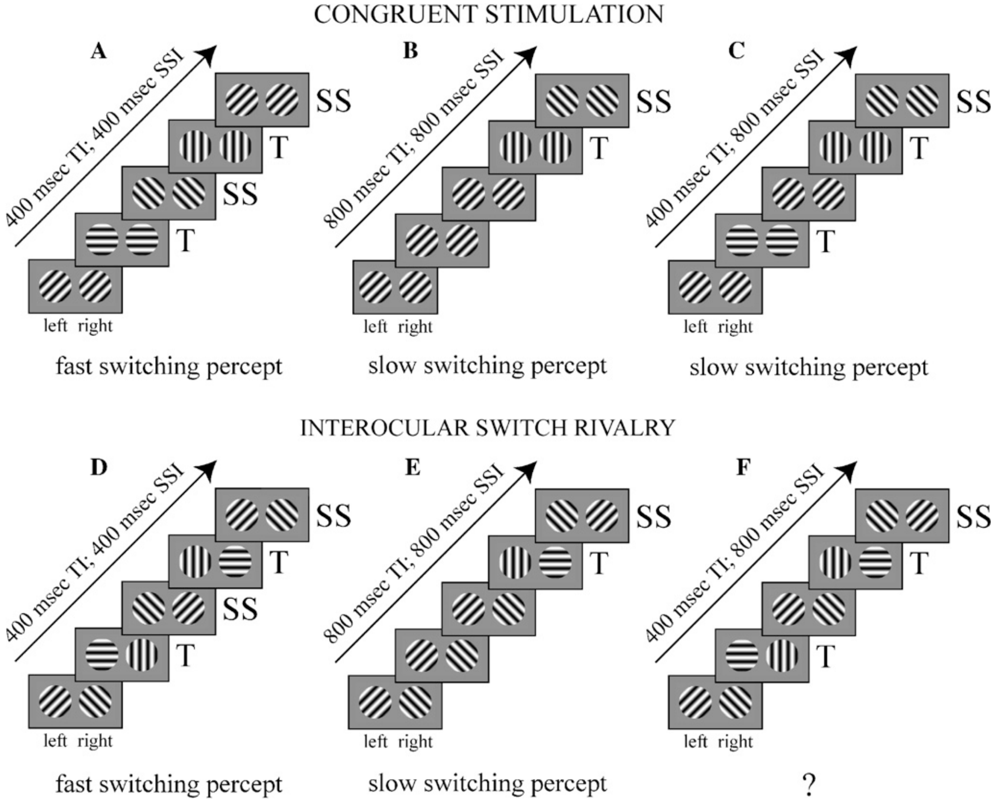

Fig. 2. Stimuli used in Experiment 1. TI = transient interval; SSI = stimulus switch interval. Percepts associated with the various stimulus configurations are shown at the bottom of each panel. T indicates the occurrence of a transient consisting of vertical and/or horizontal gratings (11–55 ms in duration). SS indicates stimulus switches, either congruent changes in grating orientation (top panels) or interocular exchanges (bottom panels). (A–C) Congruent stimulation. In these training examples (also used as catch trials), subjects were instructed to ignore the transients and to report whether the rate of orientation switches was "fast" (every 400 ms) or "slow" (every 800 ms). Thus, their behavioral responses would be expected to reflect the rate of stimulus switching (SSI). (D) IOS rivalry; fast transient and stimulus switch rates. In this condition, both transients and stimulus switches occur every 400 ms, so the expected response from the subjects is "fast" perceptual switches. (E) IOS rivalry, slow transient and stimulus switch rates. Here, transients and stimulus switches occur every 800 ms, so subjects should report "slow" perceptual switches. (F) IOS rivalry, fast transient rate and slow stimulus switch rate. In this case, transient and stimulus switch rates are dissociated. If global orientation transients drive perceptual switching in IOS rivalry, the predicted response is "fast" perceptual switching. Alternatively, if interocular stimulus switches are required for perceptual alternations, subjects should report "slow" perceptual switching.

in the two eyes) that changed orientation between 45 and 135 deg every 400 (Fig. 2A) or 800 ms (Fig. 2B and C) and contained global orientation transients (congruent horizontal or vertical, 50% probability of each) once every 400 (Fig. 2A and C) or 800 ms (Fig. 2B). In this case, the rate of alternation was unambiguous, and subjects received feedback on every trial that indicated whether the alternation rate was slow or fast. In addition, catch trials with congruent stimuli were randomly intermixed with the IOS rivalry trials to confirm that subjects understood the instructions and were correctly discriminating fast from slow perceptual alternations. These catch trials constituted approximately 15% of the total number of trials for each session. Each trial contained 8 s of stimulus presentation. Each subject participated in either 3 or 4 experimental sessions, and each session consisted of 117 trials. There were no systematic differences in responses for the different orientation transient durations, and the data were combined across the three durations (11, 33, and 55 ms). The percentage of "fast switch" percepts was computed for each combination of transient duration, experimental session, and condition, and these percentage values were the units of variance for computing the standard errors of the mean displayed in Fig. 3. All the data were pooled to generate the means and standard errors for the "All subjects" graph.

2.2. Results and discussion

Before data collection, subjects were provided with examples of slow (once per 800 ms) and fast (once per 400 ms) alternations in orientation of pairs of congruent gratings (45 versus 135 deg), and they quickly learned to discriminate the two types of stimuli. These training examples were also used as catch trials in the actual experiments. Subjects' responses to these congruent catch trials are displayed in the left side of the panels in Fig. 3 as the percentages of trials in which they reported "fast switch". In addition to periodic alternations in orientation between 45 and 135 deg, global orientation transients were introduced every 400 or 800 ms. These transients consisted of brief (11–55 ms) presentations of congruent vertical or horizontal grating pairs. The subjects were instructed to ignore these transients and simply report the rate of orientation switching. When the stimulus switch interval (SSI) was 800 ms (Fig. 2B and C), subjects consistently reported slow perceptual alternations (% "fast switch" percepts was nearly zero),

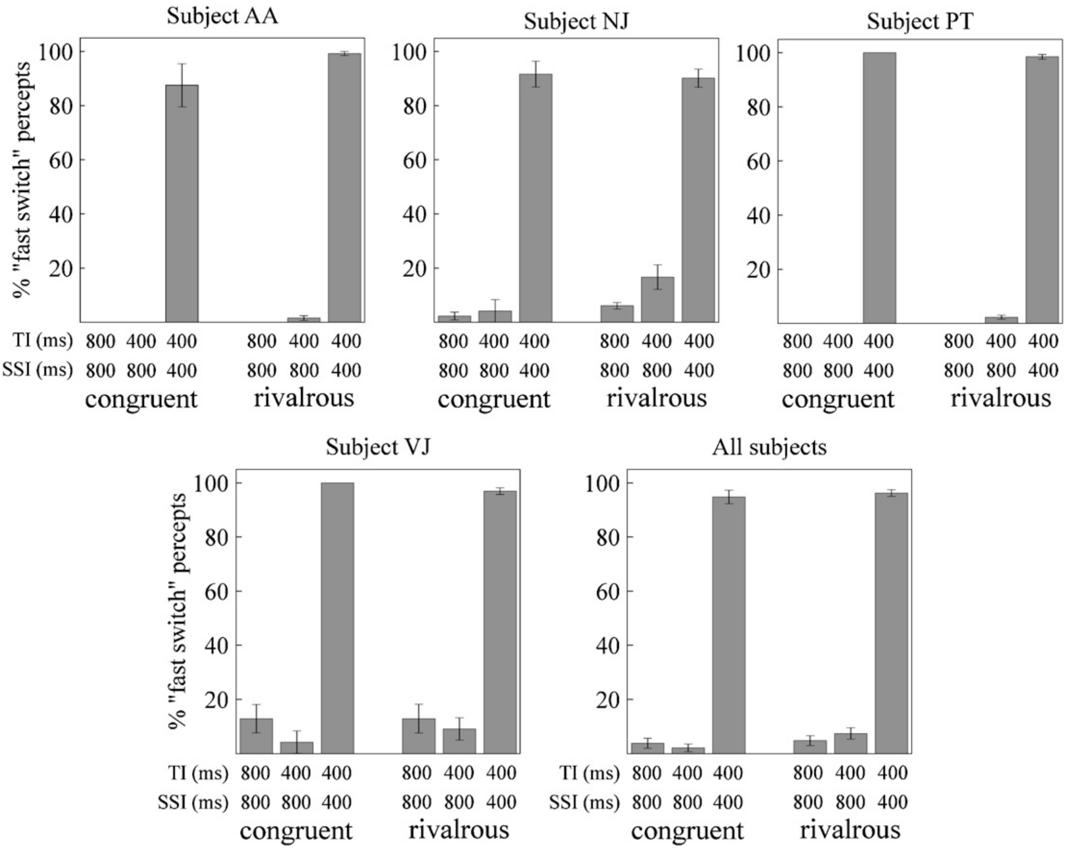

Fig. 3. Introduction of additional global orientation transients does not affect the rate of perceptual alternations in IOS rivalry. *Congruent*, gratings alternated orientation between 45 and 135 deg every 400 or 800 ms (SSI, stimulus switch interval). In addition, global orientation transients consisting of congruent vertical or horizontal gratings occurred every 400 or 800 ms (TI, transient interval). Subjects reported the rate of perceptual alternation of stimulus orientation as either "slow switch" (every 400 ms) or "fast switch" (every 800 ms) percepts. All subjects reported slow switching for 400 ms SSI and fast switching for 800 ms SSI. *Rivalrous*, pairs of dichoptic orthogonal gratings were swapped between the eyes every 400 or 800 ms (SSI, stimulus switch interval). Dichoptic orientation transients occurred every 400 or 800 ms (TI, transient interval). Subjects reported that the perceptual alternations occurred at a rate corresponding to the SSI, indicating that the alternation rate was unaffected by the introduction of additional global orientation transients.

regardless of whether the global transient interval (TI) was 400 or 800 ms (Fig. 3). When the SSI was 400 ms (Fig. 2A), subjects correctly reported nearly 100% "fast switch" percepts (Fig. 3).

When the stimuli were a pair of rivalrous orthogonal gratings (45 versus 135 deg), the same pattern of responses was observed. When the SSI and TI were both 800 ms (Fig. 2E), subjects reported slow perceptual switching, and when they were 400 ms (Fig. 2D), subjects reported fast perceptual switching (Fig. 3). The interesting case is when the global transient interval was 400 ms but the interocular stimulus switching interval was 800 ms (Fig. 2F). If global transients cause the suppressed stimulus to become immediately dominant, then subjects should have perceived a change in orientation every 400 ms (large percentage of "fast switch" percepts). If, on the other hand, the perceptual alternations were due to eye rivalry, then they should have occurred every 800 ms (small percentage of "slow switch" percepts). The results provide strong evidence against the hypothesis that fast regular switching in IOS rivalry is due to global orientation transients (Fig. 3). Additional experiments were conducted in which stimulus blanking (gray screen presentation) was used instead of global orientation transients, and these produced identical results (data not shown). Although these data do not conclusively demonstrate that the fast regular switching in IOS rivalry is due to competition between eye-of-origin signals, they are entirely consistent with this possibility.

3. Experiment 2

The IOS rivalry stimuli studied by Logothetis et al. (1996) & Lee & Blake (1999) typically result in one of two percepts: slow irregular alternations that persist over multiple interocular exchanges or fast regular alternations that are time-locked to the stimulus swaps. The existence of these two different perceptual alternations suggests that they may correspond to two different types of competition—namely, the slow irregular alternations could be due to competition between stimulus representations (Logothetis et al., 1996), while the fast regular alternations could result from rivalry between eye-of-origin signals (Lee & Blake, 1999).

We reasoned that the introduction of additional stimulus features that favored either stimulus or eye competition should bias the perceptual alternations towards either slow irregular or fast regular alternations, respectively. A temporal frequency tagging procedure was employed in which one input flickered at 9 Hz and one at 22.5 Hz. These temporal frequency tags either retained the same ocular configuration during interocular swapping of the grating orientations (Fig. 4A), or they remained associated with particular grating orientations across the stimulus swaps (Fig. 4B). In the first case, the two flicker rates labeled the monocular inputs, and in the second case, they labeled the oriented gratings. We hypothesized that tagging the eyes should enhance the fast regular perceptual alternations that have been attributed to eye rivalry (Lee & Blake, 1999), while stimulus tagging should increase the probability of slow irregular perceptual alternations characteristic of stimulus rivalry (Logothetis et al., 1996).

This temporal frequency tagging procedure introduces differences in effective contrast between stimuli flickering at 9 Hz and 22.5 Hz. Specifically, at the spatial frequencies employed in this experiment (5 cyc/deg), stimuli with low temporal frequency flicker (9 Hz) will have a higher effective contrast than those with high rates of flicker (22.5 Hz) (Robson, 1966). It is well known that higher contrast stimuli dominate stimuli of lower contrast in binocular rivalry (Levelt, 1968). To remove this possible confound due to differences in effective contrast, the stimulus contrasts were adjusted for each subject so that they had equal strength in conventional binocular rivalry. If differences in effective contrast cause more fast regular alternations with eye-of-origin tagging and more slow irregular alternations with stimulus tagging, correcting for differences in effective contrast should eliminate the effects of eye and stimulus tagging. On the other hand, if the effects of temporal frequency tagging are to bias the visual system towards either eye- or stimulus-based competition, then the introduction of contrast differences between the stimuli or between the eyes provides another tag that should increase the effects of eye and stimulus tagging compared to uncorrected stimuli.

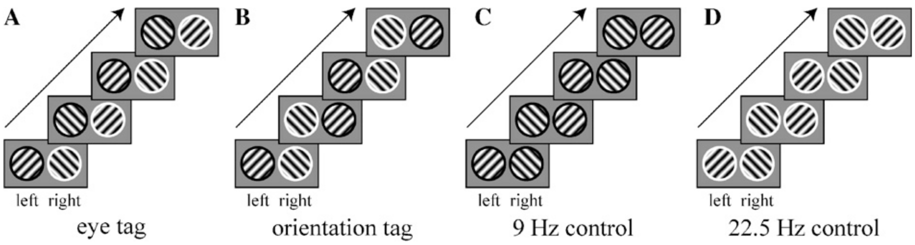

Fig. 4. Stimuli used in Experiment 2. In all conditions, a black circle surrounding a stimulus indicates that it was flickered at 9 Hz, and a white circle indicates 22.5 Hz flicker. (A) Tagging of eye-of-origin. Although the stimulus orientations were exchanged between the two eyes at 2.25 Hz, the two flicker rates were not exchanged. In this example, the left eye always viewed 9 Hz flicker, and the right eye viewed 22.5 Hz flicker. (B) Tagging of stimulus orientation. Here, the orientation swaps were identical to those depicted in (A), but the flicker rates remained associated with the respective stimulus orientations across interocular exchanges. (C) Baseline condition (9 Hz flicker). In this case, 9 Hz flicker was presented to both eyes and was also associated with both stimulus orientations. (D) Baseline condition (22.5 Hz flicker). Same configuration as in (C), except flicker rate was 22.5 Hz instead of 9 Hz.

3.1. Methods

The four subjects described in Experiment 1 also participated in this experiment, and the psychophysical apparatus was identical. In contrast to Experiment 1, it was important to adjust stimulus parameters to allow both fast regular and slow irregular perceptual alternations to occur (Lee & Blake, 1999). Specifically, the Michelson contrast of the gratings was 0.4, the interocular switch interval was 445 ms, and the spatial frequency of the gratings was 5 cyc/deg. The other stimulus parameters were identical to Experiment 1, except that no additional global orientation transients were presented. Each trial consisted of 10.67 s of viewing time, followed by a behavioral response collected using a button box.

Subjects reported their perception using a six-point rating scale. To calibrate this rating scale, training sessions were conducted in which two types of control stimuli were presented: congruent gratings that alternated between 45 and 135 deg every 445 ms (exemplifying fast regular switching), and conventional (non-switching) binocular rivalry between orthogonal gratings of 45 and 135 deg orientation (exemplifying slow irregular switching). During training, subjects were provided with feedback on every trial. The training examples were shown with all possible combinations of 9 and 22.5 Hz flicker (eye-specific: 9 Hz in both eyes, 9 Hz in one and 22.5 Hz in the other, or 22.5 Hz in both eyes, regardless of orientation; orientation-specific: 9 Hz for both stimuli, 9 Hz for one orientation and 22.5 Hz for the other, or 22.5 Hz for both stimuli, regardless of eye-of-origin). This encouraged the subjects to respond only to changes in perceived stimulus orientation, regardless of flicker configuration. Flicker was generated by alternating periods of grating presentation and periods of no grating (neutral gray luminance). At the 90 Hz monitor refresh rate employed in this study, 9 Hz flicker corresponded to 5 frames of grating alternating with 5 frames of neutral gray, and 22.5 Hz flicker was 2 frames of grating alternating with 2 frames of neutral gray. Due to the discrete refresh rate of the monitor, this procedure generated stimuli that had a fundamental frequency of flicker at the desired frequency but also had power at other temporal frequencies.

Each subject participated in either 3 or 4 experimental sessions, with each session containing 180 trials. 52 trials consisted of temporal frequency tagging of the eyes (Fig. 4A; counterbalanced across left/right), and 52 trials consisted of tagging of the stimuli (Fig. 4B; counterbalanced across 45 and 135 deg). To measure a baseline rating scale value in the absence of tagging, 26 trials were included in each session in which both eyes/stimuli were flickered at 9 Hz (Fig. 4C), and the responses on these trials were averaged with those from 26 trials in which both eyes/stimuli were flickered at 22.5 Hz (Fig. 4D). Finally, 24 catch trials were included, 12 with congruent stimulation and 12 with conventional binocular rivalry. These trials allowed us to verify that subjects were correctly using the subjective rating scale. The order of the various stimulus conditions was completely randomized. Half of the baseline, eye-tagging, and stimulus-tagging trials contained stimuli that were adjusted for contrast as described below, and the remaining trials were not adjusted. For each experiment, the mean rating scale values were separately computed for each combination of (eye tagging or stimulus tagging) and (uncorrected or corrected contrast) and were subtracted from the mean values for the corresponding baseline condition. The unit of variance for computing standard errors of the mean was the experimental session, and the significance of the differences between eye tagging and stimulus tagging was assessed using two-tailed t-tests. The effects of contrast correction were determined by measuring the difference and standard error of the difference of subjective rating values between eye and stimulus tagging and performing a two-tailed *t*-test.

To correct for differences in stimulus strength due to temporal frequency, we measured perceptual dominance during conventional (non-switching) binocular rivalry over a range of stimulus contrasts. Subjects viewed rivalrous orthogonal gratings (45 and 135 deg) with spatial frequency of 5 cyc/deg that did not switch between the eyes. One stimulus flickered at 9 Hz, and the other flickered at 22.5 Hz. Contrast differences between the two eyes were varied over trials, but the average Michelson contrast of the two stimuli was always 0.4. On each trial, subjects viewed the stimuli continuously for 1 min, and they pressed one button while the 45 deg stimulus dominated perception and the other button while the 135 deg stimulus dominated. Subjects were instructed to refrain from pressing any buttons when they experienced piecemeal rivalry or mixed dominance.

All four subjects participated in three experimental sessions. In each experimental session, each level of contrast difference was tested four times, counterbalancing across the two eyes and two stimulus orientations. Eleven contrast differences were tested, resulting in 44 trials per session. The percentage of viewing time for which subjects reported dominance of either the 45 or 135 deg grating was computed and plotted as a function of contrast difference between the two stimuli (Fig. 5). For equal contrast levels, the 9 Hz flickering stimulus always dominated the stimulus with 22.5 Hz flicker (Fig. 5). However, as the contrast of the 9 Hz grating was lowered and the contrast of the 22.5 Hz grating was increased, the levels of dominance of the two stimuli became more similar and eventually reversed. The intersection of these curves represents the point at which the effects of temporal frequency are balanced by the contrast differences between the two stimuli. This point was determined for each of the three sessions for each subject and averaged across the sessions. The resulting contrast difference value represents the point at which the two stimuli have equal dominance in conventional binocular rivalry.

3.2. Results and discussion

Subjects used a six-point subjective rating scale to quantify the relative amounts of slow irregular and fast regular

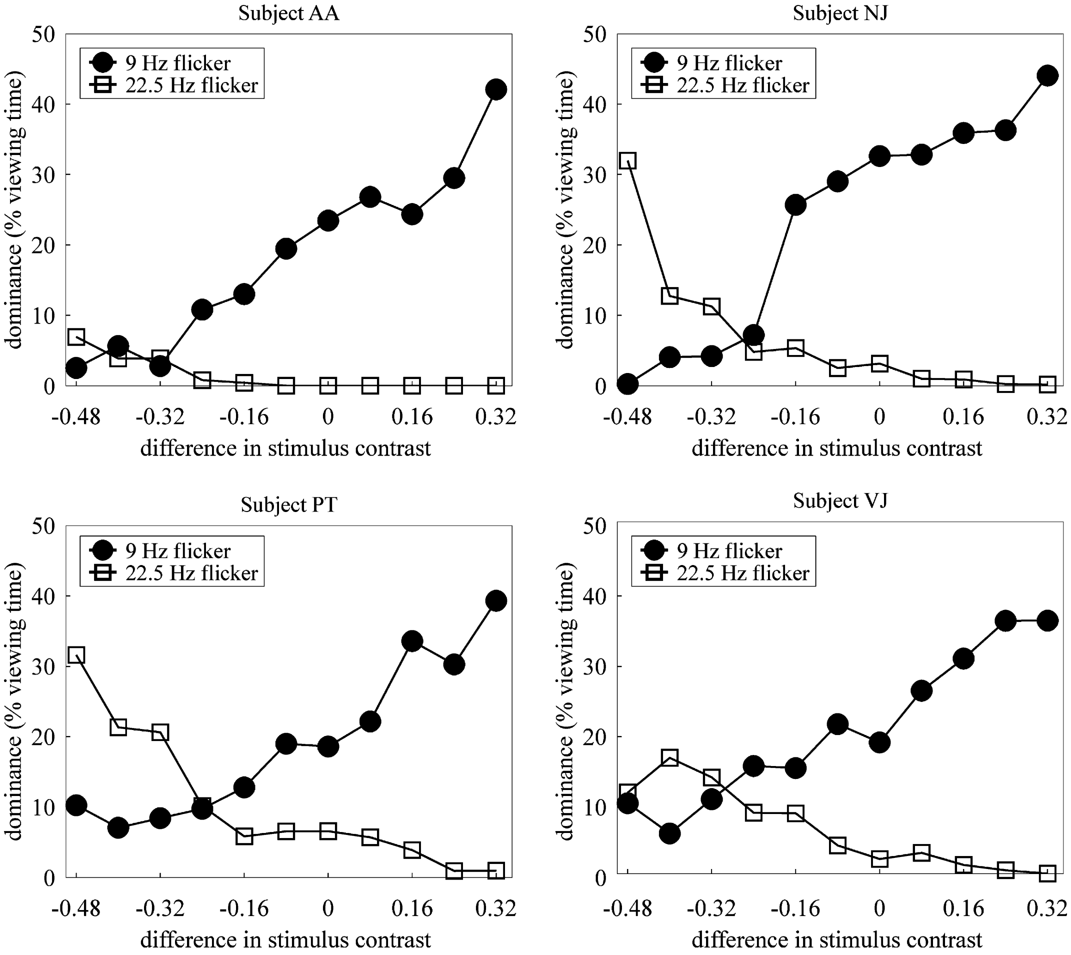

Fig. 5. Determination of the amount of contrast adjustment required to offset differences in stimulus strength due to temporal frequency. Subjects viewed pairs of non-switching orthogonal rivalrous gratings for periods of 1 min and continuously reported periods of dominance of each stimulus. One oblique stimulus was flickered at 9 Hz, and the other had 22.5 Hz flicker. When the contrasts of the stimuli were identical (corresponding to a value of zero on the *x*-axis), the 9 Hz stimulus was dominant more often than the 22.5 Hz stimulus. For negative contrast differences, the relative dominance of the 9 Hz stimulus decreased compared to the 22.5 Hz stimulus. The intersection of the two curves for each subject defines the point at which the two stimuli had equal levels of dominance in binocular rivalry. Graphs show an example experimental session for each subject.

perceptual alternations during IOS rivalry. Control trials were used both as training examples and as catch trials to insure that subjects were following the task instructions and to calibrate the rating scale. For congruent stimulation trials, both eyes viewed gratings that alternated between 45 and 135 deg orientation at 2.25 Hz, resulting in a fast regular perceptual alternation (1 on the rating scale). Conventional (non-switching) binocular rivalry between orthogonal gratings (45 and 135 deg) was used as an example of slow irregular alternations (6 on the rating scale). Subjects responded appropriately on catch trials (1.13 ± 0.06 for congruent stimulation; 5.77 ± 0.08 for non-switching rivalry), thereby validating the rating scale.

Baseline rating scale values were obtained by averaging responses to IOS rivalry stimuli with either 9 (Fig. 4C) or 22.5 Hz (Fig. 4D) flicker in both eyes/stimuli. The mean rating scale response across all four subjects for this baseline condition was 3.94. Given that the mean of the six-point rating scale was 3.5, this result indicates that the choice of contrast, spatial frequency, and stimulus switch rate in this experiment resulted in approximately equal probabilities of fast regular and slow irregular switching.

Tagging of either the eye or the grating orientation with different rates of flicker systematically shifted the perceptual alternation towards fast regular or slow irregular switching, respectively. Three of four subjects showed a decrease in rating scale values when the temporal frequency tags were associated with eye-of-origin (Fig. 6, “eye tag-uncorrected” bars) compared to when they were associated with stimulus orientation (Fig. 6, “orientation tag-uncorrected” bars). This difference between eye tagging and stimulus tagging was highly significant at the group level. In general, eye tagging caused a shift in subjective rating scale values towards the fast regular perceptual alternations that have been attributed to eye rivalry (Lee & Blake, 1999), while stimulus tagging shifted behavioral responses towards the slow irregular alternations associated with stimulus rivalry (Logothetis et al., 1996). Subject NJ showed little effect of temporal frequency tagging, regardless of whether the eyes or the orientations were tagged.

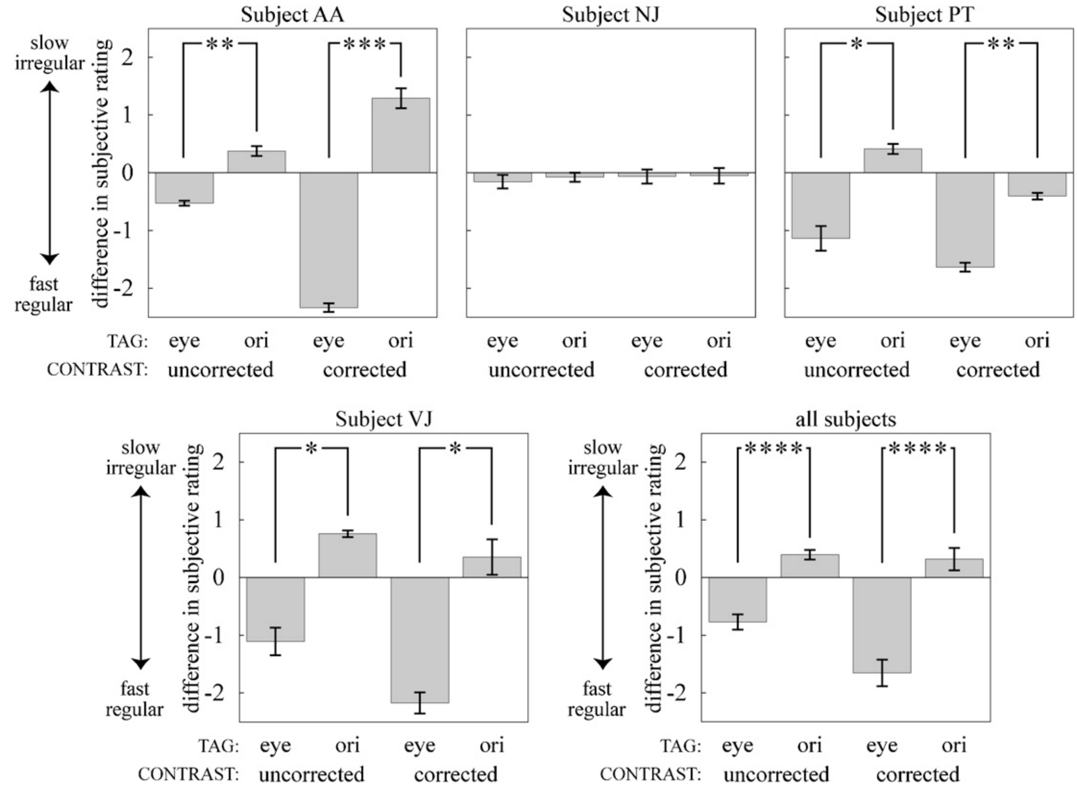

Fig. 6. Temporal frequency and contrast tagging of eye-of-origin or stimulus orientation biased perceptual alternation in IOS rivalry. Subjects used a six-point subjective rating scale to report the relative amounts of fast regular switching (rating of 1) versus slow irregular switching (rating of 6). Rating scale values are plotted relative to control baseline conditions in which both eyes and stimuli were flickered at 9 Hz (Fig. 4C) or 22.5 Hz (Fig. 4D), and a value of zero corresponds to the average of these control conditions. *Eye tag*, the stimuli presented to one eye had 9 Hz flicker, and the other eye's stimuli were continuously flickered at 22.5 Hz across multiple stimulus swaps (Fig. 4A). This resulted in a decrease in mean rating scale values relative to baseline, indicating a shift towards the fast regular perceptual alternations that have been attributed to eye rivalry. *Orientation tag*, one orientation was flickered at 9 Hz and the other at 22.5 Hz, independent of the ocular configuration (Fig. 4B). Orientation tagging enhanced slow irregular perceptual alternations, consistent with a shift towards stimulus rivalry. *Uncorrected*, contrast was 0.4 for both eyes and both stimuli. *Corrected*, contrast was added to the 22.5 Hz eye or stimulus and subtracted from the 9.5 Hz eye or stimulus to equate the stimulus strength of the eyes and of the stimuli. The amount of contrast correction was determined for each subject based on the procedure shown in Fig. 5. Contrast correction provided an additional tag that always corresponded to the temporal frequency tag applied to the eyes or to the orientations. The effects of temporal frequency tagging on perceptual alternation in IOS rivalry shown in the uncorrected conditions in this figure were increased by the addition of contrast tagging. $^{*}p < 10^{-3}$; $^{**}p < 10^{-4}$; $^{***}p < 10^{-5}$; $^{****}p < 10^{-6}$.

The responses of this subject on catch trials were similar to those of the other subjects, suggesting that this subject was correctly following the task instructions.

While these results clearly indicate that eye tagging enhanced fast regular switching and stimulus tagging enhanced slow irregular switching, there is an alternative interpretation of these data. Consider the outcomes in which the low temporal frequency stimulus almost always dominates perception in IOS rivalry. For eye tagging, the low temporal frequency stimulus would always be presented to the same eye, resulting in a predominantly monocular percept corresponding to fast regular switching—exactly the result shown in the "uncorrected" bars of Fig. 6. For the stimulus tagging case, the low temporal frequency stimulus would be associated with a particular orientation. In the extreme case, the subjects would perceive only the orientation associated with the low temporal frequency tag. In a more realistic case, there would be some periods of dominance of the high temporal frequency stimulus, but these would be briefer than the dominance phases for the low temporal frequency stimulus. The result of this would probably be a shift towards slow irregular switching—again corresponding to the results shown in the "uncorrected" bars of Fig. 6.

To eliminate the advantage that low temporal frequency stimuli have over stimuli with high flicker rates, the contrasts of the stimuli were adjusted based on perceptual reports during conventional (non-switching) binocular rivalry. Subjects viewed orthogonal oblique grating pairs and reported periods of dominance for the two stimuli. Fig. 5 shows the amount of dominance (% of viewing time) for the low (9 Hz) and high (22.5 Hz) flicker stimuli as a function of contrast differences between the two stimuli. The crossing point of the two curves represents the point at which the advantage of low temporal frequency in binocular rivalry is balanced by interstimulus contrast differences. The contrast differences corresponding to this intersection point were computed for all four subjects.

These contrast differences were used in contrast "corrected" trials in IOS rivalry, in which the same tagging procedure and behavioral report as the "uncorrected" trials were employed, but the 9 Hz stimulus had a lower contrast than the 22.5 Hz stimulus, based on the matching procedure shown in Fig. 5. The contrast differences always corresponded to the temporal frequency differences, so temporal frequency tagging of the eye also resulted in constant contrast differences in the two eyes over multiple stimulus switches. Similarly, stimulus tagging meant that a given orientation was associated with a particular temporal frequency as well as a particular contrast on a given trial.

If the results shown in the "uncorrected" bars of Fig. 6 were due to the fact that low temporal frequency stimuli dominate high temporal frequency stimuli in IOS rivalry, than equating the strength of the two stimuli by contrast adjustment should have eliminated the effects of eye and stimulus tagging. The "corrected" bars in Fig. 6 demonstrate that this was not the case: as for "uncorrected" trials, eye tagging with temporal frequency and contrast resulted in a shift towards fast regular switching compared to stimulus tagging. This was observed in three of four subjects and was highly significant at the group level.

In addition to eliminating the confound based on differences in stimulus strength due to temporal frequency, these data also support the notion that tagging can provide additional information that biases the type of competition in IOS rivalry towards eye or stimulus rivalry. For the group of four subjects, the difference between rating scale values for eye tagging and orientation tagging was 1.17 ± 0.16 in the uncorrected case, and this difference increased to 1.97 ± 0.30 when contrast differences were introduced. This enhancement of eye and stimulus tagging effects due to stimulus contrast differences was statistically significant (two-tailed t-test, $p < 0.05$). Notably, the effects of contrast tagging were primarily due to changes in perception during eye tagging. A comparison of the group rating scale reports for eye tagging trials revealed that the "corrected" stimuli resulted in significantly lower values (shift towards fast regular switching) compared to the "uncorrected" stimuli (two-tailed t-test, $p < 0.01$). No significant effects of contrast correction were observed at the group level for stimulus tagging trials.

It should be noted that although the group mean difference between eye and stimulus tagging represented a relatively small fraction of the 6 point rating scale (approximately 25% of the full range for uncorrected trials and 40% for corrected trials), this does not necessarily indicate that the perceptual differences between the eye-tagged and stimulus-tagged configurations were subtle or unimportant. First, the effects of eye and stimulus tagging were highly statistically significant, as described above. Second, the use of conventional binocular rivalry and congruent stimulation as training examples and catch trials served to compress the rating scale for the IOS rivalry stimuli. For example, subjects could only have reported a rating scale value of 1 for IOS rivalry if the perceptual alternations were indistinguishable from those occurring during congruent stimulation. If the subjects had made judgements based only on IOS rivalry stimuli, they presumably would have made use of more of the rating scale. However, in this case, the rating scale could have been calibrated differently across subjects, thereby increasing variability. By using training examples representing pure fast regular and slow irregular switching, we were able to fix the endpoints of the rating scale for all of the subjects, as verified by their responses on catch trials. One consequence of this is that the rating scale differences between eye and orientation tagging were probably reduced. However, our interpretation of the data depends on reliable shifts in perceptual alternations, not on the absolute rating scale differences.

In conclusion, temporal tagging of either the eye or stimuli systematically biased the type of perceptual alternation reported by subjects. Eye tagging enhanced perceptual alternations associated with eye rivalry, while stimulus tagging increased perceptual alternations associated with stimulus rivalry. These results suggest that the temporal frequency tag provides additional information that is used by the visual system to favor one of these forms of rivalry over the other.

4. General discussion

4.1. The role of transients in fast regular perceptual alternations in IOS rivalry

Interocular switching of dichoptic pairs of orthogonal gratings with high contrast, low spatial frequency, and slow switch rates tends to produce fast regular perceptual alternations that are time-locked to the stimulus swaps (Lee & Blake, 1999). This perceptual alternation is similar to what would be experienced if the IOS display was only viewed with one eye, suggesting that it may be due to interocular competition (Lee & Blake, 1999). However, both eyes are presented with the same periodic sequence of alternating orientations that differs by only a few hundred milliseconds in the two eyes, making it extremely difficult to link the percept at any given time with the inputs to the left eye, right eye, or some alternation between the two eyes.

An alternative to the eye rivalry account is based on the fact that each stimulus switch is associated with global orientation transients that could drive a perceptual switch from one orientation to the other. Abrupt transients delivered to a suppressed eye or stimulus can cause it to immediately become dominant during binocular rivalry (Blake et al., 1990; Walker & Powell, 1979), and brief flashes in background luminance can initiate perceptual switching in other bistable stimuli such as the Neckar cube and structure-from-motion stimuli (Kanai, Moradi, Shimojo, & Verstraten, 2005). In addition, brief presentation of a target stimulus followed by abrupt onset of a rivalrous pair of stimuli (Wolfe, 1984) or a textured surround (Wilke, Logothetis, & Leopold, 2003) can lead to perceptual suppression of the target. This flash suppression occurs for target presentation times as short as a few hundred milliseconds (Wilke et al., 2003; Wolfe, 1984), corresponding to the transient intervals employed in the present study. However, it should be noted that the results of Wolfe (1984) indicate that a wide range of adapting stimuli can result in perceptual suppression of a grating in the adapted eye, suggesting that the suppression is interocular in nature. Wilke et al. (2003), on the other hand, demonstrated that the flash suppression effect was reduced if the orientations or retinotopic locations of the adapting and test stimuli were significantly different (although suppression was much stronger if the textured surround and target stimuli were presented to different eyes).

If the abrupt changes in orientation associated with stimulus switches in IOS rivalry also cause the suppressed orientation to become dominant, this would result in fast regular perceptual alternations. We directly tested this hypothesis by introducing additional transients in the form of global orientation changes between interocular stimulus swaps. These transients had no effect on the rate of perceptual alternations, supporting the notion that the fast regular alternations in IOS rivalry are due to interocular competition.

4.2. Stimulus competition in binocular rivalry

The fact that IOS rivalry can produce periods of stable perception of a single orientation that persist over multiple interocular stimulus exchanges provides very good evidence that competition can occur between stimulus representations (Logothetis et al., 1996). During these periods of stable perception, both eyes view both the dominant and suppressed stimuli multiple times, eliminating any explanation based on interocular competition. The analog of this phenomenon in the spatial domain is interocular grouping, in which portions of the two eyes' inputs are combined to generate a perceptual alternation between coherent patterns (Diaz-Caneja, 1928; Kovács et al., 1996). It should be noted that experiments in which interocular swapping of small regions of stimuli was performed during interocular grouping have demonstrated a role for interocular competition as well (Lee & Blake, 2004).

Neurophysiological studies in monkeys have reported binocular neurons whose activity is modulated as a function of the dominant percept in binocular rivalry (Leopold & Logothetis, 1996; Sheinberg & Logothetis, 1997), but the activity of monocular neurons has been shown to reflect the physical presence or absence of the stimuli, independent of percept (Lehky & Maunsell, 1996; Leopold & Logothetis, 1996). These results provide evidence against perceptual selection based on interocular competition in binocular rivalry. Blood oxygenation level-dependent (BOLD) signal changes have been found to correlate with the percept in binocular rivalry in the blind spot representation in cortical area V1, an area that receives only monocular inputs (Tong & Engel, 2001). However, these BOLD signal changes could be due to modulatory top-down inputs from other cortical areas that may have only small effects on the firing rates of V1 neurons (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001).

4.3. Interocular competition in binocular rivalry

A number of studies have shown that detection of probe stimuli is impaired when the probes are presented to a suppressed eye, even when the probe does not share any features with the stimulus presented to the suppressed eye (Blake & Fox, 1974; Blake, Yu, & Lokey, 1998; Fox & Check, 1966, 1968; Wales & Fox, 1970). These studies suggest that suppression is non-selective over a wide range of stimuli and have been interpreted as evidence for eye rivalry. Additionally, single interocular stimulus exchanges cause the previously suppressed stimulus to immediately return to dominance (Blake et al., 1980). In other words, the dominant eye remains dominant following the stimulus exchange, consistent with eye rivalry. The summary of evidence for stimulus and eye rivalry presented here is far from comprehensive, and there are several reviews in the literature that provide more complete accounts (Alais & Blake, 2005; Blake & Logothetis, 2002; Logothetis, 1998; Tong, 2001).

4.4. Coexistence of stimulus and eye rivalry

A number of investigators have proposed that both eye and stimulus rivalry can take place and that they are resolved at different levels of the cortical hierarchy (Blake & Logothetis, 2002; Bonneh et al., 2001; Haynes & Rees, 2005; Ooi & He, 2003; Wilson, 2003). A computational model of IOS rivalry can generate two types of alternations, one time-locked to the stimulus switches and one that is stable over multiple stimulus switches (Wilson, 2003). The rapid switching is due to mutual inhibition between pools of monocular neurons, and the introduction of stimulus flicker overrides this inhibition, resulting in stimulus-based competition at a binocular second level (Wilson, 2003). Haynes & Rees (2005) trained a pattern classifier to accurately predict alternations in perception during dichoptic viewing of orthogonal colored rotating gratings, based on fMRI activity patterns in human early visual cortex. When the colors of the two stimuli were reversed in the two eyes, the predictions of the classifier fell below chance in cortical area V1 and remained above chance for area V3. This indicates that the activity patterns used by the classifier were based largely on eye-of-origin signals in V1 and stimulus features in V3 (Haynes & Rees, 2005).

Perhaps the most compelling evidence for the coexistence of eye and stimulus rivalry comes from a demonstration that both fast regular and slow irregular alternations can be simultaneously perceived (Bonneh et al., 2001). In this experiment, an array of small vertical grating patches were superimposed on an oblique large grating in one eye, while the other eye viewed the same pattern rotated 90 deg. On some trials, subjects reported both slow irregular alternations of the large background gratings and fast regular alternations of the small grating patches. These results are consistent with other experiments that demonstrate a transition between fast regular and slow irregular alternations based on a number of factors correlated with stimulus coherence in arrays of grating patches, including orientation uniformity and proximity of the patches (Bonneh et al., 2001).

4.5. Biasing perceptual alternations in IOS rivalry

The results from the present study extend existing findings by showing that labeling of either the eyes or the two stimuli can shift the type of perceptual alternation towards interocular or interstimulus competition, respectively. When differences in stimulus strength due to temporal frequency were eliminated by adjusting the contrast of the stimuli, the size of the tagging effects increased. This was probably due to the fact that the interocular or interstimulus contrast differences provided an additional eye or stimulus label that was consistent with the temporal frequency labels, thereby augmenting the effects of temporal frequency tagging. Crucially, the differences in temporal frequency and contrast introduced by the tagging procedure do not result in rivalry in the absence of dichoptic differences in contour orientation, color, or motion direction (Levelt, 1968; O'Shea & Blake, 1986).

More generally, the present results support a model of perceptual organization in which ambiguity in sensory inputs can be resolved by weighting evidence from different stimulus features. Further evidence for this model comes from experiments in which color was used to label stimulus orientation during IOS rivalry between orthogonal gratings. This color tagging procedure enhanced the incidence of the perceptual alternations characteristic of stimulus rivalry (Bonneh et al., 2001; Logothetis et al., 1996). For the IOS rivalry described in the present study, there appears to be an ambiguity based on two possible perceptual conflicts: incompatibility of eye-of-origin signals and of stimulus orientation. The results suggest that the visual system can process these conflicts differently, depending on the "evidence" favoring one or the other. Evidence for interocular competition can be experimentally provided by labeling eye-of-origin signals with temporal frequency and contrast. Similarly, labeling stimulus orientation biases the system towards competition between stimulus representations. In natural vision, it is likely that the many ambiguities in visual scenes are resolved by a similar weighting of evidence from various visual features.

Although the psychophysical tagging procedure employed in this study reliably biases perceptual alternations in a manner that is consistent with eye rivalry and stimulus rivalry, the behavioral data do not specify the levels of visual processing at which these alternations occur. In particular, the neural substrates underlying these two types of perceptual alternations are unknown. However, the ability to tag either eye-of-origin or stimulus inputs with temporal frequency and to observe corresponding differences in type of perceptual alternation raises the possibility of using this psychophysical method in neurophysiological experiments. Temporal frequency tagging has been used to label neural responses to rivalrous stimuli with both electroencephalography (Brown & Norcia, 1997) and magnetoencephalography (Srinivasan, Russell, Edelman, & Tononi, 1999; Tononi, Srinivasan, Russell, & Edelman, 1998). In these studies of conventional binocular rivalry, eye-of-origin and stimulus inputs were confounded. We have described a psychophysical method to dissociate eye-of-origin and stimulus inputs as well as the two types of perceptual alternations in IOS rivalry. This method lends itself well to physiological studies of the neural correlates of these two types of perceptual selection.

Acknowledgments

The authors thank Pedro Duay for excellent technical assistance and David Leopold for many helpful discussions.

References

Alais, D., & Blake, R. (2005). *Binocular rivalry*. Cambridge, MA: MIT Press.

Alais, D., O'Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception, 29*, 1437–1445.

Blake, R., & Fox, R. (1974). Binocular rivalry suppression: insensitive to spatial frequency and orientation change. *Vision Research, 14*, 687–692.

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience, 3*, 13–21.

Blake, R., Westendorf, D., & Fox, R. (1990). Temporal perturbations of binocular rivalry. *Perception and Psychophysics, 48*, 593–602.

Blake, R., Westendorf, D. H., & Overton, R. (1980). What is suppressed during binocular rivalry? *Perception, 9*, 223–231.

Blake, R., Yu, K., & Lokey, M. (1998). Binocular rivalry and motion perception. *Journal of Cognitive Neuroscience, 10*, 46–60.

Bonneh, Y., Sagi, D., & Karni, A. (2001). A transition between eye and object rivalry determined by stimulus coherence. *Vision Research, 41*, 981–989.

Brown, R. J., & Norcia, A. M. (1997). A method for investigating binocular rivalry in real-time with the steady-state VEP. *Vision Research, 37*, 2401–2408.

Diaz-Caneja, E. (1928). Sur l'alternance binoculaire. *Annals d'Oculistique, October*, 721–731.

Fox, R., & Check, R. (1966). Forced-choice form recognition during binocular rivalry. *Psychonomic Science, 6*, 471–472.

Fox, R., & Check, R. (1968). Detection of motion during binocular rivalry suppression. *Journal of Experimental Psychology, 78*, 388–395.

Haynes, J-. D., & Rees, G. (2005). Predicting the stream of consciousness from activity in human visual cortex. *Current Biology, 15*, 1301–1307.

Kanai, R., Moradi, F., Shimojo, S., & Verstraten, F. A. J. (2005). Perceptual alternation induced by visual transients. *Perception, 34*, 803–822.

Kovács, I., Papathomas, T. V., Yang, M., & Fehér, Á. (1996). When the brain changes its mind: Interocular grouping during binocular rivalry. *Proceedings of the National Academy of Sciences of the United States of America, 93*, 15508–15511.

Lee, S.-H., & Blake, R. (1999). Rival ideas about binocular rivalry. *Vision Research, 39*, 1447–1454.

Lee, S.-H., & Blake, R. (2004). A fresh look at interocular grouping during binocular rivalry. *Vision Research, 44*, 983–991.

Lehky, S. R., & Maunsell, J. H. R. (1996). No binocular rivalry in the LGN of alert macaque monkeys. *Vision Research, 36*, 1225–1234.

Leopold, D. A., & Logothetis, N. K. (1996). Activity changes in early visual cortex reflect monkeys' percepts during binocular rivalry. *Nature, 379*, 549–553.

Levelt, W. J. M. (1968). *On binocular rivalry*. The Hague: Mouton.

Logothetis, N. K. (1998). Single units and conscious vision. *Philosophical Transactions of the Royal Society of London B, 353*, 1801–1818.

Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivalling during binocular rivalry? *Nature, 380*, 621–624.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature, 412*, 150–157.

Ooi, T. L., & He, Z. J. (2003). A distributed intercortical processing of binocular rivalry: psychophysical evidence. *Perception, 32*, 155–166.

O'Shea, R. P., & Blake, R. (1986). Dichoptic temporal frequency differences do not lead to binocular rivalry. *Perception and Psychophysics, 39*, 59–63.

Robson, J. G. (1966). Spatial and temporal contrast-sensitivity functions of the visual system. *Journal of the Optical Society of America, 56*, 1141–1142.

Sheinberg, D. L., & Logothetis, N. K. (1997). The role of temporal cortical areas in perceptual organization. *Proceedings of the National Academy of Sciences of the United States of America, 94*, 3408–3413.

Srinivasan, R., Russell, D. P., Edelman, G. M., & Tononi, G. (1999). Increased synchronization of neuromagnetic responses during conscious perception. *Journal of Neuroscience, 19*, 5435–5448.

Tong, F. (2001). Competing theories of binocular rivalry: a possible resolution. *Brain and Mind, 2*, 55–83.

Tong, F., & Engel, S. A. (2001). Interocular rivalry revealed in the human cortical blind-spot representation. *Nature, 411*, 195–199.

Tononi, G., Srinivasan, R., Russell, D. P., & Edelman, G. M. (1998). Investigating neural correlates of conscious perception by frequency-tagged neuromagnetic responses. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 3198–3203.

Wales, R., & Fox, R. (1970). Increment detection thresholds during binocular rivalry suppression. *Perception and Psychophysics, 8*, 90–94.

Walker, P., & Powell, D. J. (1979). The sensitivity of binocular rivalry to changes in the nondominant stimulus. *Vision Research, 19*, 247–249.

Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron, 39*, 1043–1052.

Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of the National Academy of Sciences of the United States of America, 100*, 14499–14503.

Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research, 24*, 471–478.