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Distance in feature space determines exclusivity in visual rivalry

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Abstract

Visual rivalry is thought to be a distributed process that simultaneously takes place at multiple levels in the visual processing hierarchy. Also, the different types of rivalry, such as binocular and monocular rivalry, are thought to engage shared underlying mechanisms. We hypothesized that the amount of perceptual suppression during rivalry as measured by the total duration of fully exclusive perceptual dominance is determined by a distance in a neurally represented feature space. This hypothesis can be contrasted with the possibility that the brain constructs an internal model of the outside world using full-fledged object representations, and that perceptual suppression is due to an appraisal of the likelihood of the particular stimulus configuration at a high, object-based level. We applied color and stereo-depth differences between monocular rivalry stimulus gratings, and manipulated color and eye-of-origin information in binocular rivalry using the flicker & switch presentation paradigm. Our data show that exclusivity in visual rivalry increases with increased difference in feature space without regard for real-world constraints, and that eye-of-origin information may be regarded as a segregating feature that functions in a manner similar to color and stereo-depth information. Moreover, distances defined in multiple feature dimensions additively and independently increase the amount of perceptual exclusivity and coherence in both monocular and binocular rivalry. We conclude that exclusivity in visual rivalry is determined by a distance in feature space that is subtended by multiple stimulus features.

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1. Introduction

In perceptual rivalry perception alternates between several more or less equally valid interpretations of a stimulus that are mutually exclusive. The fact that the stimulus remains the same while phenomenal perception changes has resulted in great interest from researchers attempting to investigate the neural correlates of visual awareness (Blake & Logothetis, 2002; Leopold & Logothetis, 1999). In several types of rivalry, orthogonal gratings are presented to the observer. These gratings may be presented dichoptically, resulting in binocular rivalry between the two eyes' images (Wheatstone, 1838), or dioptically, resulting in monocular rivalry between the two grating patterns (Breese, 1899). Binocular rivalry has traditionally been cat-

egorized separately from monocular and other types of perceptual rivalry, occupying a category of its own, because of the evident low-level and eye-based characteristics of binocular rivalry suppression (Blake, 1989; Blake, Westendorf, & Overton, 1980). Not consciously accessible as an independent information source (Helmholtz, 1910–1924), the eye-of-origin information that plays a role in binocular rivalry is represented in low-level neural structures that subserve interocular gain control (Ding & Sperling, 2006; Sengpiel & Vorobyov, 2005). However, it is also widely accepted that the mechanisms behind rivalrous alternations are multifaceted (Alais & Parker, 2006; Freeman, 2005; Grossmann & Dobbins, 2006) and must span multiple functional areas in the brain (Blake & Logothetis, 2002). This is evidenced by the fact that both the occurrence and the strength of binocular rivalry suppression are subject to contextual modulation through center-surround (Paffen, Alais, & Verstraten, 2005), grouping mechanisms (Alais & Blake, 1999) and perceptual meaning (Andrews

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& Lotto, 2004). Monocular or pattern rivalry is also subject to center-surround pattern completion interactions (Maier, Logothetis, & Leopold, 2005). Not only are the mechanisms behind perceptual rivalry generally considered to be distributed, there is also evidence that the different types of visual rivalry are dependent on shared neural circuitry (Bonneh, Sagi, & Karni, 2001; Logothetis, Leopold, & Sheinberg, 1996; Pearson & Clifford, 2005; Wilson, 2003).

There are many examples of rivalrous stimuli for which the rate of perceptual alternations depends on the strength of the conflict between them (Brouwer & van Ee, 2006; Hupe & Rubin, 2003; van Ee, van Dam, & Erkelens, 2002). When contrast, the main determinant of interocular gain control (Ding & Sperling, 2006), is decreased in a binocular rivalry stimulus, the source of conflict decreases in strength, resulting in fusion of the two stimulus half-images: plaid percepts (Liu, Tyler, & Schor, 1992). We hypothesized that, as a general mechanism, the neural inhibition that results in completeness of perceptual suppression during visual rivalry is determined by a distance in a low-level neurally represented space subtended by features such as orientation, color, or eye-of-origin information, before these features are integrated into object representations. Our hypothesis can be contrasted with the possibility that the brain constructs an internal model of the outside world, and that perceptual suppression is due to an appraisal of the stimulus configuration likelihoods in this internal model based on the properties of fully elaborated object representations. This latter hypothesis would imply that rivalry acts at a relatively high neural level as opposed to a feature-based hypothesis, which assumes that integration and suppression occur at lower levels in the visual processing hierarchy. To test our hypothesis, we parametrically varied the feature-based distance between the two grating patterns of a monocular rivalry stimulus by applying distances in both stereo-depth and color feature spaces.

Color differences between stimulus gratings affect the speed of monocular pattern rivalry alternations (Wade, 1975), as does the angle between the stimulus gratings (Crassini & Broerse, 1982; Mapperson & Lovegrove, 1978). The stereo-depth difference causes the gratings to appear at different depths. This change in stimulus configuration strongly decreases the likelihood that the two gratings coincide spatially. Real-world occlusion constraints play a profound role in determining whether binocular rivalry occurs at any location in the visual field (Ooi & He, 2006; Shimojo & Nakayama, 1990), and the addition of stereo-depth difference provides a way to assess the role of depth ordering in monocular rivalry. If, for instance, the likelihood of real-world conflict (i.e. a collision in three dimensional space) between the stimulus gratings when represented as objects, plays a definitive role in the generation of perceptual suppression, the amount of time spent in fully exclusive perceptual dominance should decrease as a result of the addition of stereo-depth differences. Conversely, our hypothesis regarding the distance in a low-level feature space between the neural representations of the two

gratings predicts that the amount of fully exclusive perceptual rivalry must increase.

Another issue is whether in binocular rivalry, eye-of-origin information can be seen as a segregating signal, much as we regard color and stereo-depth differences. That is, we wanted to investigate whether a difference in eye-of-origin combines with other stimulus features to produce perceptual suppression. Recently a new type of presentation paradigm has been developed in which the stimulus presentation is dichoptic and the stimulus halves are switched between the eyes at 3 Hz while being flickered at a rate of ca. 20 Hz (Logothetis et al., 1996). This flicker & switch (F&S) rivalry presentation may, when using the right stimulus conditions (Bonneh et al., 2001; Lee & Blake, 1999), result in percepts that survive switches between the eyes, implying that perceptual suppression is not eye-image based but based on pattern identity under these conditions. The fact that eye-of-origin information is dissociated from alternations in visual awareness allows us to specifically address the role of eye-of-origin information as a segregating feature in binocular rivalry by varying color differences between dichoptically presented orthogonal gratings in situations of binocular and F&S rivalry.

Total dominance time is a measure of the vehemence of the rivalry process as it is defined by the lack of intermediate, non-exclusive states such as fused plaid percepts or piecemeal rivalry.¹ In our experiments, we have used the sum of all perceptual durations in which observers reported a completely exclusive percept as a measure for the completeness of suppression. So, observers were reporting full suppression of one grating and the concomitant full dominance of the other grating, a phenomenon we refer to as full exclusivity. The dependent variable in our experiments was the sum of the durations of full exclusivity in any one trial, divided by the duration of that trial, yielding the 'full exclusivity fraction'.²

¹ In monocular and binocular rivalry the complementary percepts of what we term full exclusivity constitute different perceptual impressions. The complement of full exclusivity in binocular rivalry is characterized by a spatial break-up of exclusive perception such that the observer's percept is dominated by one stimulus half-image at a certain spatial location, whereas the other stimulus half-image dominates the remainder of the spatial extent of the stimulus. This type of perception is called piecemeal rivalry, as opposed to the wholesale or coherent perceptual dominance that we term full exclusivity. Therefore, in the case of binocular rivalry, 'full exclusivity' could be exchanged with 'coherence'. In monocular rivalry however, the percept seen when perception is not fully exclusive is a fusion of the two constituent gratings into a plaid pattern. In contrast, these types of plaid pattern percept do not occur in binocular rivalry apart from the first 150 ms of presentation (false fusion, [Blake, Yang, & Westendorf, 1991]), and/or at very low stimulus contrasts [Liu et al., 1992]. In the case of monocular rivalry, the most coherent possible percept is a mixture of the two grating patterns fused to a plaid percept and because of this, we cannot use the phrase 'coherence' but refer to this most exclusive perceptual state as 'full exclusivity' in both binocular and monocular rivalry.

² Note that what we term 'full exclusivity' does not imply strength of suppression as defined by the difference in detection or discrimination threshold during either dominance or suppression of the percepts. This long-standing method [Fox & Check, 1972] for probing the depth of suppression during binocular rivalry directly probes the strength of gain-control [Alais & Parker, 2006; Alais & Melcher, 2006], whereas in our research we have not.

2. Methods

2.1. Apparatus and stimuli

Eight observers participated in the different experiments, one of whom was aware of the hypotheses (author T.K.). At least six observers participated in each condition. All had normal or corrected-to-normal vision, and could reliably discern the stereo-differences in our stimuli. Subjects viewed orthogonal grating stimuli through a mirror stereoscope at a viewing distance of 47 cm. The stimuli were presented on a 22" LaCie monitor (1600 × 1200 75 Hz) with linear γ using custom software.

A rendering of a monocular rivalry stimulus is shown in Fig. 1. Centrally a fixation mark was projected, composed of half-rectified concentric circular sine-wave gratings with a gaussian envelope and a total visible size of 1.4. Surrounding the fixation mark a gaussian enveloped (eccentricity μ 1.8, σ 0.4) annulus filled by a plaid consisting of half-rectified sine-wave grating (spatial frequency 1.1 cycles/degree) patterns was drawn. The background was black (luminance 0.0 cd/m²), and a surrounding pattern (white, luminance 69.8 cd/m²) of crosses together with a concentric circle directly surrounding the stimulus provided ample aid for correct binocular fusion, and a reference for any disparity signal in the stimulus. To control one segregating signal, the colors of the gratings making up the plaid were varied from isochromatic (i.e. both were yellow) to full color difference (i.e. one was green, one was red) in eight steps. Care was taken to ensure objective isoluminance of both gratings in all color separation conditions. A control experiment with patterns made subjectively isoluminant using a flicker isoluminance test showed highly similar results in two subjects (data not shown). Peak luminance of the plaid was 12.6 cd/m² at the junctions, and each grating had a peak luminance of 6.3 cd/m².

Stereo-depth differences between the two gratings were implemented by varying the spatial phase of the gratings between the eyes to a maximum of 0.15 disparity in four steps. In a control experiment we examined the possible effect of vergence eye position by placing the fixation mark in the stereoscopic depth plane of either the nearer or farther grating.

For the second experiment, a binocular rivalry stimulus was constructed by projecting one of the monocular rivalry gratings in each eye, with orthogonal orientations. Peak luminance of these gratings was set to 12.6 cd/m² to equate the total amounts of luminance in the stimuli of binocular and monocular rivalry conditions. Binocular rivalry stimuli were presented under conditions of normal continuous viewing, synchronous on-off flicker at 19 Hz, and flicker and switch stimulation, during which the stimulus was flickered at 19 Hz and the monocular half-images were switched between the eyes with a full period of 660 ms, i.e. the dura-

tion of each of the two eye-pattern combinations was 330 ms. Note that this means that the pattern in both eyes is replaced at 3 Hz, whereas a full cycle takes place at 1.5 Hz.

2.2. Procedure

In all experimental sessions the subjects' task was identical; Subjects were instructed to fixate the fixation mark and report the orientation of the dominant grating percept by depressing keys. They were specifically instructed not to press when either a plaid, piecemeal rivalry, or rapid 3 Hz alternations were perceived. When debriefed, none of the subjects reported problems regarding binocular fusion during the experiment, nor did stereoscopic depth and color engage in independent rivalry. As we were interested in the mechanisms that cause perceptual exclusivity or coherence, our main measure was the total fraction of a trial during which exclusive perceptual dominance was experienced. We calculated this measure by summing all the perceptual durations in a single trial, and divided this number by the total duration of that trial. In all sessions, trial duration was 30 s, and each combination of presentation regime and color or stereo-depth difference was tested twice, once for each of the orientation-color combinations. Subjects completed three sessions, amounting to approximately 2.5 h in total.

3. Experiment 1: Monocular rivalry

Subjects viewed stimuli such as those depicted in Fig. 1 and continuously reported periods of full perceptual exclusivity, meaning that when a plaid or piecemeal rivalry was perceived, no keys were pressed. The exclusive dominance durations were summed and divided by the total trial duration to yield the 'fraction of full exclusivity'. This fraction is better suited than alternation rate to probe the prevalence of intermediate perceptual states such as a plaid percept, or piecemeal rivalry percepts. We independently varied grating separation using stereo-depth differences and color differences between the two grating patterns.

3.1. Results

Our results, shown in Fig. 2a, demonstrate that the combination of stereoscopic depth differences and color differences increases the amount of full perceptual exclusivity, in some subjects to the point where the suppression likens binocular rivalry suppression in completeness and rate. The strengthening of perceptual exclusivity due to increased stereoscopic depth differences is evidence for the conjecture that pattern rivalry suppression is determined by distance in feature space and not by an evaluation of the three dimensional positions of objects (that is, at a high level of abstraction). Thus, real-world spatial relationships such as likelihood of spatial grating coincidence do not play a role in the generation of suppression in our stimuli. In addition, we find that there is no predominance of the near-plane percept that could be the result of real-world occlusion or depth-ordering constraints such as those that occur in suppression based on surface completion (Graf, Adams, & Lages, 2002; Maier et al., 2005). We also conducted a control experiment in which the fixation mark was placed in the depth plane of either the near or far stimulus plane. Fig. 2b shows the data from this con-

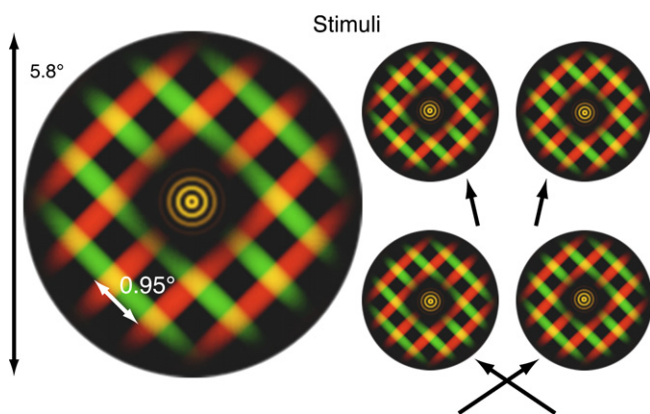


Fig. 1. Monocular rivalry stimulus. The fixation mark, consisting of concentric circles, ensures stable fixation and also provides a reference for stereoscopic signals. This rendering illustrates the maximum color difference between the two gratings. Free-fusing leads to a stereo-depth difference between the red and green gratings, which greatly increases the strength of suppression. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

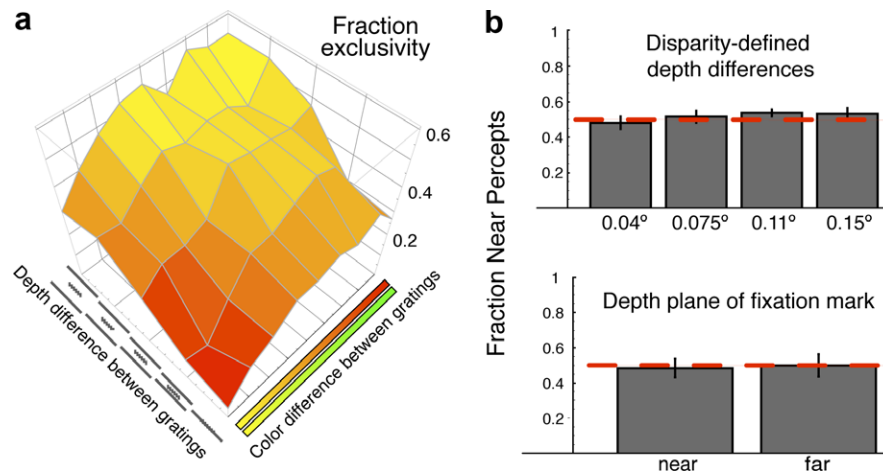


Fig. 2. (a) Monocular rivalry; exclusivity increased due to both color and stereo-depth differences results of experiment 1 plotted as full exclusivity fraction versus both color and stereoscopic depth differences between stimulus gratings. Fraction full exclusivity indicate the fraction of time subjects reported complete perceptual suppression. This measure of the amount of exclusivity combines the rate and duration of perceptual dominance periods. Both stereoscopic depth differences and color differences increase this measure, lending credence to the proposition that it is distance in a feature space that causes perceptual suppression. Moreover, the two signals additively increase the amount of exclusivity which points towards a role for distributed processing of various signals as the source of perceptual suppression. Values indicate the mean over 7 subjects. (b) No effects of depth ordering and vergence eye position; experiment 1. Top: If the rivalrous alternations that subjects reported were influenced by the depth ordering of the planes (or inferences regarding occlusions) a difference in the preponderance of near-plane and far-plane percepts should result from this influence, as has been reported for other stimuli (Graf et al., 2002; Maier et al., 2005) that rely on surface-completion for suppression. The most likely result would be a near-plane predominance bias that increases with stereoscopic depth difference. To investigate this, we took the total amount of time spent in both near-plane and far-plane percepts for all stereo-depth differences separately and calculated the ratio between the two, a measure of near-plane predominance bias. This ratio of near and far percepts is not influenced by the stereoscopic depth difference between the gratings $F(4, 30) = 1.1, p = .4$. Thus, depth ordering does not influence the predominance of the near-plane and far-plane percepts. Values indicate the mean ± 1 SEM over 8 subjects. Bottom: Changing the depth of the fixation mark to that of either the near or far plane does not affect the near/far ratio. To provide a control for the possible effect of vergence eye position on the ratio of near and far plane percepts, we changed the stereoscopic depth of the fixation mark to that of either the near or the far plane. Placing the fixation mark in either front or back plane does not change the ratio of near to far planes ($p > .8$). Together, these control results indicate that there is no effect of either depth ordering or vergence eye position on the distribution of near-plane and far-plane percepts. Values indicate the mean ± 1 SEM over 6 subjects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

control experiment, demonstrating that there is no effect of vergence eye position on the predominance of the near and far patterns.

Both color difference (Andrews & Purves, 1997; Kitterle & Thomas, 1980) and stereo-depth difference influence suppression (Fig. 2a), evident in our data from the fact that near-monotonic increases in full exclusivity fraction result from increases in either segregating signal. The effects of both features on the amount of exclusivity are additive and independent. The effects of color and stereo-depth difference are both significant ($F(4, 270) = 8.5, p < .001$; $F(8, 270) = 4.2, p < .001$), but the interaction between the two is not ($F(32, 270) = 0.24, p = 1.0$). These results can be easily seen in Fig. 2a, where at the highest level of color-separation the use of stereo-depth differences produces an almost identical increase in exclusivity as it does with no color-differences present, and vice versa.

4. Experiment 2: Binocular rivalry

To investigate whether eye-of-origin information can be seen as a segregating signal that functions in a way similar to color difference or stereo-depth difference we specifically disengaged eye-of-origin information as a signal by means of the F&S paradigm. We predict that under normal view-

ing conditions, eye-of-origin information must interact with color, in which interaction color must play a role, contrary to what has been found before (Wade, 1975). When eye-of-origin information is no longer involved in the generation of perceptual suppression, however, we expect that the role of color will equal that of color in a monocular rivalry stimulus with 0 stereo-depth difference between the gratings (experiment 1).

In this second experiment, we parametrically varied color differences between dichoptically presented (binocularly rivaling) gratings. The gratings were presented either continuously, with 19 Hz on-off flicker, or with F&S stimulation in which the stimuli were swapped between the eyes at 3 Hz and flickered at 19 Hz. Monocular rivalry stimuli with no stereo-depth difference were used as a reference condition.

4.1. Results

Fig. 3 shows that both normal and flickered binocular rivalry exhibit a strong saturation, in the sense that the fraction of full exclusivity (coherence) will generally not exceed 0.8 due to the durations of the transitions between percepts. The fact that several studies (Kitterle & Thomas, 1980; Thomas, 1978; Wade, 1975) have found no effect of

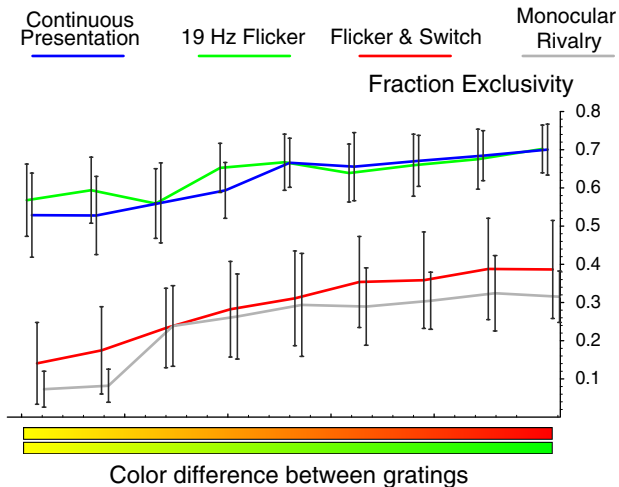


Fig. 3. Effects of color difference on binocular and pattern rivalry exclusivity. Colored lines represent conditions of normal binocular rivalry, flickering binocular rivalry, and pattern rivalry. These fall in two categories based on relative color-difference sensitivity. Binocular rivalry, flickering and continuously presented, remains close to saturation, but nevertheless shows a significant positive correlation with color difference. For both types of pattern rivalry the total amount of exclusivity is less, but the relative degree of modulation due to color differences is far greater than for binocular rivalry. Data represent the mean \pm 1 SEM over 7 subjects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

color differences on binocular rivalry rate with orthogonal gratings may be due to this saturation, which may be even greater when using smaller stimuli, because the use of smaller stimuli limits the amount of piecemeal rivalry (Bonneh et al., 2001; O'Shea, Sims, & Govan, 1997). Since piecemeal rivalry is a major complementary percept of full exclusivity (especially in binocular rivalry), larger stimuli allow for a greater increase in perceptual coherence due to color differences.

We find that the amount of suppression in both flickered and normal binocular rivalry is positively and significantly correlated with color difference between the stimulus gratings (Spearman's ρ for 71 *df*, 0.42 and 0.43, respectively, $p = .0001$ and $p < .0001$). The difference between situations in which rivalry is based on interocular differences (continuous and flickered binocular rivalry) and situations in which suppression is based on pattern (F&S and monocular rivalry) clearly demonstrates that eye-of-origin information is a very strong feature on which perceptual suppression is based, consistent with its low-level origins. As in experiment 1, a two-way ANOVA with interactions shows that whereas both the effects of color difference ($F(8, 261) = 6.5$, $p < .001$) and the effect of pattern/eye difference ($F(1, 261) = 4.6$, $p < .05$) are significant, their interaction is not ($F(8, 261) = 0.65$, $p = .74$).

The dependence of the amount of exclusive perception on both eye-of-origin information and color differences between gratings indicates that in binocular rivalry, too, multiple information sources contribute to the generation of perceptual exclusivity. Although eye-of-origin informa-

tion is a very strong and low-level segregating feature, it plays its role according to the rules of suppression based on distance in multiple feature spaces.

5. Discussion

We asked whether the strength of conflict in pattern rivalry is due to mere feature-based division between the gratings, or depends on a real-world model that the brain may construct based on the inferred spatial properties of object representations. Our data strongly favor the feature-based hypothesis, according to which rivalry is dependent on the amount of 'evidence' (independent of the cue that causes it) of the separation of two grating patterns.

There is no influence of depth order on our results. This independence of spatial scene layout implies that in our experiment, suppression occurs at relatively early neural levels at which depth ordering does not play a substantial role. This finding can be contrasted to prior results (Maier et al., 2005), where the amount of perceptual suppression reported was influenced by the depth order in the stimulus. However, as Maier et al.'s stimuli depended critically on contextual filling-in of suppression, their findings are likely the result of higher-level center-surround interactions.

Furthermore, the results of the control experiment in which we varied the position in depth of the fixation mark demonstrates that the increase in the amount of exclusive perceptual suppression due to separation in depth is independent of the depth-plane of fixation. Regarding eye posture, it has been suggested (Georgeson, 1984; Georgeson & Phillips, 1980), that there is a significant role for eye movements in the dynamics of monocular rivalry due to the fact that eye movements cause shifts in the retinal image, thereby causing interactions between negative after-images and stimulus patterns. This cannot provide a full explanation for perceptual switches during monocular rivalry, however, since these switches also occur with afterimages (Bradley & Schor, 1988; Crassini & Broerse, 1982) and without eye movements (van Dam & van Ee, 2006). In our experiments, if fixation were alternately on the depth planes of near and far planes, these eye movements would equally promote dominance of both stimulus bar patterns, as both would shift by equal amounts in the two eyes due to the fact that grating orientations in both eyes were $\pm 45^\circ$. Therefore, eye movements between the different depth planes of our stimuli cannot explain our results.

The dismissal of eye-of-origin information from binocular rivalry by use of the F&S stimulation paradigm increases the relative importance of color differences between the two grating patterns. Both F&S and monocular rivalry have been coined "pattern rivalry" (Logothetis et al., 1996; Maier et al., 2005) to illustrate the higher, eye-independent origins of the perceptual suppression that occurs. Under F&S and monocular pattern rivalry conditions, the data show a very similar monotonic increase in suppression due to the increase in color difference between the grating patterns. This correspondence between the two

types of eye-independent pattern rivalry may point to a common neural mechanism, one at which eye-independent orientation detectors engage in mutual inhibition.

Stimulus flicker does play a role in the effects of the F&S manipulation (Lee & Blake, 1999) and also increases the occurrence of interocular grouping in binocular rivalry (Knapen, Paffen, Kanai, & van Ee, 2007). However, in our experiment 2 it is the eye-swap operation that effectively eliminates eye-of-origin information as a segregating feature, suggesting a prominent role for the eye-swap transient in generating percepts that mimic normal binocular rivalry in duration. This finding is hard to reconcile with models that describe F&S rivalry (Wilson, 2003), according to which it is the flicker that causes binocular rivalry to transpire on a higher, eye-independent level and the eye-swap procedure is merely necessary to bring the resulting eye-independence to light.

The large differences in color sensitivity between rivalry based on eye and rivalry based on pattern suggest that whereas binocular rivalry may be the result of the processes that underlie interocular matching (Carlson & He, 2004; Ooi & He, 2006) and are sensitive to patterns that occur in binocular occlusion situations (Shimojo & Nakayama, 1990), pattern rivalry is more likely the result of scene segmentation mechanisms (Boutet & Chaudhuri, 2001; Maier et al., 2005).

The different information sources (color, stereo-defined depth and eye-of-origin) we used in our experiments independently affect the strength of perceptual suppression as measured by the total amount of exclusive perception. This implies that there is an important role for integrated distributed processing based on the representation of multiple information sources in the generation of perceptual suppression as measured by perceptual exclusivity.

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