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Stimulus flicker alters interocular grouping during binocular rivalry

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Abstract

When the two eyes are presented with sufficiently different stimuli, the stimuli will engage in binocular rivalry. During binocular rivalry, a subject's perceptual state alternates between awareness of the stimulus presented to the right eye and that presented to the left eye. There are instances in which competition is not eye-based, but instead takes place between stimulus features, as is the case in flicker and switch rivalry (F&S). Here we investigate another such instance, interocular grouping, using a Diaz–Caneja type stimulus in conjunction with synchronous stimulus flicker. Our results indicate that stimulus flicker increases the total duration of interocularly bound percepts, and that this effect occurs for a range of temporal flicker frequencies. Furthermore, the use of contrast-inversion flicker causes a decrease of total dominance duration of the interocularly bound percepts. We argue that different flickering regimes can be used to differentially stimulate lower and higher levels of visual processing involved in binocular rivalry. We propose that the amount of interocularly combined pattern-completed percept can be regarded as a measure of the level at which binocular rivalry is resolved.
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1. Introduction

There has been ongoing debate regarding the nature of binocular rivalry, the process of perceptual alternation that occurs when the two eyes view sufficiently different stimuli (Blake & Logothetis, 2002; Leopold & Logothetis, 1999). One subject of debate is whether suppression during binocular rivalry acts on eye-based representations or on higher level representations dependent on stimulus properties.

The first view is substantiated by the fact that when an eye is suppressed, detection thresholds in a range of modalities are increased in the suppressed eye (Fox & Check, 1968, 1972; Wales & Fox, 1970). Also, when the monocular half-image stimuli are switched between the eyes, perception will follow the switches as if suppression during rivalry were based on the eyes' images (Blake, Westendorf, & Overton, 1980). Furthermore, BOLD responses in the V1

blind spot have been shown to correlate with perceptual alternations during binocular rivalry (Tong & Engel, 2001). Since the blind spot in V1 receives solely monocular afferents, this is strong evidence for a monocular basis of binocular rivalry suppression.

There is, however, also evidence supporting the contrary hypothesis. Data from monkey physiology suggest that the suppression during binocular rivalry increases up the visual hierarchy, with relatively little percept-dependent modulation of cell activity in V1 (Leopold & Logothetis, 1996). Psychophysical examples of 'stimulus', or 'pattern' rivalry can be divided into two categories: interocular grouping and flicker and switch (F&S) rivalry. Interocular grouping occurs when the stimuli used in binocular rivalry are spatially non-uniform but can be recombined between the eyes such that uniform shapes may alternate in subjects' perception (Kovacs, Papathomas, Yang, & Feher, 1996, but also see Lee & Blake, 2004). Thus, perception alternates not between images projected into each eye, but between higher-level interpretations of the stimuli. F&S rivalry

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results from a stimulus presentation technique that is composed of two operations, both of which are necessary to create F&S rivalry. The first is to flicker the stimulus, in an on–off regime, at frequencies of 15–20 Hz. Second, the stimulus' monocular half-images are swapped between the eyes at 1.5 Hz, i.e. presentation periods are 333 ms in each eye. The effect of the combination of these operations is that subjects perceive 'normal' binocular rivalry (Logothetis, Leopold, & Sheinberg, 1996), instead of the perceptual alternations at 3 Hz predicted by an eye-based suppression hypothesis of binocular rivalry. Although dependent on a limited range of stimulus parameters (Lee & Blake, 1999, but see Bonneh, Sagi, & Karni, 2001), this phenomenon is a strong indicator that binocular rivalry can indeed occur between representations of stimulus features, and can occur independently of the stimulated eye.

We used a novel stimulus paradigm, consisting of a combination of interocular grouping and the flicker component of F&S rivalry to investigate whether stimulus flicker increases interocular grouping. To this end, we used the stimulus first conceived by Diaz–Caneja (1928), (translated by Alais, O'Shea, Mesana-Alais, & Wilson, 2000), shown in Fig. 1A. This stimulus type (which is in our case composed of horseshoe-shaped gratings presented to each eye) has been used previously, for instance to investigate the importance of interhemispheric connections during rivalry (O'Shea & Corballis, 2005). Aside from perceiving eye-based binocular rivalry between the horseshoe shapes, subjects viewing this stimulus report percepts of full circles and full line patterns. These percepts are the result of interocular grouping and pattern completion. Note that these percepts differ from F&S rivalry percepts in the way in which

they are a result of eye-independent information. In F&S rivalry, the information from the two eyes is combined temporally, leading to percepts that are based alternatingly on the right eye image and the left eye image and are in this manner independent of the stimulated eye. In pattern completion dependent on interocular grouping, information from the two eyes is combined spatially, resulting in percepts of shapes that obey, for instance, the principle of collinearity more strongly than do the respective monocular images. Both stimulus paradigms, however, elicit 'pattern rivalry' percepts that are independent of the monocular half-images and thus can be used for the investigation of the eye-dependence of binocular rivalry.

Our stimuli combine characteristics of both of these stimulus presentation paradigms and are, because they lack switches between the eyes, specifically suited for the investigation of the effects of the temporal properties of the flicker component on interocular pattern combination. We conducted three experiments designed to investigate the influence of stimulus flicker on the preponderance of interocular pattern combination. After a first proof of principle experiment, we altered temporal frequency of on–off flicker in a second experiment and also changed the type of flicker while leaving the frequency content identical in a third experiment. We show that interocular pattern combination increases due to stimulus flicker; that this effect is independent of temporal frequency; yet does depend on the on–off transients that accompany on–off flicker.

2. Experiment 1: stimulus flicker increases interocular grouping

2.1. Methods

Six observers participated in the experiment, one of which was aware of the hypotheses (author TK). All had normal or corrected-to-normal vision. They viewed the dichoptic stimuli, renderings of which are depicted in Fig. 1A, through a mirror stereoscope at a viewing distance of 57 cm. The stimuli were presented on a 22 in. LaCie monitor running at a resolution of 1600×1200 and a refresh frequency of 75 Hz, driven by an Apple G4 computer using custom software. The background was black (luminance 0.06 cd/m^2), and a surrounding pattern (white, luminance 71.9 cd/m^2) of crosses together with concentric circles directly surrounding the stimulus provided ample aid for correct binocular fusion. Stimuli were composed of circular patches (diameter 1.6 degrees) of sine-wave luminance-modulated gratings, either concentric or linear. Grating contrast was set to 75% Michelson; spatial frequency of the gratings was 5.5 cycles/degree. Gratings were bisected along the vertical meridian and recombined to produce the horseshoe shaped Diaz–Caneja stimuli. Under flicker conditions, stimuli were presented to both eyes for 2 frames, alternating with blanks of 2 frame durations resulting in a symmetric 18 Hz flicker which was in phase across both eyes.
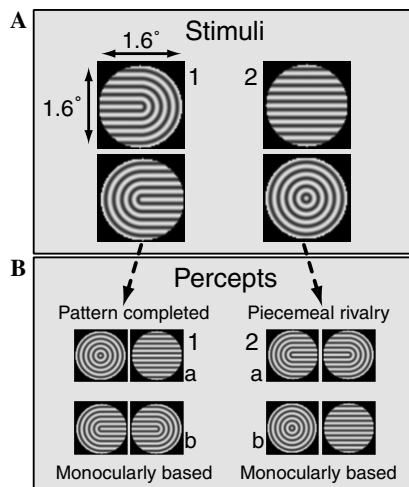

Fig. 1. Stimuli and accompanying percepts. (A) Renderings of the stimuli used in the experiments, each of which was presented to one eye while the other stimulus was presented to the other eye; (1) The Diaz–Caneja type horseshoe-shaped stimuli. (2) The circle and line stimuli. (B) Possible percepts for stimuli from panel (A1) a, pattern completion percepts (reported as circle and line percepts) b, monocularly based percepts (reported as horseshoe percepts) (A2) a, piecemeal rivalry percepts (reported as horseshoe percepts) b, monocularly based percepts. (Reported as circle and line percepts.)

The task was as follows: subjects reported percepts of either circles or lines separately by pressing buttons on the keyboard. The durations of buttonpresses were recorded separately for each type of percept. Note that for circle and line stimuli these are monocularly based percepts, whereas for horseshoe stimuli these are pattern-completed percepts (Fig. 1B). The order of trials in a session, and which eye received which input were randomized; each condition was tested once per session, with a trial duration of 60 s. Each subject completed two sessions, each of which contained four trials.

The use of interocular grouping stimuli could be considered controversial, as Lee and Blake (2004) have shown that the report of complete percepts may be dependent on subjects' reporting criterion. We have taken two measures to ensure that this is not the case in our experiments. First, we used stimuli that are very simple compared to those used in previous interocular grouping experiments (Kovacs et al., 1996; Lee & Blake, 2004), leaving less room for criterion differences to have an impact on our results. Second, we conducted a control experiment to investigate whether any effect of stimulus flicker on total dominance durations could also be due to a change in response criterion. For instance, due to stimulus flicker subjects could become less conservative in reporting circle and line percepts, thus causing the amount of circle and line percept to increase. Subjects were asked to report left-open and right-open horseshoe percepts. For circle and line stimuli, these percepts only occur during short periods of piecemeal transitions, while for horseshoe stimuli these are frequently occurring monocularly based percepts. As these percepts complement the circle and line percepts, the fraction of these percepts is also an indicator of pattern completion during horseshoe stimulus viewing. If pattern completion increases this should decrease the dominance of monocularly based horseshoe percepts for horseshoe stimuli, and vice versa. Four observers participated in this experiment, in which each condition was tested once in one session, and trial duration was 120 s. All further stimulus parameters were identical to those of the original experiment.

2.2. Results

Fig. 2 shows the results of experiment 1. As a measure for the strength of pattern completion, we summed dominance durations of both circle and line percepts to give the total time spent in pattern-completed percepts for horseshoe stimuli, and monocularly based percepts for the circle and line stimulus conditions. The fraction of time spent in circle and line percepts from experiment 1 and identical conditions from experiment 2 is shown in Fig. 2A. Monocularly based circle and line percepts (right pair of bars) were reported more than pattern-completed circle and line percepts (left pair of bars). For horseshoe shaped Diaz–Caneja stimuli, this fraction is less than that reported by Ngo, Miller, Liu, and Pettigrew (2000). This divergence may be due to spatial frequency and duty cycle differences. The application of stimulus flicker increased the pattern-completed percept for the horseshoe stimulus condition. This increase of circle and line percept is absent for circle and line stimulus conditions.
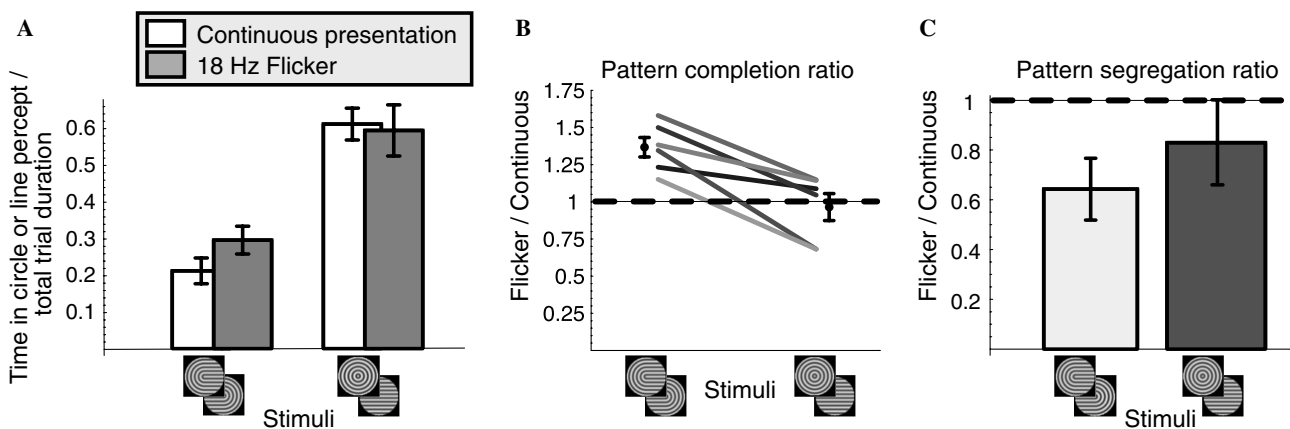

Fig. 2. Data of experiment 1, illustrating the flicker-induced increase in pattern completion. (A) Fraction of time subjects perceived circles and lines, which in cases of horseshoe stimuli were pattern-completed percepts. This fraction is greater for circle and line stimuli than for horseshoe stimuli. The amount of circle or line percept does not differ between flicker and non-flicker conditions for the circle and line stimuli. The horseshoe stimuli, however, show a significant increase in the amount of circle and line percept as a consequence of stimulus flicker. Error bars are ±1 SEM. (B) Pattern completion ratios for all individual subjects for each of the two stimulus types used. As a measure of the effect of stimulus flicker on pattern completion, we define the pattern completion ratio as the fraction of circle and line percept under flicker conditions divided by the fraction of circle and line percept under continuous presentation conditions. This ratio is significantly greater than unity for the horseshoe stimulus, indicating that stimulus flicker increases the amount of pattern completion. Each line connects data points from one subject, showing a consistent effect in all subjects. (C) Pattern segregation ratio from the control experiment in which subjects reported horseshoe percepts. Consistent with the pattern completion ratio, it is the fraction of time subjects perceived the horseshoe configuration under flicker conditions divided by the fraction of this percept under continuous viewing conditions. These percepts complement the circle and line percepts, so an increase in circle and line percepts should be reflected in a decrease in horseshoe percepts and consequently a decrease in pattern segregation ratio. This occurs for horseshoe stimuli but not for circle and line stimuli, confirming the increase in pattern completion found for circle and line percept reports.

We define the pattern completion ratio as the fraction of time spent in circle and line percepts for the flicker condition divided by the fraction of time spent in circle and line percepts for the continuous presentation condition. Fig. 2B (points with error bars) shows these ratios, which are a measure of the effect caused by flicker, for both stimulus configurations averaged over all subjects. The lines between the two conditions represent data from one subject each, and show clearly that the effect consistently occurs in all subjects. Stimulus flicker increases the amount of pattern-completed percept for horseshoe stimuli ($p = .001$, paired t-test), but does not increase the amount of monocularly based percept for circle and line stimuli ($p > .4$).

The data from the control experiment in which subjects reported horseshoe percepts are shown in Fig. 2C. The pattern segregation ratio is defined as the fraction of time spent in horseshoe percepts during stimulus flicker, divided by the fraction of time spent in these percepts during continuous presentation. An increase in pattern completion would result in a decrease of the pattern segregation ratio in the present control experiment, an effect opposite to the change of pattern completion ratio in the previous experiment. The decrease in pattern segregation ratio for stimulus rivalry shown in Fig. 2C confirms the increase in pattern completion as a result of stimulus flicker. The decrease in horseshoe percept was significant for horseshoe stimuli ($p < .05$, paired t-test), whereas the decrease in horseshoe percept that occurs for circle and line stimuli was not ($p = .2$).

3. Experiment 2: interocular grouping is independent of flicker frequency

3.1. Methods

Different flicker frequencies have successfully been used to generate F&S rivalry (Bonneh et al., 2001; Lee & Blake, 1999; Logothetis et al., 1996; Pearson & Clifford, 2005b). The range of frequencies at which it is possible to diminish the importance of monocular images in binocular rivalry is highly informative, especially regarding the relationship to physiological data, such as the different critical fusion frequencies (CFF) of different cell populations (van de Grind, 1973). Therefore, we conducted an experiment in which we varied the frequency at which on–off flicker was deployed. The range of frequencies tested was limited as for lower frequencies the transients as a result of stimulus flicker become increasingly strong perceptually and induce perceptual switches (Kanai, Moradi, Shimojo, & Verstraten, 2005). These stimulus-induced alternations are not the subject of the present paper, thus these frequencies were omitted. Higher frequencies of flicker creates monocular temporal fusion, increasing the predominance of plaid-like percepts. Monocular rivalry could ensue under these conditions of monocular temporal fusion, however, the stimulus characteristics used in the present study are quite different

from those normally required to induce monocular rivalry, such as low duty cycle, large stimuli and low contrast.

Six observers participated, five were subjects in the previous experiment. Setup and stimuli were identical to those used in the previous experiment, but flicker frequency was varied. Different flicker frequencies were implemented by varying the number of frames presented between successive blanks each lasting one frame duration (13 ms). Thus, flicker frequency was varied between 10 and 24 Hz in five steps. Subjects completed one session during which trial duration was 60 s.

3.2. Results

Fig. 3 shows pattern completion ratios for both circle and line stimuli and horseshoe stimuli, over a 10–24 Hz range of frequencies. Pattern completion ratios are greater than unity at all frequencies for horseshoe stimuli, whereas the ratios for circle and line stimuli are ∼1. Thus, there is no effect of stimulus flicker at any of the frequencies tested for the circle and line stimuli, whereas for horseshoe-shaped stimuli the effect of stimulus flicker is present at all frequencies. The difference between the two types of stimuli is highly significant (two-way ANOVA $F(1,4): 28.7, p < .10^{-5}$). Subjects, when debriefed after the experiment, reported an increase in transparent percepts at lower flicker frequencies. With less convincing percepts and more transition time, the amount of time reported as monocularly based percept diminishes for circle and line stimuli.

More importantly, for horseshoe stimuli the pattern completion ratios do not show any trend across frequencies, indicating that the increase in pattern completion as a
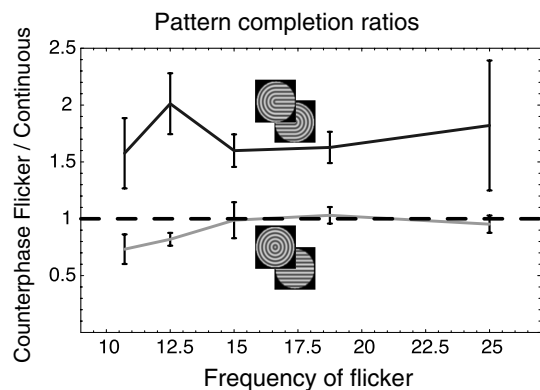
Fig. 3. Frequency-independence of the increase in pattern completion. The black line represents data for horseshoe stimuli, the light gray line represents data for the circle and line stimuli. Pattern completion ratio is defined as the total duration of pattern-completed percept during flicker divided by the total duration of pattern-completed percept during continuous stimulation. Therefore, a value of one (indicated by the dashed line) means there is no difference in pattern completion as a result of flicker. Values represent means across four subjects, error bars are ±1 SEM. It is evident that the increase in pattern completion occurs equally for all frequencies for the horseshoe stimuli. No such effect occurs for circle and line stimuli, apart from an opposite effect at lower frequencies which does not reach significant levels.

result of stimulus flicker is not dependent on flicker frequency.

4. Experiment 3: counterphase flicker decreases interocular grouping

4.1. Methods

Pattern completion increases as a result of stimulus flicker and does so approximately equally at multiple frequencies, as experiment 2 showed. Although insensitive to changes in frequency, the effect may be altered by changing the type of flicker used. To investigate this further, we modified the flicker regime to alternate not between presence and absence of the stimulus, but between two counterphased presentations of the stimuli. Under this regime there are only local inversions of contrast but no global luminance modulations at a given flicker frequency. In the presentation regime used here the patterns of circles, lines and horse-shoe shapes are continuously presented, while the frequency content of the stimulus presentation is kept equal to that during on–off flicker. Moreover, counterphase flicker introduces a variation in stimulus phase over time, and modulation of cellular responses due to varying spatial phase over time is a traditional method of separating different computational levels in primary visual cortex (i.e. simple and complex cells) (Hubel & Wiesel, 1962; Ringach, 2004). Phase-invariant cells would not change their firing behavior due to the difference between on–off and counterphase flicker. However, two separate pools of phase-sensitive neurons may respond to counterphase flicker whereas only one would respond to on–off flicker. Therefore, counterphase flicker may clarify at which neural level interocular grouping occurs.

The six observers of the first experiment participated in this counter-phasing experiment. Again, setup and stimuli were identical to those used in experiment 1. However, instead of blanks, 2 frames of each cycle were used to present a contrast-inverted version of the stimulus that appeared during the other two frames of the cycle. Thus, over time, the gratings composing the stimulus would counterphase at 18 Hz. Subjects completed one session, in which 4 conditions were sampled. Trial duration was 120 s.

4.2. Results experiment 3

Fig. 4 shows the results from experiment 3. For circle and line stimuli, no significant difference in pattern completion ratio occurs as a result of counterphasing flicker. There is, however, a marked effect of counterphasing flicker on the pattern completion ratio for horseshoe stimuli. The decrease in pattern completion is significant (paired *t*-test, $p < .01$). So, subjects perceived less pattern-completed shapes during counterphasing flickering when compared to continuous stimulation, an effect that is opposite to the effect of on–off flicker on pattern completion ratios for horseshoe stimuli as found in experiment 1.
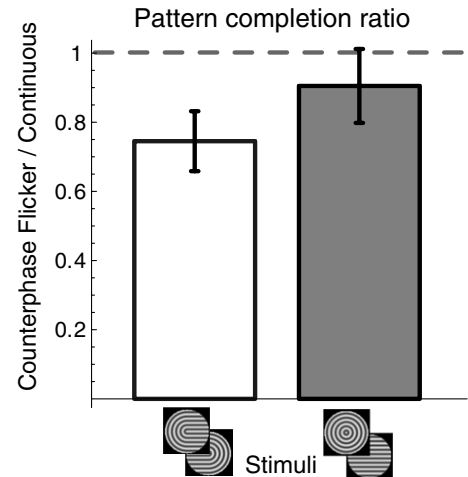

Fig. 4. Pattern completion ratios for counter-phase flicker. Counterphase flicker decreases the amount of circle and line percept when compared to the non-flicker condition for both stimulus configurations. This effect is significant for the horseshoe stimulus. Thus, counterphase flicker has opposite effects on pattern completion when compared to on–off flicker at the same frequency. Bars represent pattern completion ratios for both types of stimuli. Error bars are ±1 SEM.

5. Discussion

We conducted three experiments to investigate whether interocular grouping is increased by stimulus flicker. Our results demonstrate that on–off flicker increases interocularly combined pattern completion (experiment 1), that it does so independently of flicker frequency (experiment 2), and that this increase depends critically on the on–off luminance transients that occur during stimulus flicker (experiment 3).

Based on our results, we propose that the amount of interocularly combined pattern-completed percept can be regarded as a measure of the level at which binocular rivalry is resolved. We employ this measure to examine whether the temporal characteristics of stimulus presentation can alter the level at which binocular rivalry takes place. Local retinotopic factors are of paramount importance for the occurrence of normal binocular rivalry (Carlson & He, 2004), and the alternations between binocular rivalry percepts do occur in a retinotopically ordered fashion (Wilson, Blake, & Lee, 2001). However, binocular rivalry suppression occurs at multiple levels in the visual hierarchy, as it has been found that the depth of suppression increases with increasing stimulus complexity (Nguyen, Freeman, & Alais, 2003). In addition, the pattern that undergoes suppression alters the percept of the dominant pattern in a manner that implicates continuous interaction at multiple levels (Pearson & Clifford, 2005a). The fact that rivalry can occur independently of the eye being stimulated, as occurs in F&S rivalry, points directly to the existence of multiple rivalry stages (Lee & Blake, 1999; Logothetis et al., 1996; Pearson & Clifford, 2005b). Stimulus flicker is thought to cause rivalry to bypass lower, monocular stages and transpire at higher stages whose activity is independent

of eye-of-origin information. A putative physiological mechanism for this decrease of direct interocular inhibition due to stimulus flicker is a decrease in V1 neuron IPSP amplitude at stimulation frequencies above 6 Hz (Kuhnt & Creutzfeldt, 1971, see also Wilson, 2003). A compelling result by Bonneh et al. (2001) shows that the occurrence of F&S rivalry is dependent on the size and structural coherence of the stimulus used, under conditions of fixed spatial frequency. This strongly suggests that pattern-based representations are mediated by neurons with larger receptive fields, likely located higher in the visual processing stream. These higher stages could consist of binocular cells in V1, but also constitute activity anywhere up the ventral pathway along which the perceptual modulation of neuronal activity increases (Fang & He, 2005; Leopold & Logothetis, 1996). Interocular pattern completion is likely to be mediated by the higher stages at which rivalry may occur. The increase in interocular pattern completion due to stimulus flicker accords well with the hypothesis that rivalry may transpire at several levels simultaneously (Bonneh et al., 2001).

Previously, different frequencies of 15–20 Hz were used for the generation of F&S rivalry (Bonneh et al., 2001; Lee & Blake, 1999; Logothetis et al., 1996; Pearson & Clifford, 2005b). We show that in our stimulus paradigm, the frequency of on–off flicker has no decisive influence on the increase in pattern completion within the range of ca. 10–25 Hz. If extrapolated to F&S rivalry, our results could be construed to indicate that there is no 'sweet spot' for the on–off flicker frequency as there is for the switch frequency (Lee & Blake, 1999).

We also show that the increase in interocular pattern completion as a result of stimulus flicker is diminished and even reversed when there are no blanks in stimulus presentation (Fig. 4). Although the global patterns projected into the eyes are the same as in the other experiments, the local luminance and spatial phase change rapidly over time when the stimulus is counterphased. Geniculate and cortical simple cells are known to be sensitive to changing spatial phase, and thus might change their firing behavior as a result of counterphase flicker. These cells also have a tendency (strong for geniculate cells, less so for simple cells (Hubel & Wiesel, 1962; Gilbert, 1977; Skottun & Freeman, 1984)) to be more monocularly driven and have a higher critical flicker frequency (CFF) than complex cells that have a lower CFF than the frequencies used in the present stimulus (van de Grind, 1973). Also, complex cells would not respond to counterphase flicker in a different manner when compared to on–off flicker given their lack of phase sensitivity.

Thus, assuming that the lower stages at which rivalry occurs are stimulated twice every flicker period, we interpret the decrease in pattern completion that results from the counterphase flicker operation as a shift of the binocular rivalry process to monocular stages, that would in this view consist of monocular simple cells in V1. However, this interpretation is tentative, and should be investigated fur-

ther using a combination of physiological and psychophysical experiments.

The data presented here provide evidence supporting the hypothesis that binocular rivalry occurs at multiple stages, and provide insights in the divisions between these different stages. Further research employing the F&S stimulus or its derivatives is very likely to be of use in investigating binocular rivalry, especially in physiological studies.

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