

Removal of monocular interactions equates rivalry behavior for monocular, binocular, and stimulus rivalries

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When the two eyes are presented with conflicting stimuli, perception starts to fluctuate over time (i.e., binocular rivalry). A similar fluctuation occurs when two patterns are presented to a single eye (i.e., monocular rivalry), or when they are swapped rapidly and repeatedly between the eyes (i.e., stimulus rivalry). Although all these cases lead to rivalry, in quantitative terms these modes of rivalry are generally found to differ significantly. We studied these different modes of rivalry with identical intermittently shown stimuli while varying the temporal layout of stimulation. We show that the quantitative differences between the modes of rivalry are caused by the presence of monocular interactions between the rivaling patterns; the introduction of a blank period just before a stimulus swap changed the number of rivalry reports to the extent that monocular and stimulus rivalries were inducible over ranges of spatial frequency content and contrast values that were nearly identical to binocular rivalry. Moreover when monocular interactions did not occur the perceptual dynamics of monocular, binocular, and stimulus rivalries were statistically indistinguishable. This range of identical behavior exhibited a monocular (~50 ms) and a binocular (~350 ms) limit. We argue that a common binocular, or pattern-based, mechanism determines the temporal constraints for these modes of rivalry.

Keywords: binocular vision, perceptual organization, bistability, rivalry

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Introduction

What shapes our awareness in face of the ambiguities intrinsic in visual information? The mechanisms underlying visual awareness are often studied employing ambiguous stimuli. The merit of such stimuli is that they remain constant, while their multiple perceptual interpretations alternate, revealing the internal processes involved in resolving visual ambiguities (Crick & Koch, 1990).

An extensively studied class of ambiguous stimuli is bistable binocular rivalry. In order to instigate binocular rivalry two mutually incompatible stimuli are shown to an

observer, one stimulus to each eye. This configuration leads to perceptual alternations between the left and right eye's images.

One of the central issues in the discussions on the origin of binocular rivalry is whether it involves predominantly a competition between monocular neurons that code for the conflicting stimuli (i.e., interocular rivalry, e.g., Blake, 1989). Alternatively binocular rivalry may depend, perhaps even exclusively, on competition between stimulus representations independent of the eye of origin (e.g., Logothetis, Leopold, & Sheinberg, 1996). The current view is that visual rivalry is a complex, multileveled, and multifaceted process (Blake & Logothetis, 2002), but this

view does not tightly constrain the range of possible mechanisms that underlie binocular rivalry.

A possibly revealing direction of research is comparing binocular rivalry to other forms of rivalry that do not involve interocular interactions. The premise is that if similarities are found between these different forms of rivalry, these similarities are caused by a similar, or even identical, mechanism. Such a finding would strengthen the hypothesis that binocular rivalry and other forms of rivalry depend on a general rivalry mechanism.

Apart from binocular rivalry there exist at least two protocols to induce the alternations between perceptual interpretations: i.e., monocular rivalry (including ambiguous figures) and stimulus rivalry. *Monocular rivalry* may be instigated when two incompatible patterns are presented to the same eye. In this case one does not observe a stable superposition of the two patterns but an alternation in perceptual salience between the two patterns (Breese, 1899). Because the two patterns are presented to the same eye, the rivalry involves pattern-based,¹ not interocular, competition. *Stimulus rivalry* (Logothetis et al., 1996) may be instigated when the incompatible images are presented to different eyes, while being swapped between the eyes at regular intervals. Competition therefore may involve pattern-based processes, and—although not generally acknowledged—interocular processes.

For ease of discussion, the visual rivalries resulting from those different stimuli are called different modes of rivalry in the remainder of this report, even though they may rely on partly shared mechanisms.

Similarities between the different modes of rivalry

Monocular rivalry and binocular rivalry may be instigated with very similar image orientation differences between the conflicting patterns (Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973; Logothetis, 1998; O’Shea, 1998; Schor, 1977). Furthermore, a stimulus simultaneously engaged in different modes of rivalry at different locations induces perceptual alternations across its whole spatial extent (Andrews & Purves, 1997; Pearson & Clifford, 2005), in disregard of the different protocols with which rivalry is instigated. This finding suggests that similar mechanisms underlie the perceptual alternations in the different rivalry protocols. Moreover, changing the saliency of one stimulus interpretation in ambiguous stimuli (with foreground/background segregation cues, Leopold, Maier, Wilke, & Logothetis, 2005) or stimulus rivalry (with contrast changes, Logothetis et al., 1996) primarily influences the percept durations of the other interpretation, leaving dominance durations for the changed stimulus unaffected. This effect was first established for binocular rivalry (Levelt, 1965) and later generalized over the full range of possible contrast

differences (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006).

Differences between the different modes of rivalry

The central differences between binocular rivalry, stimulus rivalry, and monocular rivalry may be categorized in two main groups: (1) Spatial and contrast limitations on rivalry induction and (2) perceptual dynamics.

Spatial and contrast limitations on rivalry induction

Binocular rivalry can be induced over a wide range of contrasts and spatial frequencies (Blake, 1977; O’Shea, Sims, & Govan, 1997). Monocular rivalry needs low spatial frequencies and low contrast (Logothetis, 1998; Maier, Logothetis, & Leopold, 2005; Wade, 1975), while stimulus rivalry needs high spatial frequencies and low contrast (Lee & Blake, 1999; Logothetis et al., 1996).

Perceptual dynamics

Alternation dynamics between the different modes of rivalry are widely different (Breese, 1899; Tong, 2001; Wade, 1975). Binocular rivalry alternations are frequent (i.e., short perceptual dominance durations) and crisp (i.e., lacking long transition periods; e.g., Wade, 1975), although this behavior depends on contrast (Brascamp et al., 2006; Hollins, 1980). Monocular rivalry, on the other hand, shows the opposite pattern (Breese, 1899; Wade, 1975), with infrequent alternations and long transition periods. The binocular rivalry data are mimicked by stimulus rivalry (Logothetis et al., 1996), but only for certain parameter combinations (Knapen, Kanai, Brascamp, van Boxtel, & van Ee, 2007; Lee & Blake, 1999).

Considering the perceptual dynamics, some nuances need to be addressed. In some conditions perceptual alternations in monocular rivalry are reported to be quite frequent and crisp, similar to binocular rivalry (Andrews & Purves, 1997; Campbell et al., 1973; Knapen et al., 2007; Maier et al., 2005; Rauschecker, Campbell, & Atkinson, 1973). However, these studies invariably employed stimuli that differed in color. This addition may have influenced the rivalry dynamics quite drastically, because color differences by themselves are known to induce rivalry (Creed, 1935; Dawson, 1915/1917; Desaguliers, 1716; Kakizaki, 1950). The binocular rivalry-like behavior may therefore have been due to color rivalry, instead of orientation-based rivalry.

We reinvestigate the issue of the similarities between the different rivalry modes, while avoiding the use of colored stimuli. Instead, we studied the influence of several temporal stimulus characteristics. The use of temporal parameters to study the similarities between the different

modes of rivalry has the advantage that they do not lead to rivalry by themselves (O’Shea & Blake, 1986) but do provide a segmentation cue that may help to process the conflicting stimuli independently (Holcombe, 2001; Holcombe & Cavanagh, 2001; Suzuki & Grabowecky, 2002) and in turn promote rivalry. Furthermore, we employed simple grating stimuli and thereby excluded shared higher level influences, such as context (Andrews & Lotto, 2004), and therefore engaged solely the core rivalry resolution processes for grating rivalry.

The similarities and differences in spatial stimulus characteristics for both the instigation of rivalry and the different perceptual behaviors have long been a centerpiece in the debate as to whether the different modes of rivalry depend on different underlying rivalry processes (Andrews, 2001; Blake & Logothetis, 2002; Bonneh, Sagi, & Karni, 2001; Lee & Blake, 1999, 2004; Tong, 2001) or a shared rivalry process (Andrews & Purves, 1997; Kovács, Papathomas, Yang, & Fehér, 1996; Leopold & Logothetis, 1996). Our results provide one of the first extensive characterizations of temporal constraints on the different modes of rivalry. In addition, our results constrain computational models of visual rivalry.

General methods

Apparatus

Images were presented on a gamma-corrected 22" LaCie electron22blueIV monitor (1600 × 1200 pix, 75 Hz), using a conventional stereoscope with a septum dividing the screen into two equal parts. Effective screen distance was 46 cm. A chin-rest stabilized head position. Experimental procedures were reviewed and approved by the Institutional Review Board.

Stimuli

The rivalrous patterns were achromatic orthogonally oriented (± 45 deg from vertical) sinewave gratings containing 2.1 cycles/deg, subtending 1.7 degrees. The gratings were seen through a circular window. Background luminance was 1.5 cd/m², mean stimulus luminance was 10.5 cd/m². Michelson contrast was 50%. The stimulus was surrounded by a 2.7 deg binocularly visible annulus (0.06 cd/m², 0.2 deg wide), serving as a fusion aid. Blank periods were introduced by removing the stimulus and showing the background luminance. These specific parameters were chosen to produce a near exact copy of previously used stimuli in the parametric study of stimulus rivalry (Lee & Blake, 1999). Any differences between our results and those reported previously are

therefore not due to differences in spatial/contrast parameters, but instead due to temporal parameters.

Statistics

Chi-square tests between proportions were performed between overall proportions, combining data of the different subjects. A *z*-value was obtained using the following formula:

$$z = \frac{p_1 - p_2}{\sqrt{p_{tot}(1 - p_{tot})(1/n_1 + 1/n_2)}}, \quad (1)$$

where $p_{\{1,2\}}$ were the observed proportions, p_{tot} is the calculated proportion when both samples are combined, and $n_{\{1,2\}}$ were the number of observations. The *z*-value was subsequently transformed into a *p*-value.

Results

Experiment 1: The role of the interswap period and temporal duty cycle

In a first experiment, we investigated the dependence of stimulus rivalry and monocular rivalry on two main temporal stimulus characteristics: the interswap period (ISP) and the temporal duty cycle (TDC). The ISP is the period between two successive stimulus swaps between the eyes (see Figure 1), and the TDC is the portion of the ISP during which a stimulus is presented (see Figure 1).

Binocular rivalry is not very sensitive to the exact values of TDC and ISP (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens, & van Ee, 2008; van Boxtel, van Ee, & Erkelens, 2007); binocular rivalry takes place for ISPs smaller than ~350 ms (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens et al., 2008; van Boxtel et al., 2007) and is independent of the TDCs (van Boxtel, Alais, Erkelens et al., 2008).

Stimulus rivalry seems similarly limited by ISPs smaller than 350 ms (Lee & Blake, 1999; van Boxtel, Alais, Erkelens et al., 2008), but the dependence on TDC is unknown. Here we investigate the dependence of both monocular rivalry and stimulus rivalry on ISP and TDC, employing techniques similar to the conventional stimulus rivalry protocol (Logothetis et al., 1996). Two important changes to that protocol were made. First we included a blank period of variable length before the stimulus swap (Figure 1) to allow the TDC to change. Second, in the monocular rivalry condition, the stimulus rivalry protocol was shown to just a single eye. This last condition is a truly monocular form of stimulus rivalry, without the possibility of interocular interactions.

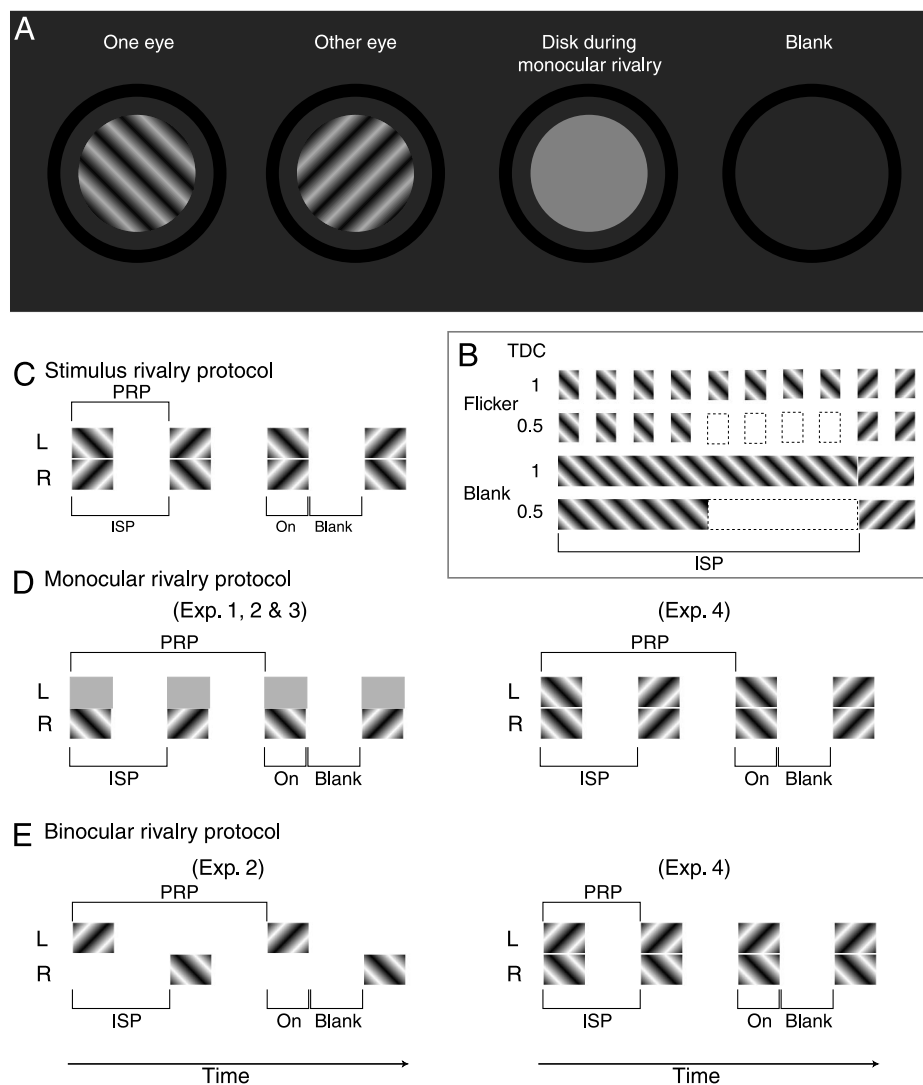


Figure 1. Spatial and temporal characteristics of the stimulus protocols evoking (C) stimulus, (D) monocular, and (E) binocular rivalries. (A) The spatial layout of the stimuli. (B) Schematic representation of the temporal duty cycle (TDC). In the flicker conditions, stimuli were 'on' and 'off' for 2 frames at a time. The dashed boxes for TDC 0.5 represent 'off' periods where otherwise a stimulus would have been presented. (C–E) Schematic representation of the temporal layout of the stimuli. To produce stimulus rivalry and monocular rivalry the patterns were swapped between or within the eyes, respectively, at each successive cycle. In [Experiment 1](#), the patterns were additionally flickered at 19 Hz during the 'on'-period. L and R denote left and right eyes, respectively. ISP denotes the interswap period; PRP denotes the pattern repetition period for identical patterns irrespective of eye of origin. Note that ISP and PRP may be identical (as in stimulus rivalry) or different (as in monocular rivalry). ISP and PRP, together with the temporal duty cycle [on / (on + blank)], define the temporal aspects of stimulation. All stimuli were achromatic.

Methods: Experiment 1

Stimulus

The interswap period (ISP) was 53, 107, 213, 320, 427, 533, or 640 ms. The temporal duty cycle of the stimuli was 0.25, 0.5, 0.75, or 1 (ignoring the blanks caused by the 19 Hz flicker, see below and [Figure 1B](#)).

In order to remain close to published stimulus protocols we flickered the stimuli at 19 Hz (by presenting the stimuli for two successive frames, i.e., 27 ms, and blanking the stimulus for two successive frames, [Figure 1B](#)). Because

of this flicker, not all TDCs could be produced exactly. Stimuli with an ISP of 53 ms and at TDC of 0.25 were produced by showing the pattern for 1 frame (=13 ms), followed by 3 blank frames. Stimuli with an ISP of 53 ms and a temporal duty cycle of 0.5, 0.75, and 1, were all produced by showing the pattern for 2 frames and blanking them for another 2 frames (therefore, all these stimuli were physically identical). Similarly, for an ISP of 107 ms, temporal duty cycles of 0.25 and 0.5 were identical (a 27 ms presentation, followed by an 80 ms blank), just as 0.75 and 1 were identified (a sequence of

27 ms ‘on’, followed by 27 ms blank, 27 ms ‘on’, and 27 ms blank). The monocular rivalry stimuli were shown to a single eye, the other eye receiving an equally sized disk with a luminance equal to the stimulus (and thus higher than the background).

Procedure

The subjects’ task was to categorize each 6-s trial as containing either rivalry, rapid and regular orientation alternations (“switches”), or a plaid (Lee & Blake, 1999). Employing this paradigm, we capitalized on the distinct

perceptual experiences (Lee & Blake, 1999; Logothetis et al., 1996) to deduce whether stimulus-based percepts (i.e., rivalry) or eye-based percepts (rapid and regular alternations: “switches”) had occurred. Subjects ($n = 5$) were asked to base their categorization on the last 3 s of a trial. Each subject performed 2 sessions, each with 2 reports per parameter combination for stimulus rivalry conditions. These sessions were followed (or preceded ($n = 2$)) by 2 sessions, each with 2 reports per condition for monocular rivalry, and 1 report per condition for stimulus rivalry. All conditions were randomly interleaved.

The temporal limit reported in Figure 2 is determined to be the ISP where the number of rivalry reports halved

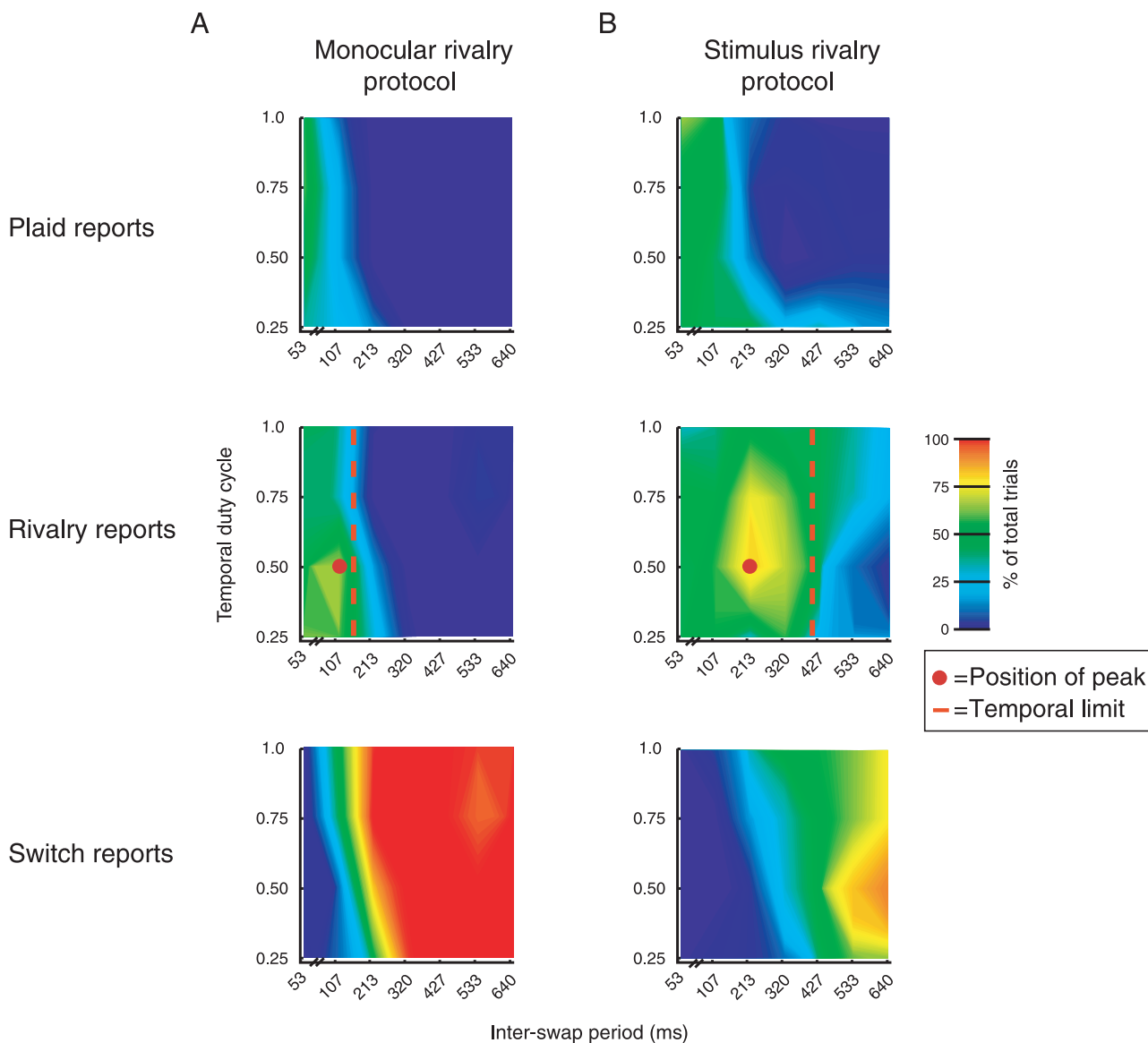


Figure 2. Dependence of plaid (top row), rivalry (middle row), and switch reports (bottom row) on the temporal duty cycle (TDC) and the interswap period (ISP). Reported the percentage of trials of a certain IDSP-TDC combination resulting in a plaid, rivalry, or switch reports. In both monocular (A) and stimulus (B) rivalry protocols, plaid reports were common for short ISPs, and switch reports were common for long ISPs. At the peak in the ISP-TDC space 66% of the trials in monocular rivalry and 79% in stimulus rivalry were categorized as containing rivalry. The occurrence of rivalry reports is largely independent of the TDC, except near a TDC of 1.

relative to the maximum. Linear interpolation was used, collapsing the data over temporal duty cycles.

Results: Experiment 1

Rivalry percepts were rather common, both in monocular and stimulus rivalry protocols (Figure 2). This finding was not anticipated because the grating stimuli had a spatial frequency (2.1 cyc/deg), stimulus size (1.7 deg), and contrast (50%) that are thought to compromise monocular (Maier et al., 2005; Wade, 1975) as well as stimulus rivalry (Bonneh et al., 2001; Lee & Blake, 1999). In fact, at optimal ISP-TDC combinations, rivalry was reported in 66% of the trials for monocular rivalry, and in 79% of the trials for stimulus rivalry. This value is not significantly different between the two rivalry protocols ($p > 0.05$, Wilcoxon signed-rank test), although the position of the peak in the ISP-TDC space was different. (We explain later why this difference exists, and why it is no evidence for a difference in underlying mechanisms.)

Figure 2 shows that rivalry reports are most common toward lower ISP values. We determined the upper temporal limit of the ISP to support rivalry (see Methods). For monocular rivalry the temporal limit was 147 ± 21.6 ms (mean \pm se over subjects), for stimulus rivalry 414 ± 76.1 ms (these limits differ significantly: $p < 0.03$, two-tailed t -test). Plaid reports were common with short ISPs (< 100 ms), in both stimulus rivalry and monocular rivalry paradigms. Switches were reported at ISPs larger than the ~ 147 ms and 414 ms ISP limit, for monocular and stimulus rivalries, respectively.

Apropos of the temporal limits, previous research had indicated that for binocular rivalry both conflicting patterns need to be repetitively shown within 350 ms from their last presentation (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens et al., 2008). The ISP for the stimulus rivalry protocol is directly comparable to the ISP for binocular rivalry. Indeed the limit of 414 ms obtained in this experiment is of similar duration. The monocular limit at 147 ms is about half the duration of the limit of both binocular rivalry and stimulus rivalry. Importantly, during the monocular rivalry protocol the patterns are also repeated at half the frequency of the stimulus rivalry protocol. Specifically, during the stimulus rivalry protocol both patterns are presented after every swap, while during monocular rivalry the patterns are only repeated every *second* swap (Figure 1). When we translate the obtained ISP limits to *pattern repetition periods* (PRP, see definition in Figure 1), we obtain ~ 294 ms and ~ 414 ms for monocular and stimulus rivalries. These limits are indeed close to the 350 ms limit and are not significantly different from each other ($p > 0.2$, two-tailed t -test).

The TDC seems to influence the occurrence of rivalry only marginally, apart from an apparent decrease of rivalry reports near TDCs of 1 (see Figure 2). This decrease in rivalry reports is consistent with the literature where rivalry was reported to be almost absent with the parameters used in the current experiment (Lee & Blake, 1999); these studies have used duty cycles of 1. It is also consistent with the literature on binocular rivalry (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens et al., 2008), which reports a large independence of TDC.

Experiment 2: Blanks are more effective than flicker and decrease the dependence on spatial frequency

Experiment 1 showed a large independence of rivalry occurrence to the temporal duty cycle (TDC), a possible exception being a TDC of 1. Since the main difference between the conditions was the presence of a large blank before a swap for $TDC < 1$ and an absence of this large blank for $TDC = 1$ (see Figure 1), it seems that a blank period just before a stimulus swap increases rivalry reports. In the following experiment we tested this prediction. We investigate rivalry occurrence in stimuli that have an ~ 70 ms blank period before the swap, but lack the 19 Hz flicker, and compare this condition to the classical stimulus rivalry protocol (with the 19 Hz flicker). We expected more rivalry reports in the blank conditions than in the flicker conditions for monocular and stimulus rivalry protocols. In the binocular rivalry protocol the influence of the blank should be minimal (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens et al., 2008), as it lacks the stimulus swap that hampers rivalry percepts in the two other rivalry protocols.

A second variable of interest is the spatial frequency of the rivalry stimuli. Both monocular rivalry and stimulus rivalry are reported to be very dependent on spatial frequency while binocular rivalry is less dependent on this variable (see Introduction section). We reinvestigated the dependence on spatial frequency while keeping stimulus conditions (Figure 1) very comparable among the different rivalry protocols.

Methods: Experiment 2

The conventional stimulus rivalry protocol (with the 19 Hz flicker) was compared to a protocol in which the 19 Hz flicker was removed and replaced by a blank of 67 ms inserted just before each stimulus swap (subjects = 5). Spatial frequencies were varied (2, 4, and 6 cyc/deg were used). All other stimulus parameters were identical to Experiment 1. The task was identical to that in Experiment 1. We also tested binocular rivalry conditions ($n = 5$), with the same procedure as monocular rivalry, but keeping

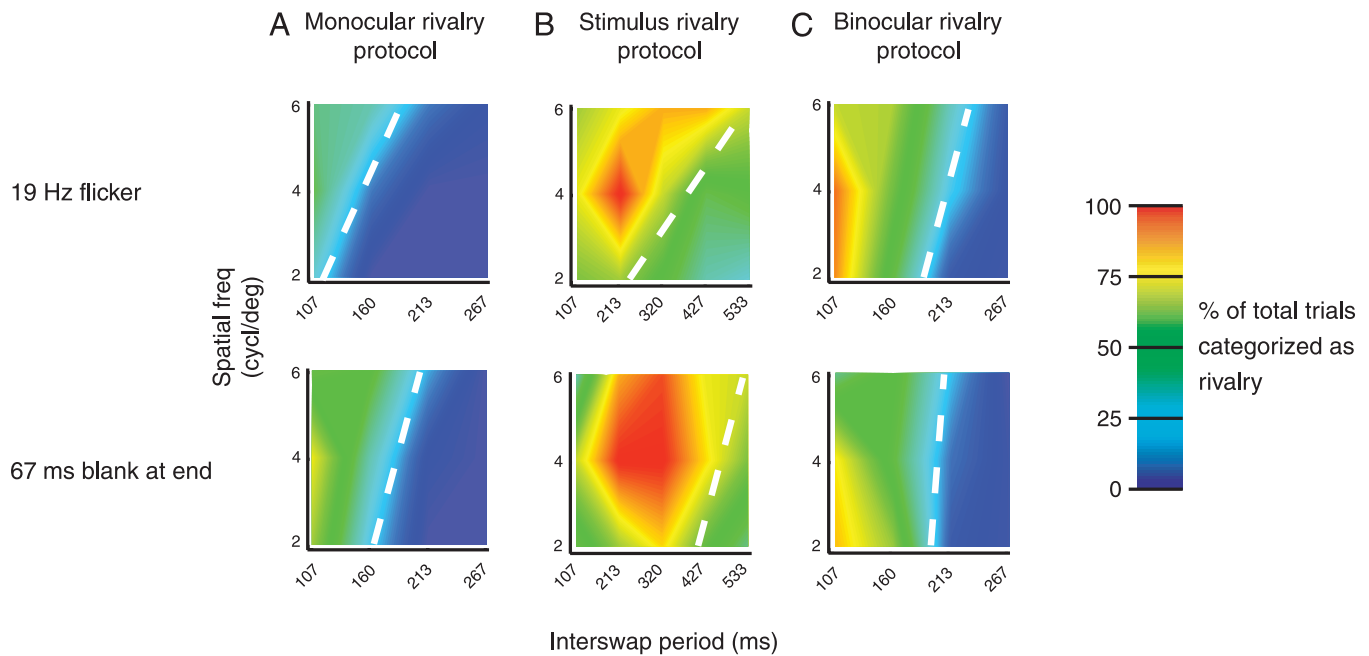


Figure 3. Dependence of rivalry reports in (A) monocular, (B) stimulus, and (C) binocular rivalry protocols, dependent on interswap period (ISP) and spatial frequency. The upper panels depict data from conditions in which the stimuli were flickered at 19 Hz (i.e., the conventional way of inducing stimulus rivalry). The lower panels depict data for conditions in which the stimuli were blanked for 67 ms before the swap. In monocular (A) and stimulus (B) rivalry protocols, rivalry was more frequently reported with the blanked stimuli than with conventional stimuli. The incidence of rivalry reports was also less dependent on spatial frequency with the blanked stimuli than with the conventional stimuli. This can be seen from the differences in slopes of the lines, which are drawn by hand orthogonal to the steepest gradient. These lines are more vertical in the bottom panels, indicating a weaker dependence on spatial frequency (which is changed along the y-axis). For binocular rivalry (C), flicker and blank conditions are very similar, and also similar to monocular rivalry ‘blank’ data, consistent with the idea the monocular interactions between the conflicting patterns are absent in the binocular rivalry conditions. Note that the blanked stimuli had an effective contrast that was higher than for the conventional rivalry protocol, for all but the 107 ms ISPs.

the two patterns in different eyes (see Figure 1). All subjects had participated in Experiment 1.

Results: Experiment 2

We found that the introduction of a 67-ms blank before the stimulus swap between the eyes enlarges the area of rivalry reports in the ISP–Spatial frequency space as compared to the conventional 19 Hz flicker paradigm (Figure 3). Comparing rivalry reports between the 19 Hz flicker condition and the 67 ms blank condition we found that rivalry reports are more frequent in monocular ($p < 0.002$, χ^2 -test) and stimulus rivalry conditions ($p < 0.05$, χ^2 -test) when the stimuli were blanked instead of flickered stimuli. (When pooling monocular and stimulus rivalry data, $p < 0.003$.) Note that this increase took place even though in most cases the effective contrast and luminance were higher in the ‘blank’ conditions than the ‘flicker’ conditions (which should have lowered rivalry reports; Lee & Blake, 1999). Therefore, it seems that, indeed, the introduction of a blank before the swap increases the number of rivalry reports. By consequence,

these results show that the 19 Hz flicker is not an essential component of the stimulus rivalry protocol. The positive effect of the 19 Hz flicker on the number of rivalry reports (Lee & Blake, 1999; Logothetis et al., 1996) may be largely due to the presence of a 2 frame (~ 26 ms) blank before the swap, which accompanies the 19 Hz flicker protocol. These results furthermore suggest that models that need the 19 Hz flicker to explain the existence of stimulus rivalry (cf. Wilson, 2003) are not likely to explain our findings.

Unlike the data for stimulus rivalry and monocular rivalry protocols, the data for the conventional binocular rivalry protocol is not different between ‘blank’ and ‘19 Hz flicker’ conditions ($p > 0.9$, χ^2 -test). This was expected, as in binocular rivalry conditions there is no stimulus swap, so adding a blank will not change rivalry dynamics, as was already reported by O’Shea and Crassini (1984).

The dependence on spatial frequency existed in both flicker and blank protocols, for both monocular and stimulus rivalries, but not, or to a much smaller extent, for binocular rivalry. The dependence on spatial frequency in the blank protocol was less than in the flicker paradigm,

as can be seen by the more vertical orientation of the white dashed line when comparing the bottom panels in Figure 3 to the top panels.

In this experiment, binocular rivalry showed a temporal ISP limit of about 200 ms, which is lower than the ~350 ms limit discussed in Experiment 1. However, the presentation protocol was also different (see Figure 1). In the current protocol, an ISP = 200 ms translates into a pattern repetition period (PRP) of 400 ms, consistent with the limits reported for monocular and stimulus rivalries (see Experiment 1).

Discussion results: Experiments 1 and 2

The experiments have shown that with the introduction of a blank period before a stimulus swap, rivalry reports are more frequent. On the other hand, the presence of a blank period does not matter for rivalry reports during binocular rivalry protocols. This finding suggests that the blank prevents monocular interactions between conflicting patterns presented in a single eye. This reasoning would also explain why rivalry is experienced over similar ranges in the flicker and blank conditions for binocular rivalry (because monocular interactions between conflicting stimuli do not occur during binocular rivalry). Moreover, because monocular interactions in the ‘blank’ condition are reduced by the presence of a blank, the blank condition in the monocular rivalry protocol leads to a distribution of rivalry reports (in the ISP–Spatial

frequency space) that is very similar to binocular rivalry protocol (see Figure 3). Specifically, the dependence on spatial frequency is reduced in the monocular rivalry protocol, mostly by increasing the rivalry reports for the lower spatial frequencies, and the total amount of rivalry reports is more similar to the binocular rivalry protocol. Nevertheless, with the current settings (i.e., a rather brief blank period of <70 ms) the total amount is still significantly lower in the monocular blank condition compared to the binocular blank condition ($p < 0.02$). For more optimal conditions (see Experiment 4), this difference disappears.

Experiment 3: A blank immediately preceding a swap is most effective

To test whether the blank before the swap was indeed important, and what aspects of it in particular (i.e., duration or position within the interswap period; ISP), we performed Experiment 3.

The ISP was set to 260 ms in both stimulus rivalry and monocular rivalry. This ISP leads to many rivalry reports for the stimulus rivalry protocol, and few for the monocular rivalry protocol (see Experiment 1). We varied the duration of the blank and its position within the ISP (see Figure 4A).

If the blank period indeed prevented monocular interactions between conflicting stimuli in the previous experiments, then a blank at the end of the ISP should give rise

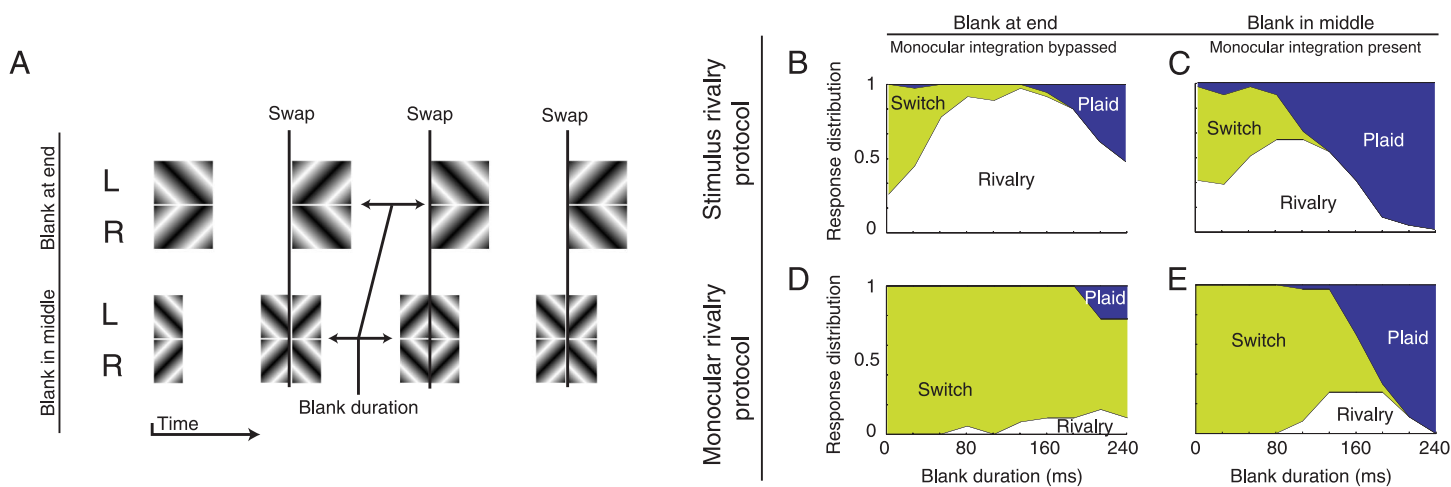


Figure 4. Blank duration before a pattern swap determines the occurrence of rivalry. (A) Stimuli were constructed with a blank just before a swap of the patterns (top), or in the middle of the interswap period (bottom). The two competing patterns were temporally separate when the blank was placed at the end of the ISP, however they were temporally abutting when the blank was placed in the middle of the ISP. It is key to note that the latter condition allowed for monocular interactions. (B, C) Responses during stimulus rivalry conditions, presented as stacked frequency distributions. Switch = green, rivalry = white, plaid = blue. Rivalry occurred frequently over nearly the full range of blank durations when the blanks were placed at the end (B) and was severely decreased when the blanks were placed in the middle (C). Plaid reports, however, gained in frequency, suggesting, indeed, that monocular interactions took place between the two patterns. (D, E) Monocular rivalry data. Consistent with Experiment 1, rivalry reports at this ISP were rare during monocular rivalry (D), and switch reports abound. Importantly, when blanks were placed in the middle of the ISP (E), plaid reports were almost as frequent as with stimulus rivalry conditions (note the similarity in plaid reports in panels (C) and (E)).

to a considerably higher number of rivalry reports than conditions with the blank placed in the middle of the ISP. Furthermore, one may expect that the longer the blank is, the larger the number of rivalry reports.

Methods: Experiment 3

Stimuli and task were identical to those in [Experiment 1](#) (except that the 19 Hz flicker was removed). The ISP, for both stimulus rivalry and monocular rivalry protocols was fixed to 260 ms. Note that with this ISP, the stimulus rivalry paradigm leads to a high amount of rivalry occurrence, while the monocular rivalry protocol should lead to very little rivalry. The temporal duty cycle was varied by inserting blanks just before a pattern swap (top row, [Figure 4A](#)), or right in between two pattern swaps (bottom row, [Figure 4A](#)). Twelve repetitions for each parameter combination were made per subject ($n = 3$, all had participated in [Experiments 1](#) and [2](#)).

Results: Experiment 3

First we discuss the results for the stimulus rivalry protocol. Conditions with blanks placed at the end of the ISP resulted in higher numbers of rivalry reports than conditions with blanks placed in the middle of the ISP (compare [Figure 4B](#) to [4C](#)). This difference was significant at all blank durations above 27 ms (pairwise comparisons at all individual blank intervals: $p < 0.05$, χ^2 -tests). As predicted, the conditions that prevented monocular interactions between the conflicting stimuli (i.e., blanks at end) lead to more rivalry reports.

These results also bore out the prediction that longer blank durations should lead to more rivalry reports. Ceiling performance was reached at blank durations of about 80 ms and remained up to blank durations of about 220 ms ([Figure 4B](#)). With blanks shorter than ~ 70 ms, switches (i.e., rapid, regular alternations) were reported. With blank durations of about 180 ms and more (and therefore presentation times of < 80 ms), plaids were also reported. These plaid reports were probably due to a fusion of the two eyes' views when stimulus presentations are very short: 'false fusion' (Blake, Yang, & Westendorf, 1991; Dawson, 1915/1917; Wolfe, 1983).

With blanks in the middle of the ISP ([Figure 4C](#)), rivalry reports also rose with increasing blank time (possibly due to a decrease in effective contrast), but not to the same extent as for conditions with blanks at the end of the ISP. Plaid reports in [Figure 4C](#) were much more frequent than in [Figure 4B](#). This finding suggests that the monocular interactions between the conflicting patterns—which were possible with blanks in the middle of the ISP—caused an integration of the two patterns into a plaid percept. This

interpretation is supported by the monocular rivalry data with blanks in the middle, reported in [Figure 4E](#). Here, the number of plaid reports was large and, in fact, about the same as in the binocular condition, consistent with the interpretation that plaid reports were caused by the monocular interaction of the conflicting grating stimuli. Rivalry reports in the monocular rivalry paradigm with blanks at the end of the ISP were rare ([Figure 4C](#)), consistent with the results of [Experiments 1](#) and [2](#) at ISPs around 260 ms.

Finally, these data again confirm that long stimulus presentations (of 180 ms or more)—which should allow for interocular inhibition to take effect (Wilson, 2003; Wolfe, 1984)—do not need to hamper the occurrence of stimulus rivalry, as opposed to previous suggestions (e.g., Wilson, 2003).

Experiment 4: The perceptual dynamics of the three modes of rivalry are statistically not different

In the above, we found that rivalry perception was common with both monocular and stimulus rivalry protocols. In fact, the occurrence of rivalry reports in these protocols was as frequent as in the binocular rivalry protocol. The occurrence of rivalry was dependent on having pattern repetition periods below ~ 350 ms, and blank periods at the end of the ISP and of a duration $> \sim 70$ ms.

Would this similarity in the parameters that induce rivalry also be found for the perceptual dynamics? To test this, we analyzed rivalry dynamics during free-running rivalry. Rivalry dynamics for all three modes of rivalry were analyzed in terms of average percept durations (defined as the time elapsed between two button presses [therefore including transition periods]), the cumulative transition duration (a marker of weak alternations), percept duration distributions, and time-until-first-percept (Fox & Herrmann, 1967; Hupé & Rubin, 2003; Levelt, 1965; van Ee, 2005).

Importantly, we either included or excluded the monocular interactions between the conflicting patterns by keeping the 'on' period at ~ 13 ms (1 frame) and varying the ISP (and therefore blank duration). With very short blank durations, monocular interactions should produce a plaid in both monocular and stimulus rivalry protocols, and consequently, we expect perceptual behavior corresponding to classically reported monocular rivalry behavior (slow alternation dynamics and long transition periods). With longer blank durations the perceptual dynamics of monocular and stimulus rivalry are expected to become more similar to binocular rivalry. This is expected because the monocular interactions between the conflicting stimuli are eliminated with the introduction of blanks (see previous experiments), which creates conditions similar to binocular rivalry, where, by construction,

monocular interactions between the conflicting stimuli are absent.

Methods: Experiment 4

Stimuli

Stimuli were identical to those in [Experiment 1](#), except that contrast was >99.99%, and monocular rivalry stimuli were shown to both eyes (see [Figure 1](#)). Trial duration was

60 s. ‘On’ times were 13 ms (1 frame). ISPs were varied by adding blank frames.

Procedure

Subjects ($n = 4$, 3 of which participated in previous experiments) indicated their dominant percept using either of two keys. They were asked not to press when a fast and regular switching of the two grating patterns was perceived, or when the two patterns were overlaid without

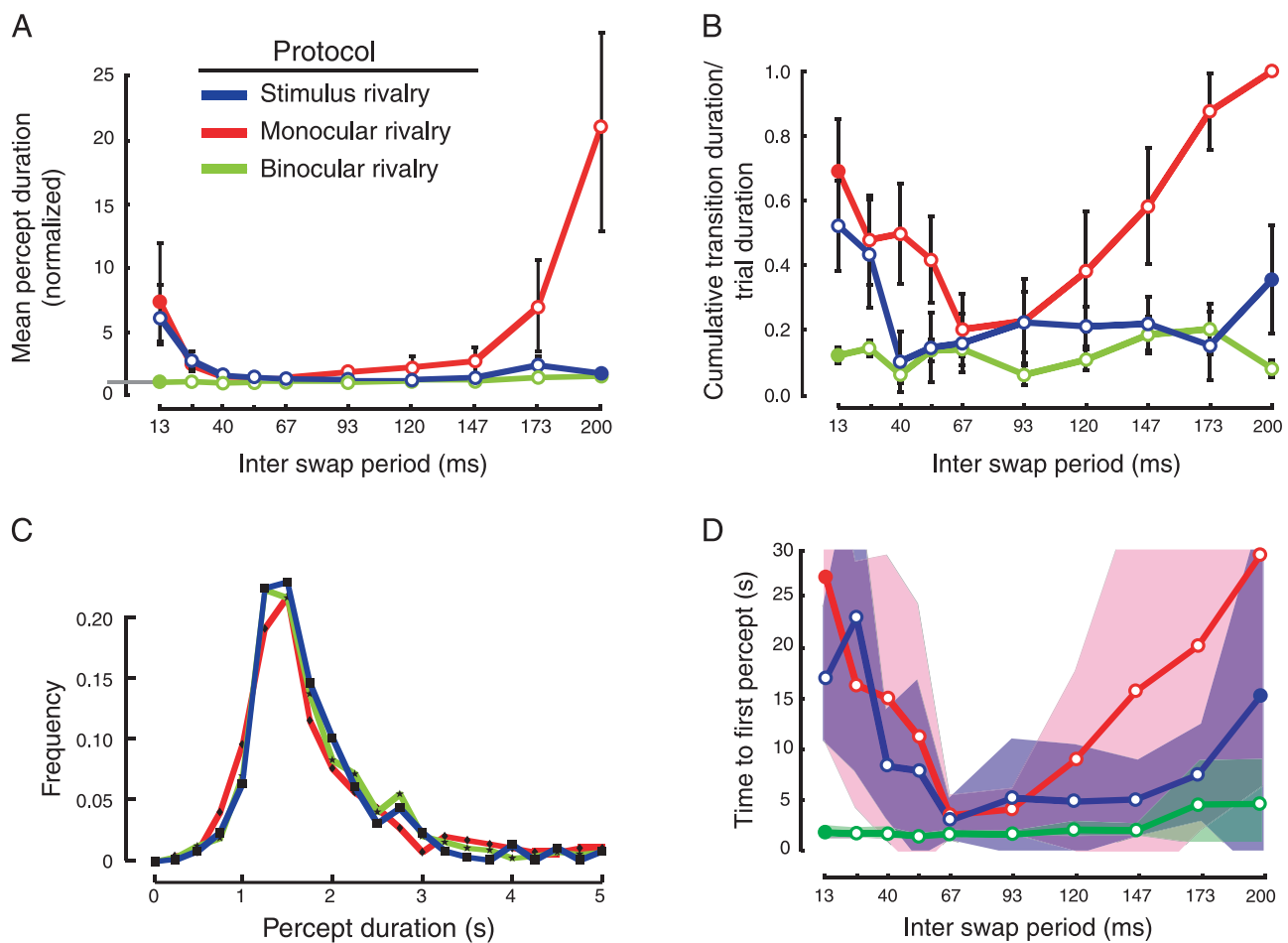


Figure 5. Perceptual dynamics of binocular (green), stimulus (blue), and monocular (red) rivalry protocols. Rapidity (A) and strength (B) of perceptual alternations were probed with the normalized average percept duration (A) and the cumulative transition duration (B), respectively. Filled circles represent stimulus conditions that most closely match conventional monocular, binocular, and stimulus rivalries. At small ISPs, monocular and stimulus rivalry alternations are slow and weak, and binocular rivalry alternations are fast and strong. The behavior of monocular and stimulus rivalries changes with increasing ISP (and therefore blank duration), obtaining perceptual dynamics identical to binocular rivalry at ISPs of about 40–90 ms. At pattern repetition periods larger than about 150–200 ms monocular rivalry is impeded, consistent with it reaching the pattern integration limit at a PRP of about 350 ms ([Figure 1](#)). Error bars are 95% bootstrapped confidence intervals (A) and *SEM*. (B). Bottom panels: (C) Frequency distributions of non-normalized percept durations. The distributions are not significantly different from each other (all pairwise Kolmogorov–Smirnov tests: $p > 0.28$), nor were the average durations (which were log-transformed to approach normal distributions; all three pairwise *t*-tests: $p > 0.35$). Data were combined for ISPs of 53, 67, and 93 ms. (D) Time until first-reported percept depends on the ISP in the same way as the average percept duration does. For small ISPs the time until the first reported percept is large for both monocular and stimulus rivalries, it decreases for larger ISPs, and for even larger ISPs, it increases again, especially for monocular rivalry, although binocular and stimulus rivalries also show an increase. At ISPs around 70–90 ms the differences between the conditions are small. The shaded areas encompass the mean ± 1 std, based on 8 data points. These combined data in this plot strongly suggest that a single rivalry mechanism underlies the perceptual dynamics for all three modes of rivalry.

any of the two being stronger. All 30 (rivalry mode \times ISP) conditions were presented once per session and were randomly interleaved. Four subjects performed two sessions each. In case a trial passed without button presses, a single transition period was recorded. Before further analysis, each percept duration was normalized by dividing it by the mean percept duration of the binocular rivalry condition with an ISP period of 13 ms. The normalization was done separately for each session. Note that this normalization did not bias our data toward similar outcomes in the three modes of rivalry, as we used only one condition as a basis of normalization, i.e., we did not normalize per ISP or per rivalry mode separately. [Figure 5C](#) shows that even non-normalized data show identical duration distributions, showing that the normalization as such was not responsible for the similarities between the rivalry conditions. The total transition duration was normalized by the trial duration ([Figure 5B](#)). The first 20 s of a trial were not analyzed for this calculation (the total trial duration was therefore 40 s). Similarly, the first 10 percepts (amounting to about 20 s) were excluded in the frequency histograms in [Figure 5C](#).

Results: Experiment 4

Consistent with the classical behavior of monocular and binocular rivalries (Breese, 1899; Tong, 2001; Wade, 1975) we found that with continuous presentations (ISP = 13 ms) binocular rivalry (green lines) shows frequent alternations (i.e., short percept durations; [Figure 5A](#)) and “strong” alternations (i.e., small amounts of transition periods; [Figure 5B](#)), whereas monocular rivalry (red lines) shows infrequent and weak alternations.

Interestingly, at ISPs between 40 ms and 90 ms (and therefore blanks of 30–80 ms), perceptual alternations of all three modes of rivalry were fast ([Figure 5A](#)) and strong ([Figure 5B](#)). In fact, dominance duration distributions were not significantly different between the different modes of rivalry ([Figure 5C](#); all pairwise Kolmogorov–Smirnov tests: $p > 0.28$); nor were the average durations different (monocular rivalry: 1.85 s, binocular rivalry: 1.66 s, stimulus rivalry: 1.70 s; all three pairwise t -tests $p > 0.35$ [on log-transformed distributions in order to approach normal distributions]). Even with ISPs up to ~ 150 ms perceptual dynamics are rather similar (see [Figure 5A](#)), and dominance was quite often complete, even for the monocular rivalry protocol. Finally, the time until the first reported percept showed trends similar to those of the average percept durations ([Figure 5D](#)).

Note that even though comparable perceptual dynamics are only found for ISP of 40 ms to about 150 ms (without significant differences between 40 and 90 ms), this is nearly the entire range of ISP that should allow for rivalry, as rivalry does not occur for the monocular rivalry protocol for ISPs above ~ 175 ms (see [Experiment 1](#)). Indeed when quantitatively assessing the limiting pattern

repetition period (PRP) for monocular rivalry in this experiment, we find a limit similar to those reported before for binocular rivalry and stimulus rivalry (see [Experiment 2](#), and van Boxtel, Alais, Erkelens et al., 2008). The limiting PRP was determined as the period where the cumulative percept duration halves compared to the maximum (which for all subjects was close to 1). This yielded an estimate of 269 ± 34 ms, which is not significantly different from the limits reported before (van Boxtel, Alais, Erkelens et al., 2008) for stimulus rivalry and binocular rivalry (all $p > 0.15$; two-tailed t -test).

Discussion

The spatial determinants of rivalry are well described (Alais & Blake, 2005; Blake & Logothetis, 2002), but the temporal characteristics are still largely unstudied. Our results describe two temporal limits to rivalry between simple grating stimuli: one large ~ 350 ms binocular window and one small ~ 50 ms monocular window. When competing patterns are presented to the observer between these limits rivalry occurs as frequent in monocular and stimulus rivalry protocols as in binocular rivalry protocols. Moreover, [Experiment 4](#) showed that rivalry behavior among the three types of rivalry is nearly identical in qualitative and quantitative terms.

The 350-ms binocular limit

We showed that rivalry ceases to occur at interswap periods larger than ~ 150 ms and ~ 400 ms for monocular and stimulus rivalries, respectively. This limit was largely independent of the temporal duty cycle (TDC) of the stimulus ([Experiments 1–3](#)), as long as the temporal duty cycle did not approach 1. In the literature, a 350 ms binocular, pattern-based, limit to binocular rivalry has been reported (O’Shea & Crassini, 1984; van Boxtel, Alais, Erkelens et al., 2008). Indeed, when transformed into pattern repetition periods (PRP; see [Figure 1](#)), the limits for all three types of rivalry, including monocular rivalry, were around 350 ms ([Experiments 1, 2, and 4](#)). In [Figure 6](#) we make a direct comparison of all the limits obtained in [Experiment 4](#) and those of previous investigations (van Boxtel, Alais, Erkelens et al., 2008). The temporal limits of all variations on the binocular rivalry, stimulus rivalry, and monocular rivalry are around a PRP of 350 ms. Clearly, the data from monocular rivalry, stimulus rivalry, and binocular rivalry are quite similar. Even though the monocular rivalry condition shows a temporal limit toward the lower end of all curves, this may well have been caused by the use of spatial frequencies and contrasts in the current study that are generally not considered optimal for monocular rivalry (cf. [Figure 3](#)).

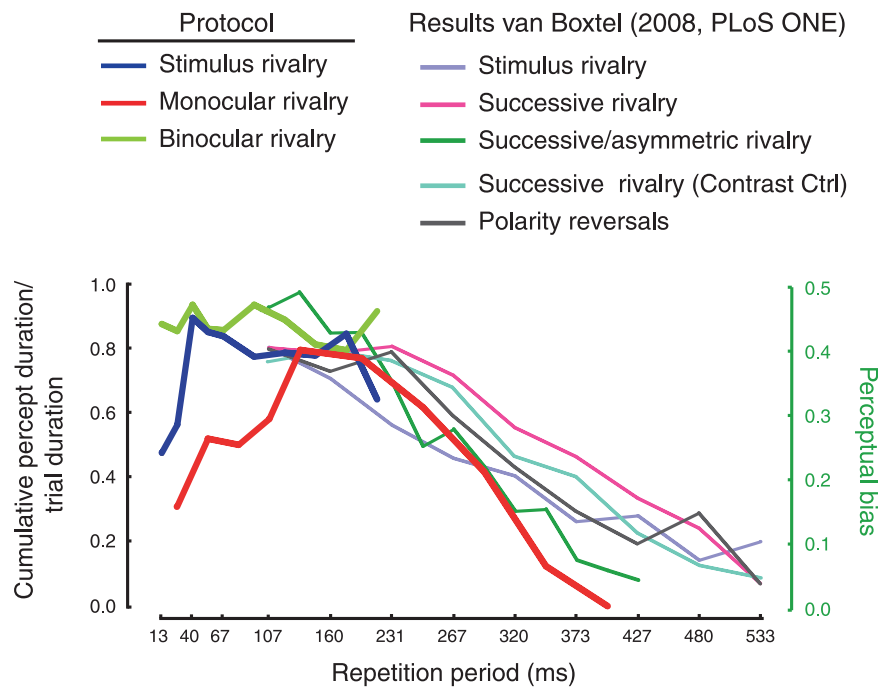


Figure 6. The temporal limits in terms of pattern repetition periods for binocular rivalry, stimulus rivalry, and monocular rivalry. The fat lines are data obtained in [Experiment 4](#). The thin lines are data obtained in a previous study (van Boxtel, Alais, Erkelens et al., [2008](#)). The average of the cumulative percept duration over subjects is plotted. The data show that the monocular rivalry data fall within the normal spread of the data obtained with other protocols. An explanation of conditions can be found in van Boxtel, Alais, Erkelens et al. ([2008](#)). Briefly, successive rivalry is induced when the intermittently shown stimuli are presented in temporal anti-phase (such as in binocular rivalry conditions, [Experiment 2](#)). Successive/asymmetric conditions are similar to successive rivalry, but the temporal phase difference is <180 degrees. In these experiments subjects either perceived binocular rivalry or repetitive dichoptic masking (van Boxtel, Alais, Erkelens et al., [2008](#)). Therefore, we used the perceptual bias as a measure (y-axis on the right), which shows the transition from binocular rivalry to dichoptic masking. In the polarity reversal experiments both patterns reversed in contrast polarity at each presentation.

Previous results on stimulus rivalry (Lee & Blake, [1999](#); Logothetis et al., [1996](#)) had hinted at the 350 ms limit to rivalry (Lee & Blake, [1999](#); van Boxtel, Alais, Erkelens et al., [2008](#); van Boxtel et al., [2007](#)). However, because in the previous studies the two eyes' views were continuously in conflict, interocular interactions might have maintained this limit. Our finding of this same limit with completely monocular presentations supports the view that it truly concerns a pattern-based limit. This temporal limit is shared by all three modes of rivalry, which is an indication of a common origin.

Where within the visual system is this temporal limit determined? Given the pattern-based processing, and the rather long temporal limit, we suggest that the probed rivalry stage is placed at a binocular level, possibly even at levels as high as V4 or LOC, which have suitable timing limits (Jiang, Zhou, & He, [2007](#); Kourtzi & Huberle, [2005](#); Mukamel, Harel, Hendler, & Malach, [2004](#)).² In possible opposition to this suggestion, the LOC and V4 have rather large receptive fields, compared to the strict dependencies of rivalry on spatial overlap between the competing patterns. However, the neurons within these areas may cooperate and together have a spatial resolution that is finer than their individual receptive field sizes

(hyperacuity, cf. Bosking, Crowley, & Fitzpatrick, [2002](#); Edelman, [1995](#)). Alternatively, it is possible that the temporal limits to rivalry are determined at another level within the visual system, say LOC, than the spatial restrictions, say V1. This would be consistent with the current view that rivalry is a multistaged process (Blake & Logothetis, [2002](#)), as deduced from neurophysiological (Leopold & Logothetis, [1996](#); Logothetis & Schall, [1989](#); Sheinberg & Logothetis, [1997](#)), psychophysical (Nguyen, Freeman, & Alais, [2003](#)), and computational findings (Freeman, [2005](#)), and it is consistent with the view that some brain areas are especially important for temporal aspects of stimulation (Battelli, Pascual-Leone, & Cavanagh, [2007](#)).

The 50-ms monocular limit

A second, ~ 50 – 80 ms, monocular window was revealed for stimulus rivalry and monocular rivalry in [Experiments 2](#) to [4](#). We found that when the two competing patterns are presented within a *single* eye within a period of ~ 50 ms the patterns interact. This interaction may lead to percepts of frequent and regular alternations in orientation when

‘on’-times are long or to plaid percepts when ‘on’-times are short. These monocular interactions therefore lead to a decrease in rivalry reports. The same 50–80 ms window was not found in the binocular rivalry protocol. This is consistent with the view that the 50 ms window is a monocular interaction window, because in binocular rivalry the two competing patterns are never presented to a single eye, and therefore, binocular rivalry should not show this limit.

The likely position of the 50-ms limit is early in the visual pathway. Firstly, the 50-ms limit is dependent on monocular interactions. Secondly, the estimated size of the monocular interaction window (~50 ms) is consistent with integration periods of early visual neurons (Hawken, Shapley, & Grosf, 1996). Therefore, the most likely neural substrate of the 50-ms monocular interaction window lies within the LGN or V1.

A link to visible persistence

Previously, we have tentatively linked the 350 ms binocular limit to the phenomenon of visible persistence (van Boxtel, Alais, Erkelens et al., 2008). These mechanisms share a similar temporal limit (Coltheart, 1980b; Meyer & Maguire, 1977; Tolhurst, 1973; Van de Grind, Gruesser, & Lunkenheimer, 1973) and phenomenological appearance (that is, a seeming visible persistence in the absence of direct stimulation).

In the literature on visible persistence, a distinction has been made between a central long-lasting form of visible persistence (limit: ~300 ms) and a peripheral short-lasting form of visible persistence (limit: ~80 ms; Coltheart, 1980a, 1980b; Engel, 1970). These limits show a similarity to the limits we identify in this report. First, the central long-lasting limit shows clear resemblance to our 350 ms binocular temporal limit, and second the peripheral short-lasting limit is very similar to our ~50–80 ms monocular limit. The monocular persistence could be the process that links the two competing stimuli together and prevents rivalry from occurring at a binocular (and central) stage.

Comparison between different modes of rivalry

Previous comparisons between the different modes of rivalry have shown that many qualitative similarities exist (e.g., Andrews & Purves, 1997; Leopold et al., 2005; Logothetis et al., 1996; Pearson & Clifford, 2005). Often however these similarities were reported to be confined to a limited parameter space (Lee & Blake, 1999), or they showed large differences in quantitative aspects (e.g., much longer percept durations in monocular rivalry protocols).

Our results, on the other hand, do show a large quantitative agreement between the different modes of rivalry. Specifically, we showed that with the introduction of blanks both monocular and stimulus rivalries lost most of the dependence on spatial frequency and the presence

of a 19 Hz flicker, and rivalry was commonly reported in parameter ranges that were previously reported not to lead to rivalry (Lee & Blake, 1999). Our results suggest that the rivalry-promoting effects of the 19 Hz flicker in the stimulus rivalry paradigm (Lee & Blake, 1999; Logothetis et al., 1996) may be largely due to the concurrent introduction of a 2-frame (~26 ms) blank before each swap. Larger blanks are even more effective in producing rivalry percepts. At interswap periods (ISPs) over a range of 40–90 ms, the perceptual behavior was statistically non-significantly different between the different modes of rivalry. Although this may seem a limited range, one should note that the upper temporal limit to rivalry is determined by pattern-repetition frequencies and not by the ISP. In this dimension the perceptual dynamics are very similar up to ~350 ms (see, e.g., Figure 6).

These findings strongly suggest that the *temporal limits* of the three modes of rivalry are determined by the same mechanism that, as we have discussed, reside at a binocular pattern-based processing stage.

This need not mean that spatial limits to rivalry are also determined by the same system for the three modes of rivalry, but it seems possible. The dependence on spatial characteristics have been reported to differ between the different modes of rivalry (e.g., Lee & Blake, 1999). However, our results suggests that when monocular interactions between conflicting stimuli are reduced, stimulus rivalry (and monocular rivalry) are induced over a wider range of spatial frequencies, being more similar to binocular rivalry (which by construction does not have these monocular interactions). However, more research is needed to see whether this increased similarity is a footprint of a single underlying mechanism in the spatial domain.

Where does competition and where does suppression take place? If spatial limitations of rivalry are indeed determined by a single system (which then is pattern-based), the frequently reported eye-based effects on rivalry (e.g., Blake, Westendorf, & Overton, 1980; Fox & Check, 1972; Wales & Fox, 1970) need to be explained through feedback (Blake & Logothetis, 2002; Logothetis, 2002; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001; Schmielau & Singer, 1977; Tong, Meng, & Blake, 2006; van Boxtel, Alais, & van Ee, 2008). In this scenario, competition between stimuli and eye-based suppression from awareness are different processes, possibly taking place at different neural sites. This idea is consistent with the idea that the site where the interocular incompatibility is registered may be different from the site where suppression takes place (Blake, 2001; Fox, 1991). Consistent with our findings and the current literature, one could envision rivalry (e.g., competition) to take place at a binocular level, while feedback to monocular neurons causes the subsequent eye-based suppression effects. Furthermore, placing the rivalry stage at a binocular, pattern-based, level is consistent with neurophysiological findings that monocular neurons do not change their firing rate when binocular conflict is present, whereas binocular

cells do (Andrews, Sengpiel, & Blakemore, 2005; Leopold & Logothetis, 1996). At the same time, supposing that the rivalry suppression occurs at a monocular level is consistent with the psychophysical (Fox & Check, 1972; Wales & Fox, 1970) and neuroimaging (Tong & Engel, 2001) literature.

Conclusion

Although well studied in terms of its spatial determinants, binocular rivalry has not been thoroughly investigated in the temporal domain. We show that temporally modulated stimuli are valuable tools in dissecting the visual system and identifying and describing the processes that conduce toward the build-up of awareness during normal vision and rivalry. We have identified two temporal limits to rivalry between competing gratings. One limit is general to the three types of rivalry and is a 350-ms binocular pattern-based limit. When each of the competing patterns is repeated within a 350-ms window, rivalry may occur. The other limit is a 50-ms monocular limit, which may impede rivalry when conflicting patterns are presented to a single eye within this time window. The importance of temporal parameters of stimulation is underlined by our finding that for temporal parameters between the two identified limits the rivalry dynamics between binocular, monocular, and stimulus rivalries are statistically non-significant. Indeed we showed that monocular rivalry may have perceptual dynamics identical to those of binocular rivalry.

The finding of a shared higher level processing in these rivalry processes may mean that other forms of rivalry will also show that same temporal limits. If rivalry is registered at a binocular, pattern-based, level, as our findings indicate, the observed eye-dependent suppression is possibly dependent on feedback from binocular to monocular levels in the visual system.

Importantly, our findings have shown that some current models of multi-level rivalry mechanisms fail to predict our data. Our results provide constraints for future computational models of binocular rivalry.

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Footnotes

¹This type of rivalry involves rivalry between neurons that encode incompatible stimulus characteristics but not necessarily (strong) eye of origin information.

²Neurons in the dorsal stream may also have long integration periods, as integration periods of over a second have been reported for optic flow processing (Burr & Santoro, 2001), showing that long integration periods may be quite common. Early motion processing has shorter integration periods (Snowden & Braddick, 1991).

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