Dichoptic masking and binocular rivalry share common perceptual dynamics

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Two of the strongest tools to manipulate visual awareness of potentially salient stimuli are binocular rivalry and dichoptic masking. Binocular rivalry is induced by presenting incompatible images to the two eyes over prolonged periods of time, leading to an alternating perception of the two images. Dichoptic masking is induced when two images are presented once in rapid succession, leading to the perception of just one of the images. Although these phenomena share some key characteristics, most notably the ability to erase from awareness potentially very salient stimuli, their relationship is poorly understood. We investigated the perceptual dynamics during long-lasting dynamic stimulation leading to binocular rivalry or dichoptic masking. We show that the perceptual dynamics during dichoptic masking conditions meet the classifiers used to classify a process as binocular rivalry; that is, (1) Levelt's 2nd proposition is obeyed; (2) perceptual dominance durations follow a gamma distribution; and (3) dominance durations are sequentially independent. We suggest that binocular rivalry and dichoptic masking may be mediated by the same inhibitory mechanisms.

Introduction

Binocular rivalry and dichoptic masking provide excellent means to study the formation of awareness, because both tools allow one to control the visibility and awareness of a stimulus by presenting a competing stimulus in close spatial or temporal proximity (reviewed in Blake & Logothetis, 2002; Breitmeyer & Ogmen, 2006; Macknik, 2006).

Even though both binocular rivalry and dichoptic masking are well-studied phenomena, their relationship is not well understood. This lack of knowledge exists because the two tools have, to our knowledge, never been studied with the same set of stimuli in a single comparative study. One other reason is that research questions for the two tools have generally differed. Research on binocular rivalry is mainly focused on the spatial determinants controlling stimulus visibility, finding for example that with increasing orientation and spatial frequency differences the rivalry rate increases between competing interpretations (e.g., Alais & Blake, 2005; Hollins, 1980; O'Shea, 1998; O'Shea, Sims, & Govan, 1997; Schor, 1977). When studied, temporal stimulus modulations in the order of hundreds of milliseconds do not seem to affect binocular rivalry (O'Shea & Blake, 1986; O'Shea & Crassini, 1984; Wolfe, 1983). Dichoptic masking research, on the other hand, is mainly focused on temporal aspects of stimulus visibility, showing, for example, that competition is strong at short stimulus onset asynchronies and decreases with longer asynchronies (e.g., Breitmeyer & Ogmen, 2006; Breitmeyer, Rudd, & Dunn, 1981; Kolers & Rosner, 1960; Macknik, Martinez-Conde, & Haglund, 2000; Michaels & Turvey, 1979; Schiller, 1965; Turvey, 1973). Interestingly, there is a distinct research direction within the dichoptic masking field that does study spatial characteristics of stimulation. This line of research uses spatially and temporally overlapping targets and masks (e.g., Baker, Meese, & Summers, 2007; Legge, 1979; Levi, Harwerth, & Smith, 1979; McKee, Bravo, Taylor, & Legge, 1994; Meese & Hess, 2004) and seems more focused on binocular interactions per se than on object or event perception.

There are hints in the masking literature that suggest a link to binocular rivalry. For example, dichoptic masking studies show that the addition of the third stimulus to the target-mask sequence may lead to the annihilation, or weakening, of mask's efficacy (dichoptic studies: Michaels & Turvey, 1979; Turvey, 1973; and monoptic studies: e.g., Breitmeyer et al., 1981; Dember &

Purcell, 1967). Furthermore, masking strength decreases with increasing number of target-mask cycles (implicit in the reports of Kolers & Rosner, 1960; Schiller & Smith, 1966; Werner, 1935), an effect reminiscent of the resurfacing of a percept of the suppressed stimulus after prolonged stimulation during binocular rivalry. In this report, we study the effects of long-lasting stimulation on dichoptic masking, and the possible relations to binocular rivalry it may reveal.

Previously we have shown (van Boxtel, Kamphuisen, van Ee, & Erkelens, 2006) that binocular rivalry may take place with intermittent stimulation (see also O'Shea & Crassini, 1984, who termed this condition successive rivalry), even when stimulation in the two eyes is asynchronous (see, e.g., Figure 1A). While viewing these stimuli, the observer perceives one of the two oriented gratings flickering on and off (being "off" most of the time), while the other stimulus remains invisible. After a certain time (~2 seconds) perception switches to the other grating, etc. (this chain of events is schematically drawn in Figure 1B, top panel). However, we also showed that with asynchronous stimulation, binocular rivalry cedes to

dichoptic masking when the period of pattern repetition exceeded ~350 ms (van Boxtel et al., 2006) (schematically drawn in Figure 1B, bottom panel). Taking these minimally different stimuli—in many cases differing only in stimulus repetition period—allowed us to investigate whether dichoptic masking and binocular rivalry are outputs of a single dynamical system, or instead are two separate processes. We focused on the perceptual dynamics of binocular rivalry and dichoptic masking employing long-lasting dynamic stimulation described in Figure 1.

For binocular rivalry, the perceptual dynamics of alternations in dominance are characterized as follows: (1) dominance durations follow a gamma distribution; (2) the dominance durations of the percepts are temporally uncorrelated (Fox & Herrmann, 1967); (3) Levelt's 2nd proposition is obeyed (Fox & Rasche, 1969; Levelt, 1967), meaning that changing the contrast of one eye's pattern will change the dominance durations of the pattern in the other eye but will leave the dominance durations of the contrast-changed pattern unchanged; or put in a modified form (which is valid over a larger contrast range): changes
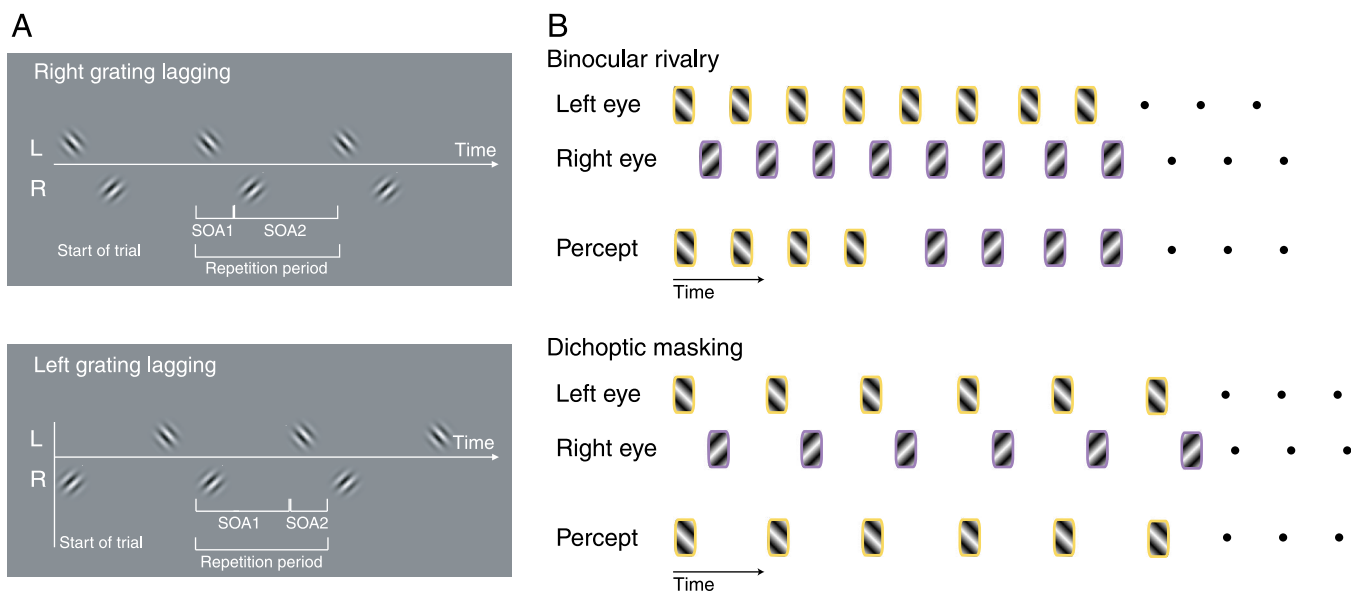

Figure 1. *Two example stimuli used in the experiment*. (A) Orthogonal gratings were presented to the two eyes. At the start of the trial, either the grating in the right eye or the grating in the left eye was temporally offset (see top panel and bottom panel, respectively). The stimulus onset asynchrony (SOA) between the first and the second presentation was termed SOA1, the SOA between the second and third presentation (which was equal to the first) was termed SOA2. The sum of SOA1 and SOA2 is the repetition period. The top panel represents a case where SOA1 is smaller than SOA2, whereas the bottom panel represents a case when SOA1 is larger then SOA2. The effective stimulation is identical in both cases, apart from the start of the trial, therefore we pooled the data of these conditions in our analysis, and in the remainder of the figures we show the dependence on the shortest of the two SOA (i.e., minSOA = MIN[SOA1,SOA2]). We refer to the stimulus that precedes the shortest SOA as the "lead" stimulus, and the stimulus that follows this SOA as the "lag" stimulus. The percepts linked to these two stimuli are called "lead" and "lag" percept (see text). (B) The perceptual consequences of stimulation with repetition cycles <350 ms (top panel) are binocular rivalry. The percept will consist of bouts of flickering leftward tilted gratings and flickering rightward gratings. Bottom panel: The perceptual consequences of stimulation with repetition periods >350 ms are dichoptic masking. The percept will consist of long stretches of a single flickering grating, only to be interrupted briefly and infrequently by the competing pattern.

in one eye's contrast mainly affect dominance durations in the higher contrast eye (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006).

We show that both successive rivalry and dichoptic masking meet the perceptual dynamics criteria set for conventional binocular rivalry. We observe as well that the first reported percept shows signs of dichoptic masking. Depending on stimulus parameters, this initial dichoptic masking may be restricted to the first percept (after which binocular rivalry takes place), or it may be sustained throughout the trial, leading to near-continuous dichoptic masking.

From the fact that the perceptual criteria for binocular rivalry are met by dichoptic masking, we suggest that dichoptic masking and binocular rivalry are mediated by the same inhibitory mechanisms.

Methods

Stimulus

Spatial characteristics

Stimuli were orthogonally oriented (45 deg from vertical) gratings, having a spatial frequency of 0.87 cycles/deg. The stimulus was drawn as seen through a circular Gaussian window with a sigma of 0.76 deg, with a spatial cutoff at a diameter of 4.3 deg. Michelson contrast was 1 at the center of the display. The leftward tilted grating was presented to the left eye, the rightward tilted grating to the right eye. Background luminance was 20.0 cd/m^2, maximum and minimum stimulus luminance (i.e., white and black parts of the grating) were 71.9 cd/m^2 and 0.06 cd/m^2, respectively. The stimulus was surrounded by a binocular annulus that was divided into 20 equally sized parts alternatively made of full contrast (white) and zero contrast (gray). The annulus was 0.1 deg wide, with a radius of 2.46 deg, and served as a fusion aid.

Temporal characteristics

The grating patterns were flickered on and off for 60 seconds. On-times were 53.3 ms (4 frames), and off-times were either 133.3 ms, or 293.3 ms, leading to repetition periods of 186.7 ms and 346.7 ms, respectively (Figure 1). These stimuli produce binocular rivalry and dichoptic masking respectively (van Boxtel et al., 2006). Left and right eye were temporally offset relative to the each other by a stimulus onset asynchrony (SOA). The SOAs ranged from 0 ms (i.e., no lag) to the size of the repetition period, in steps of 26.6 ms (i.e., two frames; Figure 1). In plotting and discussing the data, we use the shortest of the two SOAs, which we term minSOA (i.e., minSOA = MIN [SOA1,SOA2]). The pattern that preceded the shortest SOA is termed the lead pattern, the pattern following the shortest SOA is termed the lag pattern.

Procedure

Throughout the trial, subjects indicated their dominant percept using two buttons (left and right arrows for left- and right-tilted gratings, respectively). When both stimuli were perceived to be about equally salient (i.e., a spatial patchwork or a superposition of the two gratings), or when they did not engage in rivalry (i.e., they were rapidly and regularly alternating), subjects did not press any button.

Percept durations were recorded as the time between a button press and release. A percept was not used in the analysis when the end of a trial truncated it. Trials with different repetition periods were run in separate sessions, otherwise presentation order was randomized. Each condition was measured three times per subject.

Subjects

Seven subjects participated, each has normal or corrected-to-normal vision. All but one subject (the first author) were naïve as to the purpose of the experiment. As two subjects did not show signs of dichoptic masking at the repetition period of 347 ms, their data were excluded from the analysis of this repetition period. (For both subjects, we have determined that dichoptic masking does take place at still longer repetition periods in a separate experiment.)

Analysis

Perceptual bias

The total time spent in the "lag" percept (the percept of the stimulus that followed after the shortest of the two SOAs, see Figure 1) was divided by the total time spent in either percept.
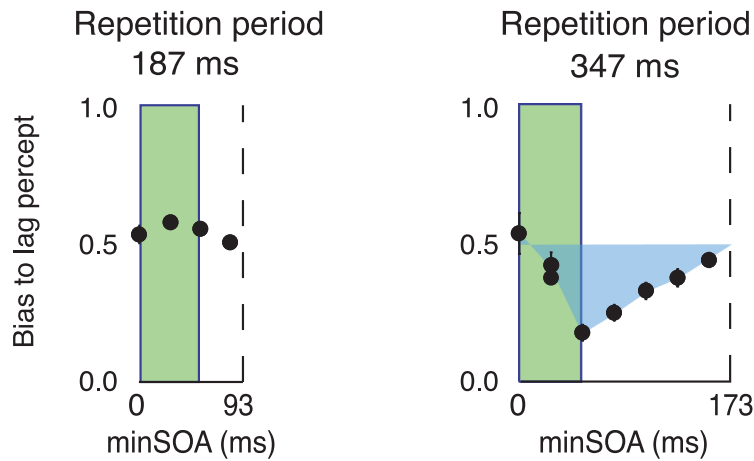
Percepts follow a gamma distribution

The reported gamma distribution fits are maximum-likelihood fits, based on all percepts of all subjects, without normalizing. We did not normalize the data in order to show the differences in mean percept durations between minSOA conditions. When each subject's data was divided by the subject's mean percept duration before pooling the data over all subjects, gamma distributions still provided good fits (all means of squared errors <0.017).
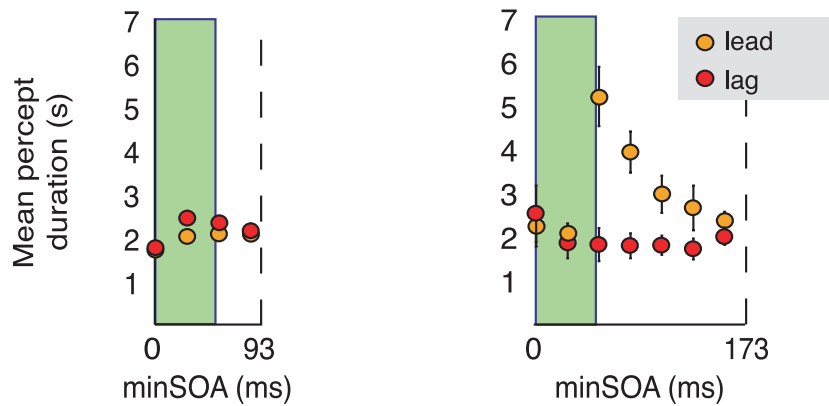
Drift analysis

Before conducting a test of independence of percept durations, we assessed whether there was drift in the data, because drift may cause spurious correlations in the percept durations. We divided each trial in 13 bins, within which the average percept duration was calculated for all
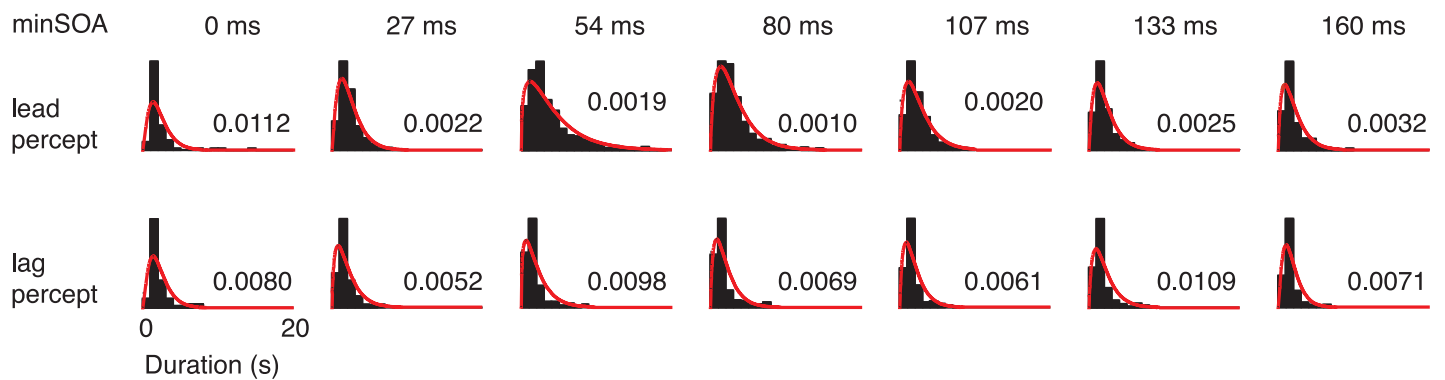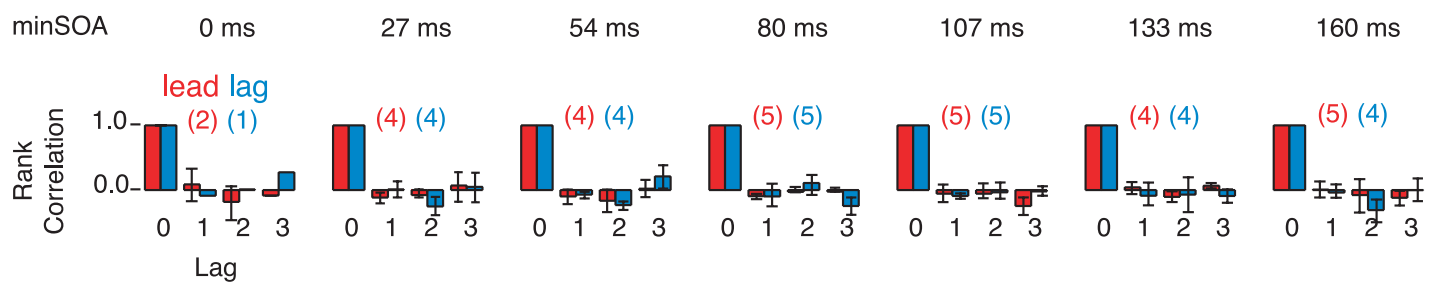
A   Perceptual Biases

B   Levelt's 2nd proposition

C   Gamma distribution fits. Period 347 ms

D   Spearman rank correlations. Period 347 ms

percepts that started within that bin. The averages of all trials were then used to calculate average percept durations per bin, per subject. A Bin × Subject ANOVA revealed no significant effect of Bin number ($p > 0.42$), but a significant effect of Subject ($p < 0.001$), post hoc Tukey analysis showed that one subject had significantly higher durations than all other subjects. The interaction Bin × Subject was not significant ($p > 0.77$). A separate analysis showed that the drift over sessions was also not significant ($p > 0.85$).

Independence of percept durations

Because of the absence of drift, we could calculate Spearman rank correlations (van Ee, 2005) over entire trials. Only trials with more than 5 reported percepts are analyzed, which caused some minSOA results not to be based on all subjects (see Figure 2D).

Calculation of bias index

A bias index was designed to describe the development of the average perceptual bias towards one or the other percept during a trial, allowing discrimination between binocular rivalry and dichoptic masking behavior trough the trial. We calculated a bias index by assigning a value of 1 to percepts of the lag pattern, 0 to percepts of the lead pattern, and 0.5 to transition periods (i.e., when no buttons were pressed). At several time points during a trial (taken 1 second apart, Figure 4), we calculated the mean over these values for all trials at that point in time. Note that we assigned a value to transition periods, as it seems they represent a separate perceptual state (Brascamp et al., 2006). Because they do not represent a bias in a particular direction, we assigned them an intermediate value of 0.5.

Results

The perceptual dynamics of the two tested repetition periods are shown in Figure 2. To show that binocular rivalry was obtained with the 187-ms repetition cycle, and dichoptic masking with the 347-ms repetition cycle, we first analyzed the overall bias in percept durations (Figure 2A). Previous work found that binocular rivalry occurred at the shorter repetition period of 187 ms (O'Shea & Crassini, 1984; van Boxtel et al., 2006) and dichoptic masking at longer repetition periods (van Boxtel et al., 2006). Therefore, we expected that short repetition periods would not lead to a strong bias toward one or the other stimulus, and hence a bias-value of around 0.5, and that longer repetition periods would show a strong bias towards one of the two stimuli, and a bias-value different

from 0.5. Both expectations were borne out by the analysis (Figure 2A; on the y-axis is shown the total time spend in the percept of the lag grating, divided by the total time spend in either percept).

These analyses, based on the biases calculated over entire trials, have revealed that conventional binocular rivalry took place for stimuli with a repetition cycle of 187 ms (O'Shea & Crassini, 1984 reported this finding for in-phase, SOA = 0 ms, and antiphase conditions), whereas strong forward masking occurred with a repetition cycle of 347 ms. Therefore, we can use these stimuli to investigate the relationship between binocular rivalry and dichoptic masking with (nearly) identical stimuli.

Is the forward dichoptic masking we observed (Figure 2A, right) a different kind of binocular conflict resolution than binocular rivalry (Figure 2A, left), or is it a biased version of binocular rivalry? In other words, do these phenomena depend on the same or different neural processes? To investigate the question, we looked at the 3 perceptual dynamics classifiers of binocular rivalry and assessed whether they applied to dichoptic masking.

Figure 2. *Testing the three classifiers of binocular rivalry on dichoptic masking data*. (A) Perceptual biases were calculated as the total time spent perceiving a "lag" pattern divided by the total time any of the two patterns was perceived. With repetition periods of 187 ms (left), the value of minSOA (i.e., Min[SOA1, SOA2]) had only a small influence on the perceptual biases, which in all cases were near 0.5. With repetition periods of 347 ms, strong (forward) masking was observed (a bias towards the "lead" pattern; shaded area). Green-shaded areas denote SOA conditions with a temporal overlap between the two stimuli. Error bars are *SEM* over trials. (B) The generalized 2nd proposition of Levelt poses that in response to changing the saliency of one of the stimuli, the percept durations of the most dominant pattern should change. The graph for repetition periods of 187 ms shows only marginal changes in dominance durations, which is consistent with the finding that these conditions show hardly any perceptual biases. The graph for repetition periods of 347 ms, however, clearly follows the generalized 2nd proposition of Levelt. Error bars are *SEM* over trials. (C) Gamma distribution (red lines) were well fit to all percept duration distributions (black frequency distributions), for both lead and lag percepts. Values reported in each graph are the means of squared errors (*MSE*), a measure of the fit quality. (D) Spearman rank correlations for both lead and lag percepts were calculated for a range of different lags. The correlation is weak at all lag values, for all conditions. Error bars are between-subject standard errors, the colored numbers indicate the number of subjects over which the mean and *SE* were calculated (see methods). Together these data show that binocular rivalry and dichoptic masking follow the same dynamic behavior. According to prevailing perceptual dynamics criteria, these results constitute evidence for the hypothesis that binocular rivalry and dichoptic masking result from the same underlying dynamical system.

Levelt's 2nd proposition

We did not explicitly change the contrast of the stimuli to which Levelt's 2nd proposition applies, but we did vary the SOAs, and as we have shown, this manipulation biased the percept towards one or the other pattern, just as contrast would. We cannot use our minSOA parameter (i.e., Min[SOA1,SOA2]) as a direct analogue of contrast, however, because our stimuli had fixed repetition periods, which meant that a change in SOA1 automatically lead to a change in SOA2 (see Figure 1), analogous to changing contrast in both eyes. However, we can test the general version of Levelt's 2nd proposition: Changes in one eye's contrast mainly affect dominance durations in the eye with the most dominant pattern (Brascamp et al., 2006), that is, the lead stimulus (see Figure 2A, right).

First, the data pertaining to conditions with repetition cycles of 187 ms show no large change in average dominance durations, and therefore these conditions do not represent a temporal analogue of Levelt's 2nd proposition. This finding is in agreement with the finding that they did not show a perceptual bias either (Figure 2A, left).

In the dichoptic masking regime, with repetition periods of 347 ms, mean percept durations did depend on minSOA. Starting, in Figure 2B (right panel), at the point where SOA1 and SOA2 are nearly identical (around minSOA = 177 ms), we observe that the percept is unbiased, which would be analogous to equal contrasts in the two eyes. Moving to the left in this graph, we observe that the mean percept duration of the lead stimulus increases whereas that of the lag stimulus does not change, which is in accordance with the generalized 2nd proposition of Levelt.

A deviation from the predicted behavior occurred when the stimuli temporally overlapped (i.e., at left of the plot). In this case, both patterns had mean dominance durations of about 2 seconds. "False fusion" (Blake, Yang, & Westendorf, 1991; Wolfe, 1983), a process causing dichoptic stimuli to fuse with short presentation periods, may have prevented strong inhibitory interactions in these cases, even though rivalry still occurred (O'Shea & Crassini, 1984; Wolfe, 1983).

Nevertheless, our results show that conditions that lead to dichoptic masking follow the generalized 2nd proposition of Levelt.

Distributions of percept durations

Both lead and lag percept duration distributions followed a gamma distribution (Figure 2C), suggesting that the perceptual dynamics followed the same set of rules in all these conditions, as well as during normal binocular rivalry. In cases of strong masking average durations of the lead percept increased while the

distribution remained gamma-shaped. The distribution for lag percept durations remained unchanged relative to the conditions in which both patterns exerted about equal inhibitory forces on each other (e.g., at minSOA = 0 ms and 160 ms).

Temporal independence of percept durations

We tested for the independence of the percept durations using the Spearman rank correlation (van Ee, 2005). Both lead and lag percept durations were temporally independent of the following percept of the same class, as evidenced by the small correlations between the different percept durations (Figure 2D).

The 187-ms period condition also met the perceptual criteria, indicating that these conditions of *successive rivalry* (O'Shea & Crassini, 1984) behaved just as conventional rivalry.

Altogether, the dichoptic masking conditions met the 3 perceptual classifiers of binocular rivalry, suggesting a common neural structure for the found percept-competition reported with both techniques.

The time course of dichoptic masking and binocular rivalry

In order to see how much of the observed biases (in Figure 2A) can be attributed to the first percept (cf. Hupé & Rubin, 2003), we calculated the biases towards either one or the other percept for the first button press. Three interesting observations were made. First, when biases are reported as the number of trials in which the first percept was that of the lag stimulus divided by the total number of trials, both the 187-ms and 347-ms repetition periods showed dichoptic masking behavior for the first percept (Figures 3A and 3B). For the repetition period of 347 ms, dichoptic masking was expected as a bias was already observed in the overall data (Figure 2A), but for the repetition period of 187 ms this was not the case (although a small bias seen at minSOAs around 27 ms might have suggested this finding; Figure 2A). Interestingly, even though the initial stimulus sequence for the stimuli with 187 ms and 347 ms repetitions cycles was identical (for the minSOA range 0–80 ms), the masking effects of the two repetition periods were in opposite directions. We have no explanation for this result, but it may be related to the observation that the addition of an additional stimulus in the DM paradigm may reduce backward masking of the mask on the target (Michaels & Turvey, 1979).

A second observation was that the first perceptual report was generally made swiftly, around 2–3 seconds after the trial began (Figures 3C and 3D, for the 187-ms and 347-ms repetition cycles, respectively). However, for
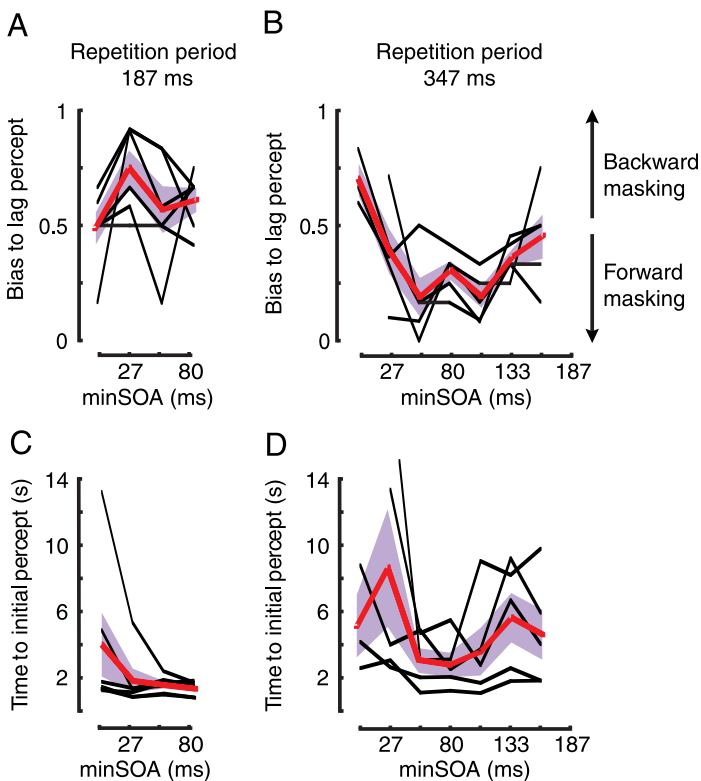
Figure 3. *Masking effects on the first perceptual report.* (A) Proportion of the initial percepts being the lag stimulus for stimuli with a repetition period of 187 ms. The bias toward the lag stimulus for short minSOAs shows evidence for backward masking. (B) Proportion of the initial percepts being the lag stimulus for stimuli with a repetition period of 347 ms. The bias towards the lead stimulus shows evidence for forward masking. (C) The average time until the first percept, for stimuli with a repetition period of 187 ms. Longer durations are observed in conditions with the inhibitory interactions being about equal between the two stimuli (that is at minSOA = 0). (D) Same as in panel C, but for stimuli with a repetition period of 347 ms. Panels C and D show that the first percept generally was formed swiftly, but it takes longer to form when inter-pattern competition is balanced. The black lines are individual subject data, the red line is the mean, the purple-shaded area is the between-subject standard error.

both repetition cycles, we observed a tendency towards longer durations for conditions when the inhibitory interactions between the patterns were equal (either because stimuli were near-simultaneous or because SOA1 was nearly equal to SOA2, see the right- and left-end side of each plot). These data suggest that the initiation of binocular rivalry is not always instantaneous (see also Liu, Tyler, & Schor, 1992). In fact we found that conditions that lead to masking lead more rapidly to an unambiguous percept than conditions that lead to binocular rivalry.

The third observation followed from the acknowledgment that the bias of the initial percept may be the main

cause of the biases observed in dichoptic masking and binocular rivalry (Figure 2A). To analyze how much of the observed perceptual biases based on the full-trial data could be accounted for by the initial percept, we calculated a bias index (see Methods). We compared the time course of the bias index for the data including only the first percept, and for the data including all percepts. As such, we investigated if the binocular interactions were changing over the course of a trial. The bias index in conditions with repetition periods of 187 ms and 347 ms are shown in Figures 4A and 4B, respectively.

We show data for the minSOA conditions with the most extreme biases (see Figures 2A and 3). The blue line shows the bias index calculated using all perceptual reports, the red line shows the bias index based solely on the first percept (all later percepts are scored as transition periods, i.e., a value of 0.5). The bias index based on all perceptual reports for repetition periods of 187 ms showed a short-lasting backward masking, which could, however, be fully accounted for by the bias caused by the first percept (the red line). The bias index for repetition periods of 347 ms showed a sustained bias that could not be explained based solely on the basis of the first percept (i.e., the red curve regresses toward 0.5, whereas the blue curve remains at ∼0.2). Therefore, the biases observed in Figure 2A are caused predominantly by the first percept for stimuli with repetition periods of 187 ms, but not for those with repetition periods of 347 ms.

General discussion

The relationship between binocular rivalry and dichoptic masking

The relationships between results from the various techniques used in the investigation of the formation of visual awareness are only beginning to be explored (Breitmeyer & Ogmen, 2006, pp. 272–275; Kim & Blake, 2005; Tsuchiya, Koch, Gilroy, & Blake, 2006). In this study, we looked at the dependence of the stimulus' visibility on temporal stimulus characteristics, and how this dependence differed during binocular rivalry and repetitive dichoptic masking. Specifically, we tested whether the classifiers related to the perceptual dynamics of binocular rivalry are also met by dichoptic masking.

We show that dichoptic masking satisfies the perceptual dynamics criteria for binocular rivalry (Figure 2), namely, (1) the patterns presented to the two eyes are dichoptic (i.e., different in the two eyes); (2) the generalized 2nd proposition of Levelt (Brascamp et al., 2006) is met; (3) dominance durations follow a gamma distribution; and (4) the dominance durations of the percepts are temporally uncorrelated.
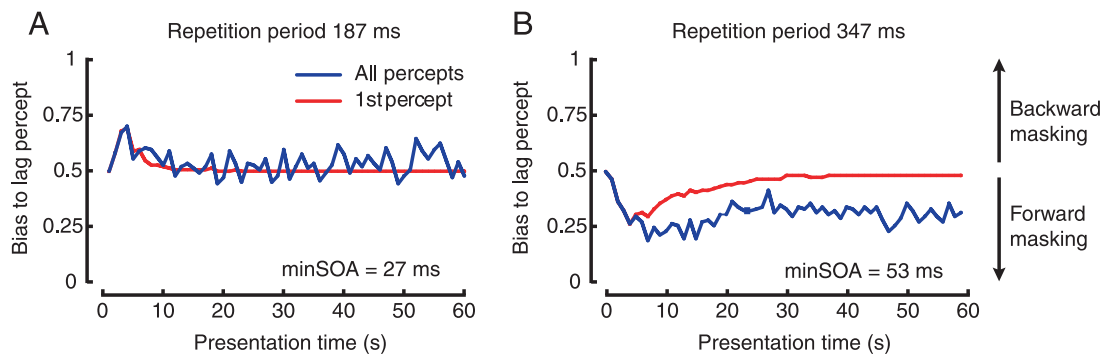
Figure 4. *Bias index during the 60-second trials.* (A) The bias index for stimuli with a repetition period of 187 ms, and a SOA of ~27 ms. The bias index calculated using all percepts (blue line) shows an initial deviation towards the lag stimulus (backward masking), but the preference rapidly fades. This bias seems to be fully caused by the first percept (red line). (B) The bias index for stimuli with a repetition period of 347 ms, and a SOA of ~53 ms. The bias index calculated using all percepts (blue line) shows an initial deviation towards the lead stimulus (forward masking), the preference weakens but remains present throughout the trial. The calculated bias index based solely on the first percept cannot explain the sustained presence of masking because the first percept does not add to the observed biases after more than 20 seconds from the start of the trial. Therefore, the bias observed in the first percept, Figure 3, can explain the bias observed in the total data, Figure 2A, only for stimuli with a repetition period of 187 ms, not for stimuli with a repetition period of 347 ms.

On the basis of these data, we would like to suggest that dichoptic masking effects and binocular rivalry are the resultant of (partly) overlapping neural mechanism. However, we have only looked at the temporal dynamics of perception, and the hypothesis is strengthened if the dependency on spatial stimulus manipulations is also similar. Indeed, it seems that binocular rivalry and dichoptic masking have a similar tuning to orientation (width of ~70 deg, Harrad & Hess, 1992; Levi et al., 1979; O'Shea, 1998; Schor, 1977), a relatively tight tuning to spatial frequency differences between the conflicting stimuli (Harrad & Hess, 1992; Hollins, 1980; Legge, 1979; Levi et al., 1979; O'Shea, 1998; Schor, 1977) and a relative independence of spatial frequency when both stimuli are large (>4 deg) and have the same spatial frequency (Legge, 1979; O'Shea et al., 1997). Some further circumstantial evidence comes from a monocular masking study, which indicated that masking and adaptation have may have a common origin (Georgeson & Georgeson, 1987). Since adaptation is one of the main components thought to underlie binocular rivalry dynamics, these results are suggestive of a link between masking and binocular rivalry. Overall, the similarity between dichoptic masking and binocular rivalry seems larger than one might expect on the basis of the very rare cross-references across the two research fields (Alais & Blake, 2005; Breitmeyer & Ogmen, 2006; Meese & Hess, 2004).

Nevertheless, a more extensive comparison is needed to establish whether binocular rivalry and dichoptic masking may indeed depend on the same (or party overlapping) underlying mechanisms.

If our suggestion of a single system for dichoptic masking and binocular rivalry turns out to be sustainable, it would provide an interesting test case for modelers, who could test whether their model can explain both dichoptic masking and binocular rivalry data.

Other studies on the relationship between dichoptic masking and binocular rivalry

In a previous study (Breitmeyer & Ogmen, 2006, pp. 272–275), the relationship between dichoptic masking and binocular rivalry was studied by presenting the observer a dichoptic masking stimulus that was surrounded by an annular binocular rivalry stimulus. It was found that the effectiveness of a dichoptic mask was contingent on whether it was being present in the eye receiving the dominant binocular rivalry stimulus. It was concluded that binocular rivalry takes precedence over dichoptic masking as it determines whether masking occurs or not, a conclusion seemingly at odds with our suggestion of a shared system. However, Breitmeyer and Ogmen (2006, pp. 272–275) used backward masking conditions, which may involve neuronal networks different from those involved in forward masking. Secondly, in our study the same stimuli induced dichoptic masking and binocular rivalry whereas Breitmeyer and Ogmen used separate, and spatially non-overlapping stimuli for binocular rivalry and dichoptic masking. This may be a crucial difference as it has been shown in monocular conditions that masking by a surrounding mask (called meta- and para-contrast masking) is different from masking by conflicting pattern information similar to the target pattern, which in turn is different from masking by noise (Breitmeyer & Ogmen, 2006). These three types of masking are currently also employed in dichoptic masking (e.g., Breitmeyer & Ogmen, 2006; Macknik & Livingstone, 1998; Meese & Hess, 2004; Tsuchiya & Koch, 2005; van Boxtel et al., 2006), but their mutual relationships have not yet been thoroughly investigated, and only recently their relationship to binocular rivalry received attention (this report, Breitmeyer & Ogmen, 2006, pp. 272–275; Macknik &

Martinez-Conde, 2004; Tsuchiya et al., 2006). So far, the differences in the employed methods and stimuli probably preclude an informative inter-study comparison.

On the time course of dichoptic masking and binocular rivalry

We found that the first-reported percept shows systematic biases towards one of the two stimuli, i.e., dichoptic masking (Figure 3). This initial bias was found to be the cause of the small bias observed for stimuli with repetition period of 187 (Figure 4A); a repetition period that would eventually lead to binocular rivalry. The reported biases for the full-trial data of repetition period 347 ms can however not be fully explained based on the initial bias, showing that the found near-continuous dichoptic masking was not fully dependent on the initial percept.

To allow for the unbiased perception, i.e., binocular rivalry, with our flickering stimuli, binocular information needs to be integrated over long periods (∼350 ms). Our study does not stand alone in presuming the existence of such long binocular integration periods, as they have been reported before (Andrews, White, Binder, & Purves, 1996; Dodwell & Engel, 1963; O'Shea & Crassini, 1984). When presentations are separated by more than 350 ms, the involved neurons cannot integrate the information over successive presentations, and transient boosts in activity of these neurons may cause transient cross-inhibition between competing representations resulting in dichoptic masking when SOA1 and SOA2 are unequal.

These particular interactions are not static, however, as we have found that many trials with repetition periods of 187 ms start with dichoptic masking. Overall, this dichoptic masking effect turns into binocular rivalry over the first 6 seconds of a trial. We may explain this finding by assuming that the binocular integration window is initially small (<190 ms) but slowly sizes up to its maximum size (∼350 ms). Initially this process allows each individual event to transiently inhibit competing patterns (causing dichoptic masking) but later causes the inhibitory forces for both patterns to become more or less equal (resulting in binocular rivalry). Consistent with this idea, is the finding that a substantial amount of cortical neurons show flicker adaptation (Van de Grind, Grüsser, & Lunkenheimer, 1973, p. 527), meaning that at first they are able to modulate the firing rate according to the flicker modulation of the stimulus, but that after a certain while they stop firing in synchrony with the stimulus, or stop firing altogether. This adaptation has a time scale of 1 to 5 seconds (Van de Grind et al., 1973, p. 527), close to the time scale we observe for the transition of masking to binocular rivalry for stimuli with repetition periods of 187 ms.

On the usefulness of continuous dichoptic masking

Our report also reveals an interesting tool for future study. Dichoptic masking conditions with repetition periods around 350 ms lead to very long dominance durations. Continuous and complete dichoptic masking, with percept durations in the order of 10 seconds (and up to 30 seconds for some subjects), is possible for repetition periods around 400 ms (data reanalyzed from experiment 2 of van Boxtel et al., 2006). Continuous dichoptic masking may be related to other effects that cause long-lasting perceptual disappearance of potentially salient stimuli, like continuous flash suppression (Tsuchiya & Koch, 2005), and the dichoptic standing wave of invisibility (Macknik & Martinez-Conde, 2004). The advantage of continuous dichoptic masking is that masking and target stimuli are identical (save for orientation) and need not differ in spatial frequency content, and luminance (Tsuchiya & Koch, 2005) or presentation duration (Macknik & Martinez-Conde, 2004), and thus may provide an additional route for the investigation of stimulus visibility (Macknik & Martinez-Conde, 2004) and the origin of visual aftereffects (Tsuchiya & Koch, 2005).

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