Cued visual selection in binocular rivalry

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Using line arrays and the technique of *cued visual selection* (Nothdurft, 2017a; www.VPL-reports.de/6/) I measured the ability of observers to identify cued targets in binocular presentations. Experiment 1 was designed to measure target visibility and was partly performed on monocular and binocularly non-rivaling line patterns. Target detection was perfect even when cues and targets were presented in different eyes. With *binocularly rivaling* stimuli, subjects saw cued targets in the dominant eye better than targets in the non-dominant eye. In Experiments 2-4, the dynamics of binocular interactions were measured by cuing lines in rivaling patterns at various delays (up to 5 s after stimulus onset). In Experiment 2, the locally orthogonal lines had similar strength; in Experiment 3, they differed in contrast; and in Experiment 4, one pattern was presented 3 s in advance for adaptation. In all experiments, there were strong modulations of monocularly cued target detection rates during the initial 500-1000 ms after stimulus onset, when perceptual reversals are rare or absent; after that period detection rates settled and remained nearly constant although perceptual rivalry is supposed to be strong during that time. This suggests that alternating percepts in binocular rivalry are likely not based on variations in ocular sensitivity alone. Target ratings with *binocular* cues, in these periods, were largely predicted by averaging the ratings with monocular cues. In Experiment 5, cued target detection was related to the observers' momentary percepts. Subjects were asked to attend to a particular line, and cues were given at various delays after a perceived line reversal. In this condition, target detection was modulated between attended and non-attended target features and locations, providing evidence for both feature-based and spatial attention effects. In all five experiments, there was a notable asymmetry of target detection rates between the dominant and the non-dominant eyes of observers.

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INTRODUCTION

One advantage of having two eyes is stereo vision, which helps to distinguish near and far surfaces and to evaluate the distance from objects to grasp and handle. In natural viewing conditions, the patterns from both eyes largely match and it is just the small local mismatches that provide the important information on relative disparity (for reviews see, e.g., Anderson & Nakayama, 1994; Qian, 1997; Blake & Wilson, 2011; Lappin, 2014). But vision researchers had not been true scientists if they had not also explored what happens when the two eyes receive largely different inputs (Wheatstone, 1838). Interestingly, as long as the structures in the two eyes are locally correlated, many brains are able to find these correlations and (re-)construct virtual depth from different disparities, even when the patterns lack visible object borders and are made of seemingly random dots (Julesz, 1971). But when no correlations can be found, for example with gratings at orthogonal orientations or with dissimilar figures like faces and houses, the two patterns compete in perception leading to what is called *"binocular rivalry"* (cf. Blake & Logothetis, 2002). The observer then sees only one pattern at a time, while the percept of the other pattern is

suppressed. Percepts of the two inputs usually alternate over longer inspection time in a way that has been described as stochastic. Patterns that evoke binocular rivalry are uncommon in visual reality (Arnold, 2011), as they would refer to two different objects at the same place in the world. They do, however, stimulate mechanisms in vision that should be interesting to study since the may elucidate important functions of visual perception.

Binocular rivalry has been a challenge to researchers since the sixteenth century (Blake & Logothetis, 2002), and particularly during the last 40 years many detailed and sophisticated studies have addressed various aspects of it. One major interest was to relate the observed perceptual fluctuations between the two ocular patterns to neural competition at various processing levels in the brain (Blake & Logothetis, 2002; Alais, 2012).

The observation that the two ocular patterns are not perceptually combined but that percepts alternate and are temporarily exclusively predominated from one or the other eye has underlined the suppressive character of binocular rivalry, which was confirmed in many studies (e.g., Stuit, Cass, Paffen, & Alais, 2009; Alais, Cass, O'Shea, & Blake, 2010; for a review, see Alais, 2012). Suppression between inputs from the two eyes was found in neurons of the primary visual cortex (Li, Peterson, Thompson, Duong, & Freeman, 2005; the paper also lists several earlier studies on this topic); according modulations were also seen in the BOLD signals of fMRI recordings (Lee & Blake, 2002), even already in the thalamus (Wunderlich, Schneider, & Kastner, 2005). There have been attempts to explain the reversals between percepts of the two ocular patterns by reciprocal inhibition (see Alais, 2012). A temporarily stronger signal from one (e.g., the left) eye will suppress responses (and reciprocal inhibition) from the other (right) eye so that the stronger (left eye) response will further increase and may finally be the only signal transferred. This might explain why the observed percept becomes exclusive. Over time, however, adaptation and other response variations will weaken that response and the suppression of the other eye, so that after a while the originally weaker (right eye) stimulus may begin to dominate. In an elegant way of relating momentary sensitivity to the long-lasting occurrence of perceptual reversals, Alais and colleagues could demonstrate the expected dynamic variations based on adaptation and reciprocal inhibition (Alais, Cass, O'Shea, & Blake, 2010). There are many observations that seem to support such an "early" model of binocular rivalry, sometimes contrary to intuition. For example, making the stimulus in one eye brighter should increase the representation of this stimulus and shorten the predominance durations of the stimulus in the opposite eye (Brascamp, Klink, & Levelt, 2015). Increasing the size of an oriented grating in one eye by adding an equal-oriented surround, does not in- but rather decrease the predominance of this grating (Fukuda & Blake, 1992; Sobel & Blake, 2002), in agreement with the reduced neural activity in many V1 neurons by iso-oriented contextual surround (e.g., Nothdurft, Gallant, & Van Essen, 1999). However, there are also findings that do not support this model. Several aftereffects which are assumed to be caused by neural adaptation in the primary visual cortex, are obtained with similar strengths when adaptation time includes suppression intervals in binocular rivalry during which the adapting stimulus is not perceived and supposed to be suppressed (Blake & Fox, 1974; Wade & Wenderoth, 1978). And interocular rivalry is also seen in the human cortical blind-spot where interocular suppression should be absent in early areas (Tong & Engel, 2001).

The exclusivity of percepts in binocular rivalry and the close link of perceptual variations to input from different eyes have biased the search for neural mechanisms to early processing stages where signals from the two eyes are reliably separated. But when the perceptual reversals are compared with the activity of single neurons, the pattern is also controversial. While some studies have reported correlations between activity changes in early visual areas and the alternating percepts in binocular rivalry (e.g., Leopold & Logothetis, 1996; Keliris, Logothetis, & Tolias, 2010) but not in neurons of the thalamus (Lehky & Maunsell, 1996), the correlations particularly in area V1 are rather weak. Better and apparently reliable correlations are seen in area IT (Logothetis, 1998) suggesting that the alternating percepts in binocular rivalry might be based on interactions of neurons at various processing levels (Leopold & Logothetis, 1996). This discrepancy is still a challenge for research on binocular rivalry.

Different patterns in the two eyes is not the only rivalry we can perceive. There is a large number of ambiguous and multi-stable patterns, which can also be seen in different ways or from different perspectives. These patterns also tend to alternate ("reverse") in perception in a similar way as conflicting patterns in binocular rivalry (cf. Blake & Logothetis, 2002, for certain differences). With these patterns, perceptual fluctuations cannot be linked to

cross-ocular suppression, as fluctuations also occur in monocular or binocularly identical presentations. In addition, the same patterns that evoke binocular rivalry when presented in different eyes can evoke similar perceptual reversals ("pattern rivalry") when frequently swapped between the eyes (Logothetis, Leopold, & Sheinberg, 1996) so that interocular suppression is strongly reduced (Bhardwaj, O'Shea, Alais, & Parker, 2008). Beyond of that, intermixed patches of different patterns presented partly to the left and partly to the right eye (so that neither eye can encode the complete stimulus) may be perceptually combined to homogeneous (and slowly alternating) patterns *across* the eyes (Kovács, Papathomas, Yang, & Fehér, 1996). All these observations show that perceptual rivalries are not necessarily caused by ocular interactions alone and that even in rivaling conditions, percepts can also be *synthesized* from information distributed in both eyes.

However, one obvious origin of binocular rivalry still *is* the dissimilar information presented in the two eyes, and it would be helpful to understand the neural mechanisms of binocular interaction before the percept is confused and eventually mixed with pattern rivalry at later processing stages. Since we are not aware of the eye of origin when seeing a rivaling pair of stimuli (except when covering one eye), we cannot easily distinguish between binocular and pattern rivalry. But given the method of cued visual selection (CVS; e.g. Nothdurft, 2017a) I wondered if the ocular origin of percepts might not be better identified. In cued visual selection, a single stimulus is cued (and hence selected) and should then be identified. By selecting individual stimuli in the left or right eye, or rivaling stimuli in both eyes, it might be possible to identify the information presented (encoded) in the according eye, before the global and rivaling percept is generated.

Selective cuing of ocular information in binocular rivalry is not a new technique. While attention effects in reaction time were found to be neutralized when cues were presented in a momentarily suppressed pattern (Schall, Nawrot, Blake, & Yu, 1993), quite a few studies have revealed attentional influences on the initial percepts and on the duration of predominance intervals (e.g., Ooi & He, 1999; Chong, Tadin, & Blake, 2005; Chong & Blake, 2006; Hancock & Andrews, 2007; Stuit, Verstraten, & Paffen, 2010; Dieter, Melnick, & Tadin, 2015; but not Meng & Tong, 2004; Jung, Kang, & Chong, 2016; for reviews see Paffen & Alais, 2011; Dieter, Brascamp, Tadin, & Blake, 2016). In particular, exogenous capture of attention by salient attractors like sudden stimulus changes or movement has been reported to terminate currently suppressive effects in binocular rivalry (Fox & Check, 1968) and to restore the percept of a suppressed stimulus (Walker & Powell, 1979).

In the present CVS experiments I have selected rivaling targets with monocular and binocular cues and have measured how often and how reliable the cued targets were seen, irrespective of the momentary global percept. I have looked for asymmetries in performance between the eyes and for the dynamics of how these asymmetries develop and eventually change. It turned out, that certain ocular modulations in binocular rivalry are less stochastic than often assumed but are instead strongly affected by individual variations between the observers. In altogether five series of experiments, I have measured target visibility and binocular rivalry in a simple binocular CVS experiment (Exp. 1) and have looked at the onset dynamics of individual preferences with cue delays of up to 5 seconds. For that I used equivalent stimuli in the two eyes (Exp. 2) as well as patterns in which one stimulus was enhanced either by stronger contrast (Exp. 3) or by previous adaptation to the other stimulus (Exp. 4). In the last experiment (Exp. 5), finally, CVS results were related and synchronized to the momentary individual percepts of the observers. In all experiments, rivaling stimuli were patterns with a regular raster of short, obliquely oriented lines, with orthogonal orientations in the two eyes. To avoid false matches between randomly oriented lines in the two eyes, the line patterns were embedded in a strong, binocularly identical stimulus that helped to align the two eyes.

GENERAL METHODS

All experiments were performed with stimulus configurations as illustrated in Figure 1. Two patterns on the monitor were separately looked at with the two eyes, by means of a mobile stereoscope attached to an otherwise empty spectacle frame worn by the observer. The patterns displayed a large amount of identical stimuli (green) for pattern alignment, and a number of oblique line bars (white) that differed between the two eyes, as test stimulus. To facilitate binocular fusion, the congruent stimuli (green) were shown at least one second before the test stimulus and remained continuously visible

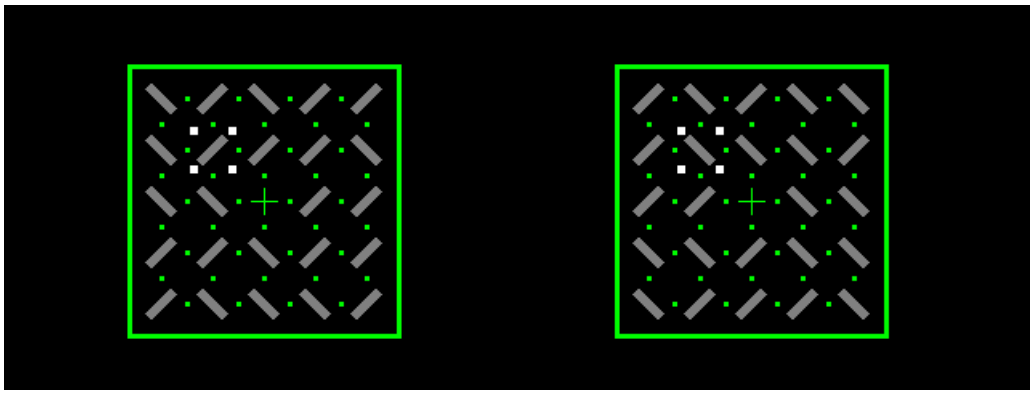

Figure 1. *Illustration of test patterns.* Patterns displayed a raster of randomly oriented (±45°) white lines and were inspected through a stereoscope, one pattern per eye. In most experiments, corresponding lines in the two patterns were orthogonal to each other thus generating binocular rivalry. In Experiment 1, also monocular line patterns or patterns with identical lines in the two eyes were used. Green items (frame, fixation cross, dots) were always identical in both eyes and were added to facilitate binocular fusion. After a variable delay, one of the line pairs was cued (as shown) and subjects had to indicate the line orientation they had seen. Cues were presented for 50 ms either monocularly or binocularly (as shown). Line patterns disappeared 250ms later. Several modifications (e.g., enhanced contrast or advanced presentation of one pattern) were tested in different experiments (see test for details).

throughout each trial and even between trials, with only a short blank after each response. At various delays after test pattern onset a "four-dot" cue pattern (white) occurred which marked one of the lines (the "target") in either the left, the right, or in both test patterns simultaneously. Subjects were asked to indicate the orientation of the cued line. There were minor modifications of this procedure which will be described in the according experiments. Aim of the study was to measure the proportion of cued targets that were correctly seen in the different cuing conditions.

Stimuli

Test patterns were 5 x 5 regular arrays of oblique lines individually tilted to the left or right (±45°); orientations were randomly assigned in every new test pattern. Except for part of Experiment 1, lines in the two patterns were orthogonal to each other so that there was strongly conflicting information between the eyes under binocular inspection. In Experiment 1, also identical lines in the two patterns or purely monocular test patterns with no lines in the other eye were used to measure target visibility. During the course of a trial, one of these lines was cued, monocularly or binocularly, at various delays (0-5 s) after test pattern onset. In a number of trials, also negative cue delays (up to -250 ms) were tested, in which the cue was presented before test pattern onset. Cues were always shown for 50 ms and then disappeared. Test patterns were shown for 250 ms if cues preceded the test pattern, or remained visible until 250 ms after the cue onset when cues were presented at or after test pattern onset. With a cue delay of 5 s, thus, the test patterns were shown for 5250 ms and could undergo one or more perceptual reversals during that time. Test lines were not masked.

All patterns were generated with standard DOS VGA technique and displayed with 60 Hz repetition rate on a 17" monitor in front of the observer (Sony multiscan 17seII). The viewing distance was 78 ±1.5 cm (including the path inside the stereoscope). Variations of the viewing distance were due to head size differences between observers, who sat relaxed with the head conveniently leaned against the wall. Monitor position was fixed. This gave a constant viewing distance for every subject; across subjects, however, the viewing distance varied with the different head sizes. All stimulus size computations below are based on the mean viewing distance of 78 cm.

Line elements in the stimulus patterns were 0.5 deg x 0.15 deg at 18 cd/m² on a background of 10 cd/m², presented in a regular raster (width 1.1 deg) around the binocular fixation cross. Each line array was presented in a rectangular binocular frame (5.8 deg x 5.8 deg, green) at 39 cd/m²; the binocular central fixation cross (0.6 deg x 0.6 deg) and blobs to facilitate stereo fusion (0.1 deg x 0.1 deg) had the same color and luminance. Target selection was achieved by white four-dot cues (each dot 0.1 deg x 0.1 deg; 61 cd/m²) centered at a midpoint distance of 0.6 deg around the target (cf. Fig. 1).

Subjects

Altogether seven observers (19-37 yrs; four females), mostly students of the Göttingen University, who were paid for their time in experiment, plus the author (male, 68 yrs) served as subjects in different parts of the study. All except the author were naïve as to the purpose of the experiment, and all had, at least, normal or corrected-to-normal visual acuity. In addition to stereo acuity (all better than 50"; Titmus stereo test), their ocular dominance was quickly assessed by binocular alignment of a distant object with the raised thumb at the stretched arm and subsequent verification, which eye was aligned (Porta sighting test; Porta, 1593, cited after Mapp, Ono, & Barbeito, 2003; cf. Coren & Kaplan, 1973; Mendola & Conner, 2007).

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Procedures

Training, test sequences and blocking. All but two subjects had already performed CVS experiments before. Of the remaining two subjects (who participated only in Exp. 1) one was highly experienced in cuing and attention tasks of earlier projects, the other had not performed such experiments before. However, the experiments of the present study were not particularly difficult (quite different to CVS tasks with very short stimulus durations; Nothdurft, 2017a) and were not considered to require previous training. In fact, this new and untrained subject performed perfectly right from the beginning.

In all experiments where that was applicable (Exp. 2-4), cues were presented monocularly and binocularly on both eyes (three conditions), at each tested cue delay. The cue delay was varied in 20 steps from -250 ms (cues presented before the test pattern) to 5000 ms (cues presented 5 s after test pattern onset). This multiplied to a total of 60 test conditions. In experiments with asymmetries between test patterns, the asymmetry was tested on both eyes, thus doubling the number of test conditions. That is, the brighter (Exp. 3) or delayed stimulus (Exp. 4) was presented, in different conditions, to the left and to the right eye. The various test conditions were blocked in 2-3 different runs with 5 repetitions of each condition in a single run. Runs were performed and repeated in interleaved sequence, so that final data curves represent at least 25 repetitions of every single test condition.

Target identification. Trials began with a 1 s presentation of the green pattern for fixation and stereo fusion, before the cue or the test pattern appeared. Observers entered the seen orientation of the cued target as being tilted to the left or right by pressing left-hand and right-hand keys, respectively (< and - keys; German keyboard with QWERTZ layout). Immediately after key pressing, there was a short blank (<200 ms), before the next trial started. Subjects were not forced to make fast responses but could take all time they wanted to respond. The task itself was a modified two-alternative forced choice (cf. Nothdurft, 2017b); subjects could terminate and reject a trial if they noticed that they had lost fixation (which was thought to be particularly useful with long cue delays). Rejected trials were then repeated, with a new pattern, later in that run. Subjects made very rare use of this opportunity. Since lines at corresponding locations in the two eyes were orthogonal (except for some patterns in Exp. 1), both tilt perceptions are virtually correct; thus there were no correct or false answers. All subjects showed high performances in Experiment 1 where target visibility was tested (and answers *could* be correct or false). Therefore, responses were generally taken as correct identifiers of the seen line orientation, which then allowed conclusions about the eye of origin. In the rare case of double pictures or when subjects could not see a clear target, they were asked to guess and to indicate the stronger percept.

Target locations. To avoid disturbances from crowding effects (Nothdurft, 2017a), possible target positions were not selected from allover the test pattern but were restricted to certain locations (Fig. 2). Subjects were not informed about these restrictions. Experiment 5 was performed with altogether eight possible target locations next to the fixation cross (Fig. 2b).

Fixation. Subjects were asked to fixate the binocular central cross. All (but one) had performed principally similar experiments without a stereoscope, in which eye

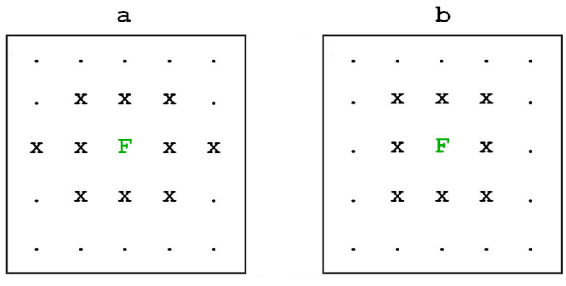

Figure 2. *Possible target locations cued in Experiments 1-4 (**a**) and Experiment 5 (**b**).* Only line pairs at marked (x) locations were randomly selected as targets. F, fixation point.

movements and fixation had been controlled, and all had been able to perform the task without gaze shifts. In addition, target presentation was generally too short (250 ms after cue onset, except for negative cue delays) to achieve improvements in target visibility from gaze shifts toward the cue (Fischer *et al*., 1993).

Analysis. To improve the readability of data curves in the figures below, the original data points are usually accompanied by smoothed curves based on the weighted averages of neighboring points. In some figures, when curves were based on few repetitions like, e.g., in the data of individual subjects, this double data presentation looked confusing and only the smoothed averages are shown. Smoothing was obtained by gliding, weighted averaging of three neighboring data points, in which the middle data point had double weight. With x_i *(i=1, 2, ..., n)* representing the ratings of the *i-th* cue delay, smoothed values x'_i were calculated as

$x'_i = 0.25 \cdot x_{i-1} + 0.5 \cdot x_i + 0.25 \cdot x_{i+1}$ *(for i=2, ..., n-1),*

with special care at the extremes,

$x'_1 = (0.5 \cdot x_1 + 0.25 \cdot x_2) / 0.75$ and

$x'_n = (0.25 \cdot x_{n-1} + 0.5 \cdot x_n) / 0.75$.

Statistics. The evaluation of statistical significance of certain findings was generally based on two-way ANOVA with or without replication (Excel) depending on whether analysis was applied to the full data sets or the means or individual subjects' data. Comparisons between cuing conditions were always restricted to data obtained with positive cue delays ≥ 0. For certain analyses, also one-way ANOVA and/or paired and non-paired t-tests were used.

Nomenclature

Unfortunately, the literature on binocular rivalry does not always make a clear verbal distinction between the different phenomenons of ocular asymmetries. The *ocular dominance* of an observer, i.e. his or her preference to use the left or right eye when pointing to a distant object, was found to be an important parameter that could predict response variations between the *dominant* and the *non-dominant* eye. This static property must be distinguished from dynamic variations, when the momentary percept of a rivaling stimulus was temporarily *predominated* by the left or right eye, while information from the other eye was (temporarily) suppressed. This eye was then also referred to as the momentarily *leading eye* or *eye of origin.* To avoid confusion, only five abbreviations are used, to specify the according eyes; left (L), right (R), dominant (D), non-dominant (nonD), and both eyes (B).

RESULTS

The stimuli for binocular rivalry in the present study are new in several aspects (Fig. 1). Many early studies had used patterns with large homogeneous gratings in different orientations for the two eyes (e.g., Levelt, 1965), but several studies have claimed that binocular rivalry manifests locally and then appears to spread over to a larger region in the form of traveling waves (Wilson, Blake, & Lee, 2001; Lee, Blake, & Heeger, 2005; cf. Alais, 2012). This general impression of asynchronous, "piecemeal"-like reversals was also seen with the patterns of the present study. While line elements in each pattern differed in orientation thus avoiding the impression of a homogeneous field of similarly oriented lines, the reversals of individual lines could happen at different times and lines could change their orientations in asynchrony.

One particular difficulty with these patterns, however, is their intrinsic structure and the random distribution of line orientations. While there is locally rivaling information from the two eyes at every line position, neighboring lines with different orientations will match across the eyes at a different disparity and may thus generate a strong binocular fusion signal. What should be see in that case, however, is a double frame and two neighboring fixation crosses. To avoid such mismatches, subjects were instructed to keep fusing the binocular fixation cross and take care that no double crosses nor double frames were seen. Since the (correct) binocular fusion stimulus (green) was shown most of the time and always one second before test pattern onset, false disparity matches have not been a problem.

Experiment 1: Target visibility, binocular rivalry, and ocular dominance

Aim of the experiment was to measure the general visibility of cued targets and the ocular selection of rivaling stimuli under different cuing conditions.

Methods

In this experiment, the cue delay was fixed. Test patterns were always shown for 450 ms; cues were

presented (for 50 ms) 200 ms after the test pattern onset. Tests were performed in two separate blocks. In *block A*, there were no rivaling stimuli at all. Test patterns were shown in the L or R eye (monocular presentations; no test lines on the other eye), or with *identical* lines in both eyes (binocular presentations, B). For each of the three test pattern conditions, cue presentations were similarly varied and cues were shown either monocularly in one and the other eye, or binocularly in both eyes together. The same set of nine test conditions was used in *block B*, except that lines in binocular test patterns were now non-identical and competitive, i.e. each line in the one pattern was orthogonal to the according line in the other pattern. Conditions with monocular test patterns were identical to block A.

The two blocks were tested in interleaved sequence on eight subjects (four female). Two subjects (31-37 yrs, 1 female) were later included to increase the general variety of individual ocular dominance settings and did participate only in Experiment 1. Five observers had been classified as being L eye dominant, three as R eye dominant.

Results

Target visibility.

Subjects were generally not aware on which side (eye) the test patterns or the cues occurred, and just entered the line orientations they had perceived. Performance rates for target visibility were high and close to 100% (Fig. 3a). Test conditions included patterns in which test lines and cues were presented monocularly on the same eye but also patterns in which test lines and cues were presented dichoptically on different eyes (empty bars in Fig. 3a). The cues then marked an empty raster field, but the corresponding line in the other eye was nevertheless correctly identified. Binocularly presented (identical) lines were generally seen a little better. While seven of eight subjects made minor mistakes with monocular test lines (29 errors = 1.9%, in total), only two subjects gave (very few) incorrect answers to binocular test patterns (3 errors = 0.7%) and only when these were monocularly cued. No error was encountered with binocularly presented cues and test patterns.

Figure 3b shows the data re-plotted for the dominant (D) vs. the non-dominant eyes (nonD) of observers. Since performance was generally very high, the differences to Figure 3a are negligible. Statistically, performance variations between the different conditions are not significant [one-way ANOVA; $F(6,49)=1.18$].

Binocular rivalry.

Performance was quite different however, when test lines in the two eyes were dissimilar. Test patterns in this part of analysis were always presented binocularly, with orthogonal line orientations; cues were presented monocularly or binocularly. Subjects saw more frequently, but not always, the test lines on the cued side (Fig. 3c). The mean data show a small but not significant preference for L cued over R cued targets [red and green bars; $F(1,14)=0.67$]; a small preference for the L eye target was also seen when cues were applied simultaneously to both eyes (black bar). There was considerable variation between subjects (larger s.e.m. than in Fig. 3a). The reason becomes obvious when the individual performances are plotted (Fig. 3d). Subjects behaved quite differently in their perception of rivaling stimuli. Subject NQ, for example, always perceived the L target when cues were presented on that eye, but never the R target when cues were presented there. Accordingly, she identified almost always the L test pattern when cues were presented binocularly on both eyes (dark bar). DQ, on the other hand, saw only few L cued targets on the L eye but almost all R cued targets on the R eye. Accordingly, he identified all targets on the R side when cues were presented binocularly. (Note that black bars in Fig. 3d plot the percentage of L eye targets seen. Since L and R stimuli were orthogonal, poor performance with L targets means automatically high performance with R targets.)

In Figure 3d, the observers' data are ordered for decreasing L preferences with binocular cues (black bars); values >50% indicate a preference for L targets, values <50% a preference for R targets. By and large, the ratings correspond to the simple ocular dominance test performed before the experiments (Porta test; see General Methods), with two deviations. Subjects HCN was clearly R dominant, even though his performance in Experiment 1 revealed a small preference for L targets under binocular cuing. Subject NMB, on the other hand, was classified as L dominant but revealed a small preference for R targets under binocular cuing. Note however, that the preference biases are rather small in these two subjects (black bars close to 50%). All other subjects showed stronger biases which replicated the preferences measured in the ocular dominance test (NQ, CF, LL, and PP were L dominant; MM and DQ were R dominant).

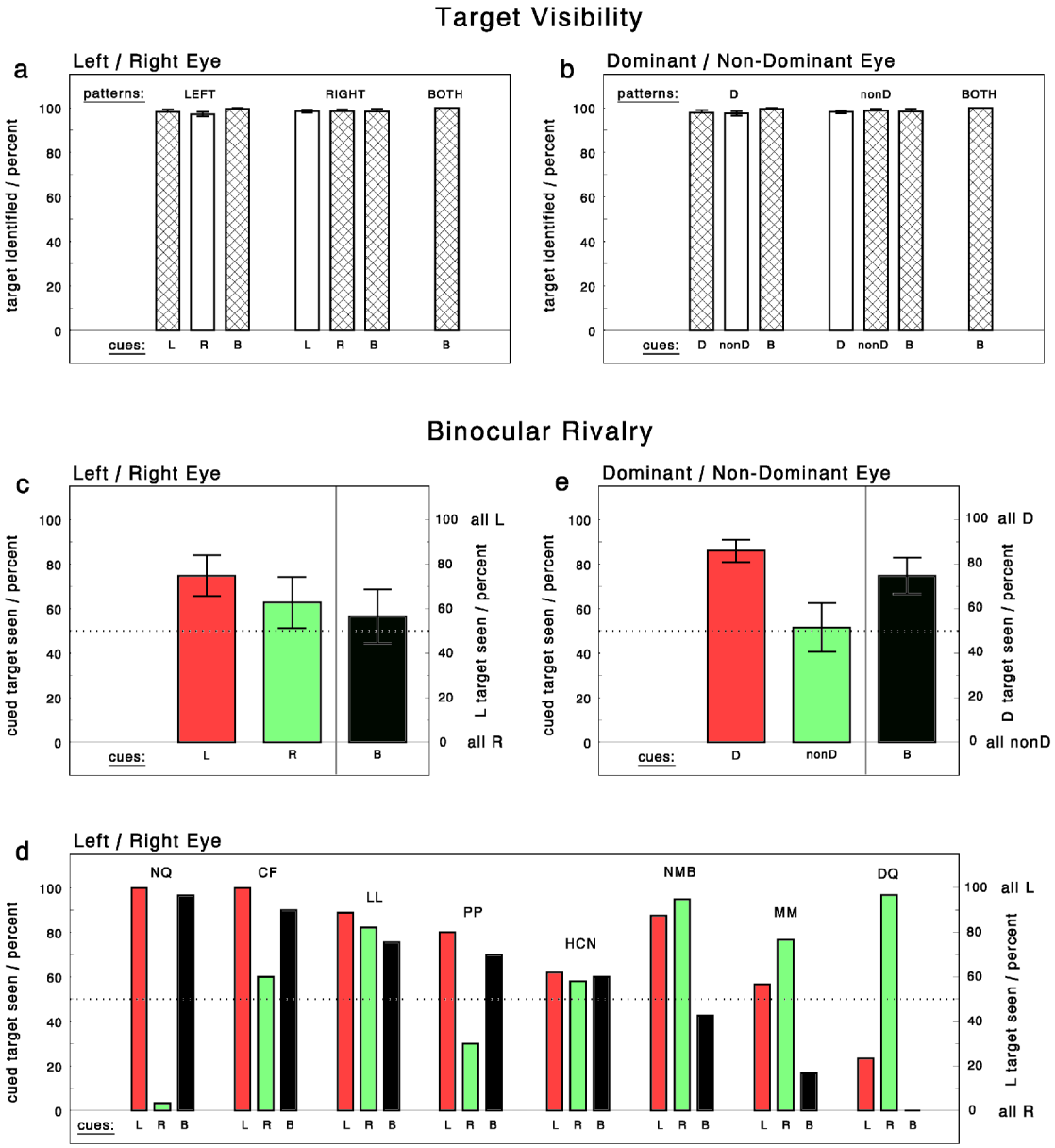

Figure 3. *Results of Experiment 1.* The experiment was split in two parts measuring the visibility of cued targets and the individual target preferences under binocular rivalry. ***a., b.*** Data from eight subjects obtained with monocular or binocularly identical patterns (indicated on the top of each graph) and various cuing conditions (indicated on bottom). Performances with dichoptical presentations (cues around blank regions in the other eye) are plotted as empty bars. Target detection rates were high with both eyes *(a)* and naturally remained high when performance was re-sorted for the individual eye dominance of observers. ***c.-e.*** Data from the same subjects obtained with binocularly rivaling patterns. Please note the different scales in these plots. For colored bars (monocular cues), the left-hand scale of each graph gives the percentage of tests in which the according cued target was seen. For black bars (binocular cues), the right-hand scales indicate the percentage of patterns in which the target in the left (L) or in the dominant (D) eye was seen. Since corresponding targets in the two eyes were orthogonal, detection rates were complementary; i.e., ratings above or below 50% indicate preferences for either eye. Performance averages across subjects *(c)* indicate small preference variations between the left and right eye, but stronger preference variations when the data are re-sorted for the dominant and non-dominant eyes of the observers *(e)*. The reason are individual variations in ocular preference *(d)* here sorted for decreasing preference for the target in the left eye (black bars). Abbreviations in this and all following figure legends refer to ocular pattern presentations: L=left eye, R=right eye, B=both eyes, D=dominant eye, nonD=non-dominant eye. Error bars indicate the s.e.m.

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The bias observed with binocular cues is also reflected in different performances with monocular cues (Fig. 3d, colored bars). L dominant observers saw L cued targets better (i.e., more frequently) than R cued targets; R dominant observers saw R cued targets better than L cued targets. This bias was also reproduced in subjects HCN and NMB who had been differently classified in the ocular dominance test before the experiment. While the observers' percepts in binocularly cued rivaling patterns correlate with the performance bias under monocular cuing (and by and large with the Porta sighting test of ocular dominance), there were considerable variations in the amount of how many L or R cued targets were seen (colored bars in Fig. 3d plot the percentages of targets seen on the cued side). The percepts of NQ and DQ were rather exclusive; other observers showed different performance levels with R and L cued targets. Subject CF, for example, saw almost all cued targets in the L eye but only about 60% of the targets cued in the R eye. Subjects NMB and HCN, on the other hand, revealed similar detection rates with monocularly cued targets in the two eyes but at different performance levels (80% and 60%, respectively).

The large variation of ocular preferences in individual observers suggested to relate performances to ocular dominance. Figure 3e shows a re-plot of Figure 3c when data are averaged over the dominant (D) and non-dominant eyes (nonD), not L and R. This re-plot increases the differences between test conditions. On average, 87% of the cued targets in the D eye were seen but only 52% of the targets cued in the nonD eye (that is, in 48% of the presentations the non-cued target in the D eye was seen instead). In binocularly cued patterns, 75% of the targets were seen in the D eye. These differences were significant [$F(2,21)=1.18$, $p<0.05$], in particular for the rating differences between D and nonD cued targets [$F(1,14)=8.24$, $p<0.02$].

Discussion

Experiment 1 has revealed three major findings. First, concerning target visibility, monocularly presented targets were correctly identified independent of whether the cue was presented together with the target in the same eye or around an empty region at the corresponding location in the opposite eye. Subjects did not distinguish between monocular and dichoptical presentations of targets and cues; in fact, they were not even aware of these differences. Six (of eight) subjects made a few mistakes in dichoptical presentations, whereas only two made mistakes with binocularly presented line patterns and none when also the cues were binocularly presented. However, this small (and statistically not significant) difference is likely the result of the generally better visibility of binocular stimuli due to binocular summation (e.g., Georgeson & Schofield, 2016) rather than an indication of a poorer performance when cues and targets are presented in different eyes. Second, with rivaling patterns, subjects saw preferentially the target in their D eye. This was not only the case when this side was cued but a bias was also seen under binocular cuing. Even when the target in the nonD eye was cued, many subjects did often not see that cued target but instead the corresponding (non-cued) target in the D eye. However, neither the bias nor performance in the D eye were complete; in about 50% of the trials (averaged from all subjects, cf. Fig. 3e), the cued nonD target was still reported and even reports with cued D targets did not reach the higher performance found with single or binocularly identical targets (cf. Fig. 3b). Thus, rivalry had a measurable effect on the identification of cued targets. This is remarkable, as it anticipates binocular competition at an early presentation time, at which perceptual reversals are rarely reported, and relates it to the ocular dominance of the observer. Third, variations in ocular dominance were far more graded than one might have expected, and were more subtle than could be evaluated with the simple sighting test. As later experiments will show, these differences were not simply a random manifestation of individual variations but seem to be accompanied by differences in the onset dynamics of ocular preferences with binocular rivaling patterns. Due to these dynamics, ocular preferences with monocular or binocular cues that remained relatively fixed during longer presentation times, varied strongly at short presentation times immediately after stimulus onset.

The small deviations of ocular preferences in Experiment 1 and ocular dominance measures with the Porta sighting test for subjects HCN and NMB are not surprising. Ocular (or eye) dominance is defined and measured in different ways, and the results do not necessarily correlate (Coren & Kaplan, 1973; Mapp, Ono, & Barbeito, 2003; Mendola & Conner, 2007). Thus, it is rather remarkable that the two measures indeed did closely correlate in the data of the other six subjects. The fact that subjects develop an eventually even strong preference for

one eye (e.g. subject NQ) may have various reasons, including small differences in visual acuity between the two eyes. Even when both eyes have normal or better acuity, small differences might cause an observer to bias the usage of one or the other eye in critical situations, which might then have developed to a strong and constant eye preference in life.

Experiment 2: Dynamics of ocular sensitivity

In Experiment 2, the rivalry measurements of Experiment 1 were expanded and cues were presented at various delays, from -200 ms to 5000 ms relative to test pattern onset.

Methods

Cuing variations were the same as in Experiment 1; cues were presented monocularly in the L or R eye and binocularly in both eyes simultaneously. Test patterns were always presented to both eyes with orthogonal lines at corresponding locations. In different test conditions, cues were presented before the test patterns (which then were shown for 250 ms) or together with them at various delays (test patterns then always remained visible until 250 ms after the cue onset). Test conditions were blocked (cue delays -200 ms to 500 ms, and cue delays 750 ms to 5000 ms); the two blocks were performed in interleaved sequence. Four subjects including the author performed the tests; two were female (CF, MM) and two showed R eye dominances in the initial Porta sighting tests (MM, HCN). In a modification of the experiment, additional keys to indicate intermediate percepts were introduced (Exp. 2a, see below).

Results

Figure 4 shows the mean performance of all four subjects in Experiment 2. Data are plotted as percentages of targets seen in the D eye; since corresponding lines in the two eyes were orthogonal, these ratings are inversely related to the percentage of targets seen in the nonD eye. Values below 50% then indicate increased ratings for the nonD target. The three cuing conditions are color-coded in Figure 4. When cues were presented alone in the D eye (red), mainly (but not always) the target in that eye was seen. When cues were presented alone in the nonD eye (green), mainly (but usually less often) that target was seen. There was an overall asymmetry between the two eyes both in long-lasting detection rates (red curve is closer to 100% than green curve to 0%) and in the onset dynamics until these levels are reached (steep increase of the red curve, slower decrease of the green curve). To make the latter differences seen better, performances with the two monocular cues are replotted in Figure 4b, now both showing the percentages of cued targets seen. Targets in the D eye were already seen at maximum rate with a cue delay of only 50 ms, whereas it took up to 1000 ms until maximal performance was reached with targets cued in the nonD eye. When cues were presented before the test stimulus (negative delays), performance was closer to chance (50%) but already began to increase with decreasing onset delays even when cues were still switched off before the test lines occurred.

With binocular cues (B; black curves) responses were less biased and observers sometimes saw the target on the D and sometimes on the nonD eye. (Note however that subjects never knew which target was on which side, nor on which eye(s) the cue(s) occurred.) Accordingly, mean performance with binocular cues was close to 50%, with a small bias towards the dominant eye. The differences between curves in Figure 4a are statistically significant [two-factor ANOVA with replication; $F(2,135)=238.73$, $p<0.0001$; in this and all following statistical evaluations, only cue delays ≥ 0 are included], both in the means [two-factor ANOVA w/o replication; $F(2,28)=255.67$, $p<0.0001$] and in the individual data of each subject [$F(2,28)>46.33$, $p<0.0001$]. However, when the ratings of monocularly cued targets are directly compared (Fig. 4b), the statistical significance is slightly reduced [all data, $F(1,90)=44.25$, $p<0.0001$; means, $F(1,14)=47.94$, $p<0.0001$] and is not valid in the individual data of two subjects.

Two observations in Figure 4 must be emphasized. First, except for the modulations immediately after test pattern onset, the performance with binocular cues (black curves) often matched the averaged performances of trials with monocular cues (gray crosses). Target selection with binocular cues could thus be largely predicted from measurements with the two monocular cues. In the entire data set, measured and predicted data are not significantly different [$F(1,90)=1.87$, $p>0.17$], although the differences

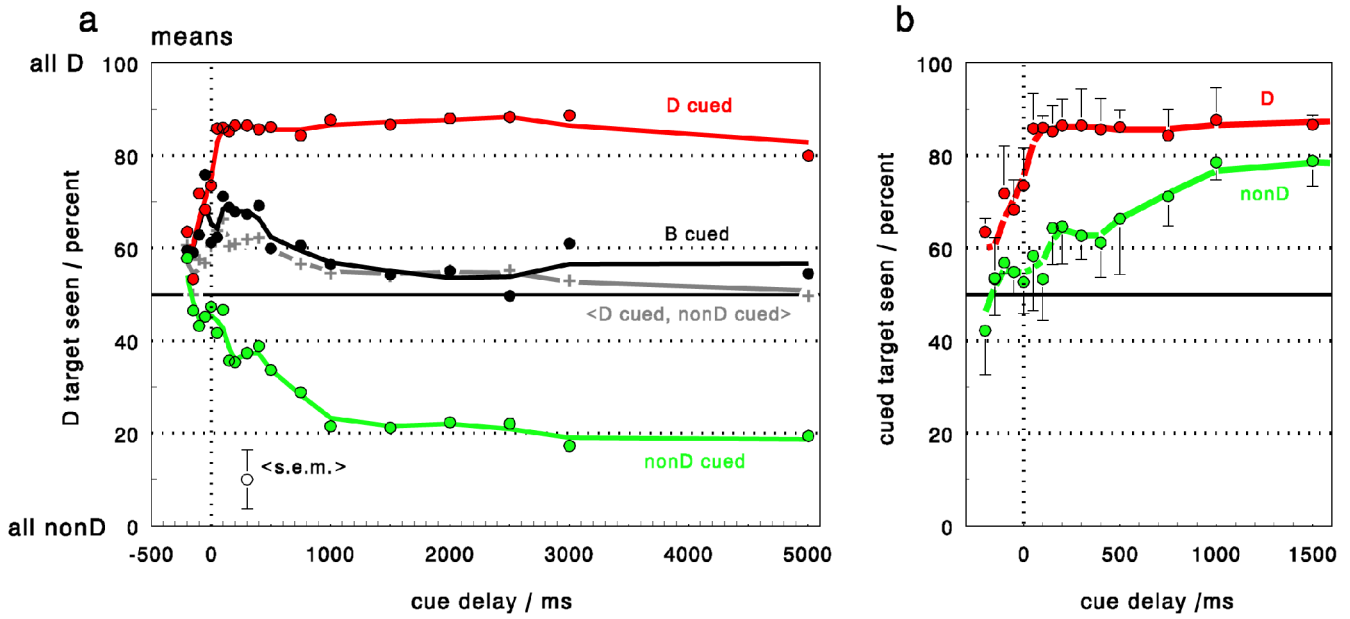

Figure 4. *Mean data of observers in Experiment 2.* ***a.-b.*** Target detection at various cue delays in different cuing conditions, plotted as percent of targets seen in the dominant eye *(a)* and plotted as percent of the cued targets seen *(b)*. Since lines pairs were orthogonal, hits in the dominant and non-dominant eyes are complementary. Targets cued in the dominant eye were often (but not always) correctly identified (red curves near 100%), while targets cued in the non-dominant eye (green curves) were rarely (but still sometimes) identified as the dominant target (green curves in *(a)* far below 50%), which in turn means, they were often, but not always, correctly identified as the cued non-dominant target (green curves in *(a)* close to 0%). In *(b)* the green curve is inverted to illustrate the performance differences between targets in the dominant and the non-dominant eye. Detection rates increase faster and to higher levels in the dominant eye. Black curves *(a)* show the ratings with binocularly cued targets; there was a small but notable bias to see the target in the dominant eye (values above 50%). Gray curves *(a)* represent the averages of target ratings with monocular cues in the dominant (red) and non-dominant eye (green). These averages often match the ratings obtained with binocular cues (black curve). Standard errors (s.e.m) are indicated in *(b)* and averaged over all data points in *(a)*. Original data points and smoothed curves (see General Methods).

were weakly significant in the data of one subject and, in consequence, also in the means [F(1,14)=5.5 and 8.57, respectively, $p<0.05$]. This suggests that target selection in monocular and binocular cuing was controlled by the same mechanism. This was not true, however, during the first 500-1000 ms after the test pattern onset, where stronger deviations are found in the data of all subjects. The second and rather surprising observation is that performance curves, after that time, remained rather flat over all cue delays up to 5 seconds, with no or only little modulations from any perceived rivalries. We do not know what subjects saw during that time (see Exp. 5 for a link to the individual percepts), but it is likely that they should have seen reversals of perceived line orientations in many if not all trials during that long presentation time (cf. analysis of Exp. 5). This is not reflected in the detection of cued targets.

The apparently constant detection levels in Figure 4 could be misleading however, if ratings of individual observers did vary but the variations had been averaged out in the means. To document the variations seen in single subjects, their individual performances are also shown in this and the following experiments. Figure 5 shows the individual data of all four subjects in Experiment 2. While their performances also remained rather constant after the initial period with strong modulations, some curves do indeed show minor variations at longer delays (marked by asterisks). Compared to the much stronger modulations at and shortly after test pattern onset, these variations were, however, small and seemed to occur more frequently in the nonD than the D eye or with binocular cues. The figure also illustrates variations between subjects when establishing their individual ocular preferences shortly after stimulus

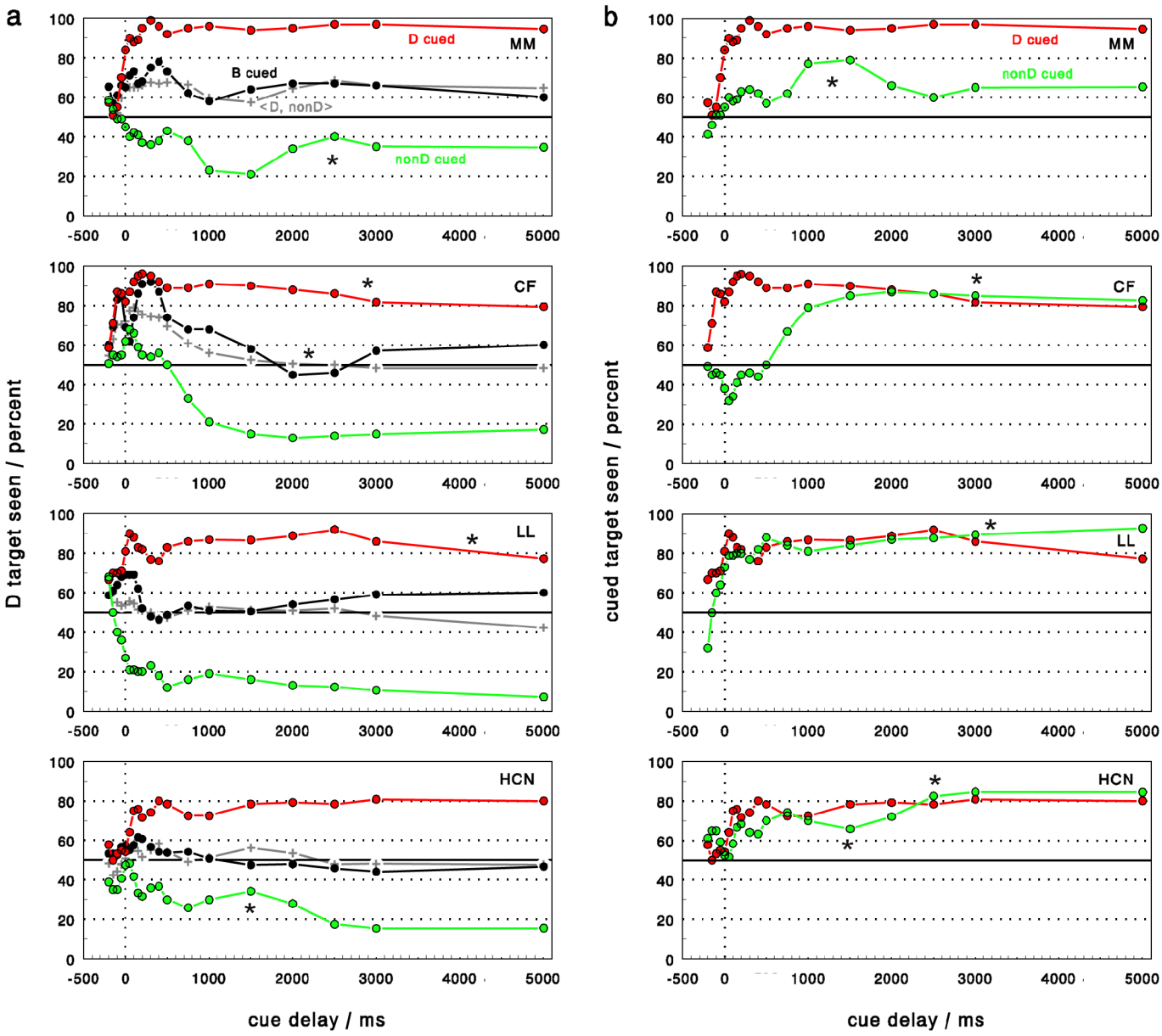

Figure 5. *Performance of individual subjects in Experiment 2.* ***a.-b.*** Target detection rates at various cue delays in different cuing conditions. Presentation as in Fig. 4 but now separately for each observer. Strong modulations in performance are mainly seen during the first 1-2 s after stimulus onset. At longer presentation times, there were occasionally gradual modulations (*) that are discussed in the text. Smoothed data.

onset (Fig. 5b). All subjects were able to detect monocularly cued targets on either eye but only two of them revealed a strong bias for the D eye by reporting the D cued targets (red curves) more frequently than the nonD cued targets (green curves). While this bias remained nearly constant in subject MM and did not change with longer cue delays, it quickly disappeared in subject CF, who could detect D cued and nonD cued targets equally well from presentations times above 2 s. In fact, three of the four subjects showed (very small) reversals of ocular preferences at long presentation times (green curves above red curves in Fig. 5b).

In terms of individual rating modulations, it may be also important to mention the small "switches" of target

preferences seen with binocularly cued targets (Fig. 5a); black curves sometimes shift above and below the 50% level thus indicating that either the D or the nonD cued target was seen (slightly) better. But when comparing the variations in different curves one must keep in mind that all curves in Figure 5a and 5b were collected from different trials each covering only one particular cuing condition. Some subjects (e.g., MM) did not reveal such preference shifts.

Discussion

Experiment 2 revealed two major observations; (i) subjects saw monocularly cued targets over long presentation times at fairly constant rates but (ii) showed strong modulations and variations at and immediately after test pattern onset. The additional observation that binocularly cued targets were closely predicted by the average of the two monocular cues, by and large fitted into that scheme; deviations were particularly strong mainly immediately after the test pattern onset. It is difficult however, to relate these two observations to the percept of binocular rivalry. Observers never reported to have seen unclear patterns or pattern reversals immediately after the stimulus onset (when the ratings of cued targets varied considerably) but all should have seen one or more reversals in long lasting stimulus presentations (when rating variations were rather small or even absent). As Experiment 5 will show, the medians of percept durations of the tested observers were typically below 3 s (except for subject HCN), which suggests that they should have seen line reversals in almost every trial. But the detection rates of cued targets do not indicate modulations strong enough to represent true perceptual reversals. Although the smoothing operation (cf. General Methods) might have flattened some humps and bumps, the generally small rating modulations in Figure 5 do not indicate alternating and exclusive representations of the two eyes, as they are reported for perceptual reversals in binocular rivalry.

It is important to recall that each data point in Figure 5 represents the average of 25 repetitions; thus targets seen at 90% or more (and accordingly 10% or less) were indeed seen (or not seen) in almost every trial. If reversals had occurred and were stochastic, then either the D or the nonD eye should have been leading in different trials, and detection rates should have averaged to nearly 50% in all cuing conditions. This was obviously not the case. Despite perceptual rivalry, the monocular cuing was apparently strong enough to bring the cued targets to awareness whatever the momentary percept was. On the other hand, monocular cuing was not strong enough to let observers *always* see the cued target, which should then have produced ratings of 100% and 0%, respectively. Only subject MM did reliably see the cued target in the D eye (ratings close to 100%), all other subjects sometimes saw the non-cued target in the nonD eye instead (lower ratings). We have already seen that in Experiment 1; monocular cuing of rivaling stimuli did not always let observers see the cued target. Overall, there was a bias for D targets, which was strong for subjects MM and CF and small for subjects LL and HCN (cf. Fig. 3d). Over the five seconds presentation time tested in Experiment 2, the bias did not change in subject MM but was apparently reduced and even slightly reversed at longer delays in subject CF (Fig. 5b, better ratings for targets in the nonD than in the D eye). Slightly stronger preference reversals are seen with subjects LL and HCN, who both had shown only a small bias between the eyes in Experiment 1. It is unlikely, however, that these small preference shifts from cue delays 2500-3000 ms onwards would reveal *perceptual* reversals which should be much stronger, as they lead to an exclusive representation of one or the other stimulus.

On the basis of all these data it seems unlikely that the perceptual reversals in binocular rivalry are evoked alone from interocular suppression. They may reflect other (not primarily ocular) competition effects as they, for example, are seen with ambiguous patterns (Logothetis, Leopold, & Sheinberg, 1996). In the cuing data, late modulations of target preferences were absent or very small, quite in contrast to the early modulations right after test pattern onset. Both observations differ from the typical dynamics of perceptual reversals (Bosten *et al.*, 2015) which were confirmed for the present observers (see Exp. 5). Only the early modulations right after stimulus onset may indeed reflect variations in ocular sensitivity and interocular suppression (Carter & Cavanagh, 2007). These variations are not stochastic but can be reliably reproduced under repetitive stimulation, as is seen in the high target detection rates in some test conditions (e.g., MM and CF at cue delays up to 500 ms). But these variations do not reach awareness.

In comparison with the previous experiment however, it is quite remarkable that monocular cues, in Experiment 2, have produced systematic differences in target detection rates depending on which eye was cued, whereas the

ocular origin of monocular cues was not distinguished (and not even recognized) in Experiment 1.

Target identification of rivaling stimuli with *binocular cues* is particularly challenging. The fact that detection rates often reflected the average of detection rates in the two monocular cuing conditions indicates likely similar underlying processes. On the other hand, deviations (like those at short or particularly long cue delays) suggest that this balance could be temporarily disturbed. This was clearly the case right after stimulus onset, when ocular interactions started and sensitivities of the two eyes were not yet balanced. It was apparently also the case at intermediate and longer delays when small variations in the selection rates of monocular or binocular cues affected the matches.

In summary, Experiment 2 has revealed strong modulations of target preferences soon after test pattern onset, which differed between monocular D and nonD cuing and settled within one second leading to nearly continuous preference settings for up to five seconds. While the initial modulations may reflect ocular interactions in establishing the ocular dominance of a subject, later modulations were not unequivocally linked to ocular or perceptual processes. They were smaller than the initial modulations (that do not reach awareness), may be related to perceptual (or experimental) uncertainties, but do not nearly reflect the alternating, exclusive percept of single patterns as found in binocular rivalry. The later modulations are reduced in larger data samples (cf. single data and mean responses in Figs. 4 and 5) but without reaching averages of nearly 50%. None of these modulations could unequivocally be related to perceptually alternating patterns of binocularly rivaling stimuli.

Experiment 2a: Modification of response categories

All subjects (including the author) reported that they occasionally saw the two orthogonal lines superimposed and sometimes no clear line at all, at the cued location. These percepts were not predominant but also not absent. In the previous experiments, subjects were asked to decide which of the two lines was stronger and better seen and had to guess if percepts were not unique and exclusive. There were only two valid responses in the 2AFC task, reporting a line tilted to the left or a line tilted to the right. In Experiment 2a this was modified and subjects could also indicate that they had seen "double lines" or "nothing".

Methods

The new response keys were "y" for double lines and "ä" for nothing (German keyboard with QWERTZ layout). The previous keys (< for left-tilted and - for right-tilted lines) remained valid. The same four subjects as in Experiment 2 also performed Experiment 2a; both experiments were run in interleaved sequence; test conditions and blocking were the same as in Experiment 2.

Results

The usage of the additional keys is criterion-dependent; subjects might have decided to guess on the line orientation as often as possible, or to hit one of the new keys if the line percept was not very clear. As a consequence, the new ratings were used with slightly different frequency by the individual observers (19.5% to 25%). However, the goal of this modification was to look for variations between cue delays and cuing conditions, and the criterion each subject used had likely been constant over a run so that the relative variations should be informative.

In general, the ratings in Experiment 2a (Fig. 6a) were similar to the ratings measured in Experiment 2 (cf. Fig. 4), in particular for monocularly cued targets. When the number of cued lines seen is divided by the number of line responses made in that condition, percentages are slightly higher than when the number is related to the number of all responses in that condition. This indicates that "double lines" and "nothing" responses were encountered in all test conditions. Even in the monocular cuing conditions with high target detection rates in Experiment 2, some targets were either not seen or not clearly perceived as single lines in Experiment 2a. But this led only to a shift of the rating curves; the general characteristics (modulations at test pattern onset, constant ratings at long cue delays, different onset dynamics for D and nonD targets) were similar to those in Experiment 2. Only the ratings with binocular cues (black curves)

deviated more strongly and did not meet the predictions from monocular cuing conditions (gray) as closely as in Experiment 2.

The ratings of intermediate percepts are shown in Figure 6b and c. While "double targets" were reported at rather constant rates over all cue delays (dark blue curves), the ratings of "nothing" were modulated along the stimulus presentation time (light blue curves). When cues were shown early before stimulus onset and hence were indeed presented without test lines, "nothing" ratings were increased (delays -200 ms and -150 ms). But when cues were shifted closer to the line pattern onset, subjects could already identify the targets even when they appeared shortly after the cue (delays -100 ms and -50 ms). "Nothing" ratings strongly decreased at cue delays 0-500 ms, particularly in the monocular cuing conditions (Fig. 6b). Obviously, monocularly cued targets then were very clear. Note, however, that "nothing" ratings did strongly increase with presentation time in binocular cuing conditions (Fig. 6c). At the longest cue delay tested, the sum of "double lines" and "nothing" percepts in the means reached nearly 50% indicating that at least some subjects had rated their percepts as unclear for about half of the binocularly cued targets. This was however not the case with monocularly cued targets (Fig. 6b)

While the overall differences between "double" and "nothing" ratings were generally not significant [$F(1,90)=0.94$, $p>0.33$], except for one subject [$F(1,14)=5.88$, $p<0.05$], the differences of summed "not single lines" ratings ("double lines" + "nothing") between monocular and binocular cuing conditions were highly significant [$F(1,90)=84.03$, $p<0.0001$], also for each individual subject [$F(1,14)=6.65$, $p<0.05$, to $F(1,14)=40.88$, $p<0.0001$].

It is important to mention that when line ratings from Experiments 2 and 2a are combined, the late and small modulations in the individual ratings (asterisks in Fig. 5a) are diminished, but not however the early and strong modulations immediately after stimulus onsets.

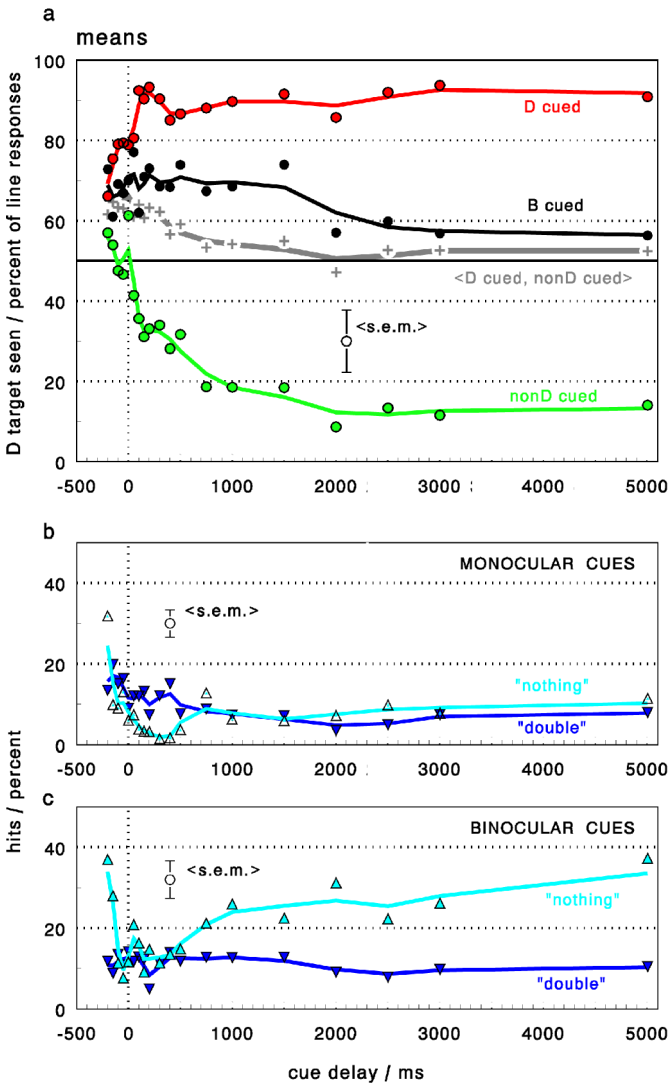

Figure 6. *Mean performance in Experiment 2a.* The experiment was a replication of Experiment 2; subjects could now also indicate that they had seen "double lines" or "nothing". ***a.*** Presentation as in Fig. 4a. Performance in cued line detection was similar to Experiment 2 when ratings are plotted as percentage of the line responses made in that condition. But ratings with binocularly cued targets (black curves) deviated from the monocular averages since subjects made fewer line responses with binocular cues (thus increasing the relative ratings). ***b., c.*** The new ratings of percepts as "double lines" or "nothing", for monocular *(b)* and binocular cues *(c)*. While "double lines" responses were entered fairly constantly in all conditions and over all cue delays, "nothing" responses were notably increased with binocular cues. Original data points with smoothed curves.

Discussion

The data confirm the conclusions from Experiment 2. The differences in cued target detection between the D and the nonD eye were preserved; strong rating modulations right after stimulus onset were also seen in Experiment 2a, whereas the later modulations in individual subjects were less pronounced and disappear when data from both experiments are averaged. This does however not mean that strong modulations from perceptual reversals might

have been present and averaged out; averaged ratings were still high but should have been strongly reduced if collected from complete perceptual reversals between the eyes. Instead, the high and nearly constant ratings indicate that perceptual reversals were not reflected in the ratings of cued targets.

Wolfe (1983) reported that a binocularly rivaling percept needs more than 150 ms to develop from rivaling stimuli. In shorter presentations, observers did see both lines superimposed. This was not observed in the present data. "Double lines" percepts were not notably increased at short cue delays (short stimulus presentation times) but were encountered with similar frequency at all tested cue delays (cf. Fig. 6b, c). "Nothing" percepts, on the other hand, were *reduced* at short cue delays when targets were apparently particularly clear. But given that target presentation time was at least 250 ms in all tests of the present study, this does not disprove the findings by Wolfe. Subjects had always enough time to see a (potentially rivaling) line pair after 150 ms. Nevertheless, rivaling percepts were apparently rare at short delays, since ratings with monocular cues quickly increased to maximal values and even binocularly cued targets were frequently rated as lines, not as "double lines" or "nothing", at these delays.

The following two experiments were designed to introduce an asymmetry between the ocular patterns. This was achieved in two ways. In Experiment 3, the line contrast in one pattern was increased. According to Levelt's second proposition (Brascamp, Klink, & Levelt, 2015) this should affect the dynamics of interocular suppression and mainly reduce the predominance periods of the other eye. In Experiment 4, subjects were adapted to one pattern before the second pattern was presented. This, too, has been reported to have dramatic consequences on the visibility of subsequently presented patterns in binocular rivalry (Wolfe, 1984). Adaptation should reduce the sensitivity for the stimulus in the adapted eye and increase the visibility for the non-adapted stimulus in the other eye. Wolfe (using a different paradigm and slightly shorter adaptation times) found effects lasting up to 1s after the adaptation.

Experiment 3: Rivalry of patterns with different line contrast

The asymmetry between patterns doubled the number of test conditions, as both patterns had to be presented to either eye.

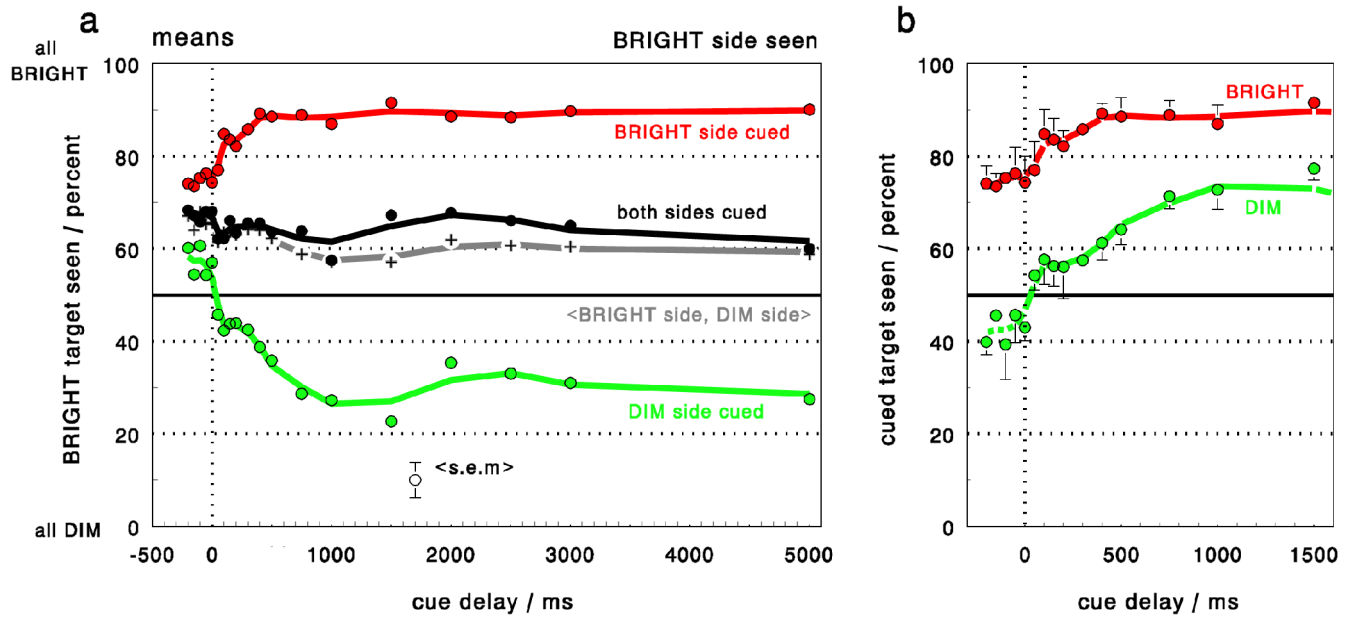

Figure 7. *Mean results of Experiment 3 (one pattern at higher contrast).* Presentation as in Fig. 4. Test conditions from the dominant and non-dominant eyes are accumulated. ***a.*** Detection rates of BRIGHT targets when either the BRIGHT targets (red), the DIM targets (green), or both targets were cued. Performance is notably better with BRIGHT than with DIM targets (red curves closer to 100% than green curves to 0%). ***b.*** Performance differences between BRIGHT and DIM cued targets. Curves are re-plotted from *(a)* with the DIM side cued data inverted. Original data with smoothed curves.

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Methods

Line luminance in one of the two patterns was increased (lines 26 cd/m^2); background luminance and cue contrast were unchanged. This doubled the Weber contrast of lines from the standard setting (18-10)/10 to (26-10)/10. The larger number of tests was split into three blocks (cue delays -200 ms to 200 ms; cue delays 300 ms to 1500 ms; and cue delays 2000 ms to 5000 ms), which were tested in interleaved sequence. All other test variations were the same as in Experiment 2. The test was again performed in the modified 2AFC task of Experiments 1 and 2 (no reports of "double lines" or "nothing"). The same four subjects (two female) from Experiment 2 also performed Experiment 3; two were L eye, two R eye dominant.

Results

Data presentation is similar to that of Experiment 2, except that we should now distinguish between normal ("DIM") targets, as before, and "BRIGHT" targets, at increased contrast. To keep the data presentation readable, performances with the two patterns are plotted in separate figures. In the averages from both eyes, however, these data are complementary. Since the DIM and BRIGHT test patterns were shown together, detection rates with one pattern will be inversely related to the detection rates with the other pattern. Differences may however occur when responses are split and performance with the D or nonD eyes is separately analyzed.

Figure 7 shows the mean data curves in different cuing conditions when the BRIGHT target was seen (Fig. 7a); data curves with the DIM target seen would be inverted. Preference variations look similar to those in Figure 4; with increasing presentation time, ratings of cued targets increase until they reach, after about 1000 ms, an almost constant level which does not further change until the longest cue delay tested. Ratings with the BRIGHT targets cued increase faster and to higher levels than ratings with the DIM targets cued. Ratings from D and nonD eyes are averaged in Figure 7 but will be split below. Please note again, that in this plot, due to the complementary ratings, values above 50% indicate a preference for the target in the BRIGHT line pattern and values below 50% a preference for the target in the DIM line pattern. The difference between targets is seen directly in Figure 7b;

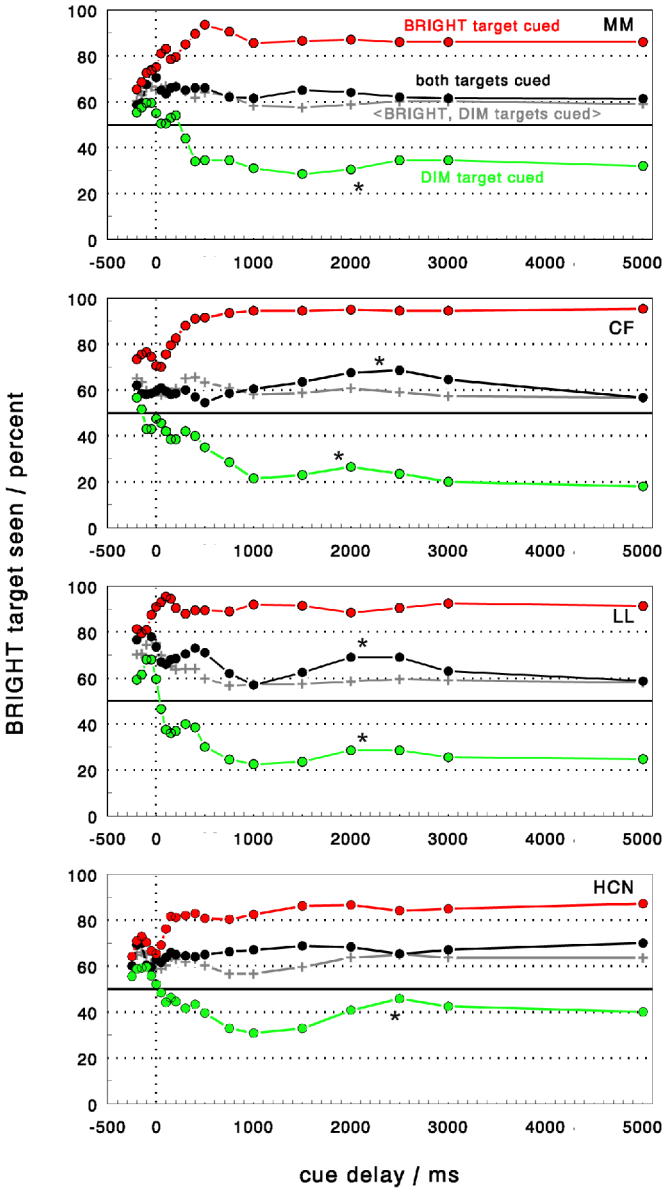

Figure 8. *Individual performance data in Experiment 3.* Presentation as in Fig. 7a but separate for each subject. Target detection was always better with the BRIGHT (red curves above 50%) than with the DIM targets cued (green curves below 50%); binocular cues (black) produced a consistent preference for the BRIGHT targets. Even outside the first 1000 ms, there were small but notable modulations (*) of detection rates which did however never change the preference for the dominant target. Smoothed data.

cued BRIGHT targets (red curves) were seen more often than cued DIM targets (green curves). Ratings in binocular cuing conditions (Fig. 7a, black curves) are again closely

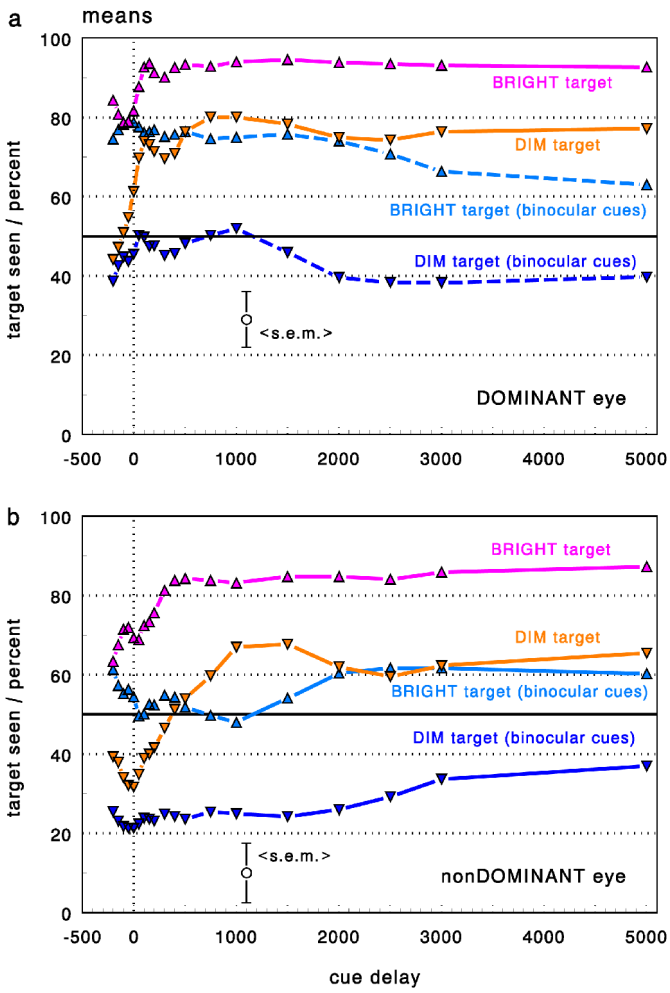

Figure 9. *Mean data of Experiment 3, split for* ***a.*** *the dominant and* ***b.*** *the non-dominant eye.* Due to stimulus conditions, curves with binocular cues are pairwise complementary. In both eyes, BRIGHT targets were better seen than DIM targets both in monocular as well as binocular cuing conditions. Across eyes, cued targets in the dominant eye *(a)* were better seen and did faster reach performance maximum. The different slopes in *(a)* and *(b)* indicate that the performance differences between the eyes cannot be fully compensated by increased pattern contrast. Smoothed data.

predicted by the averaged ratings in the two monocular cuing conditions (gray). In comparison to the patterns with equal line contrast tested in Experiment 2 (Fig. 4), the red curves in Figure 7 (BRIGHT lines) raise more slowly, but notice that here ratings from the D and nonD eye are averaged, whereas curves in Figure 4 distinguish D and nonD eye ratings (of targets with equal line contrast).

The ratings of individual observers (Fig. 8) revealed notable modulations right after stimulus onset, similar to Experiment 2. With increasing cue delays, however, these modulations flattened and ratings settled.at nearly constant values. In some observers smaller modulations were also seen at longer delays (asterisks). It also seems that the initial preference modulations immediately after the test pattern onset were less pronounced in Figure 8 than in Figure 5, where the two patterns had the same contrast. This is mainly due to the fact that DIM targets were generally less often seen than BRIGHT targets. All subjects revealed continuously higher ratings with cued BRIGHT than with cued DIM targets (red curves closer to 100% than green curves to 0%), thus confirming the different strength of pattern presentation in the eyes. Also ratings with binocular cues revealed a constant preference for the BRIGHT targets and did not shift and switch preferences.

To look for asymmetries associated with the individual ocular dominance, Figure 9 evaluates the data separately for the two eyes. (Due to stimulus conditions, the *binocular cuing* data are pairwise inversely related.) BRIGHT targets were generally seen better than DIM targets, even in binocular cuing conditions. Ratings generally increase faster with targets presented in the D (Fig. 9a) than in the nonD eye (Fig. 9b); the differences between BRIGHT and DIM targets are multiplexed into these variations. The differences between targets in the D and nonD eyes are directly plotted in Figure 10. They were smaller for BRIGHT (Fig. 10a) than for DIM targets (Fig. 10b), in which ratings of nonD targets fell initially below 50% indicating that the non-cued BRIGHT targets in the D eye were then seen instead.

Statistical analysis revealed the significance of differences in Figure 7 [two-factor ANOVA with replication, $F(2,135)=170$, $p<0.0001$] and Figure 9 [$F(3,180)=108.47$, $p<0.0001$, and $F(3,180)=121.06$, $p<0.0001$, for D and nonD cued targets, respectively], also for all individual observers [$F(2,28)\geq 56.31$, $p<0.0001$, Fig. 7; and $F(3,42)\geq 50.24$, $p<0.0001$, Fig. 9], while the differences between measured and predicted ratings with binocular cues (gray and black curves in Fig. 7) were generally not significant [$F(1,90)=0.03$, $p>0.86$], even not on an individual subject's basis [$F(1,14)\leq 3.58$, $p>0.07$], except for subject LL [$F(1,14)=7.51$, $p<0.05$]. The D vs. nonD cued rating differences in Figure 10 are also significant; $F(1,90)=34.64$, $p<0.0001$, for BRIGHT targets; $F(1,90)=36.27$, $p<0.0001$, for DIM targets.

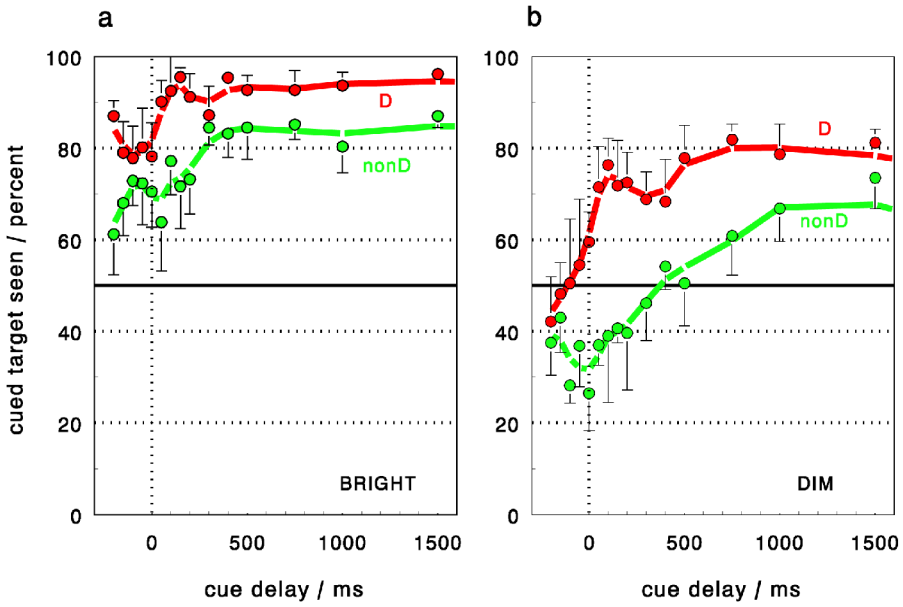

Figure 10. *Re-plot of ocular differences with **a.** BRIGHT and **b.** DIM targets in Experiment 3.* The differences document a generally better performance with the dominant eye.

Discussion

The main question is: Do we see any systematic differences in the data of this experiment compared to the data obtained with equal-contrast patterns in Experiment 2? On the first view, the answer is no, which is astonishing given the different pattern contrast and the proposed effects on reversal rates (e.g., Brascamp, Klink, & Levelt, 2015). In both experiments, detection rates of cued targets increase with stimulus presentation time and then remain about constant with only little modulations (here mainly with DIM targets) over the measured range. The initial slopes of increments are similar for BRIGHT and DIM targets but, similar to Experiment 2, differ between D and nonD cued targets (Fig. 9a and b). BRIGHT and DIM targets cued in the D eye reach maximal detection rates at cue delays of 100-150 ms, only slightly later than with equal-contrast patterns in Experiment 2 (Fig. 4, red curves; 50 ms). In the nonD eye, both targets need notably longer to reach their maximum, BRIGHT targets about 400 ms, DIM targets about 1 s. The difference in the initial slopes of D and nonD cued targets underlines that differences between the eyes cannot be compensated for by increasing the stimulus contrast; while the BRIGHT targets cued in the nonD eye were actually seen better than the DIM targets cued in the D eye, their initial ratings increased with different slopes (Fig. 9). This difference might have affected the initial predominance of the two patterns seen.

On the second view, more differences between the rating curves are found. In Experiment 3 but not Experiment 2, detection rates of the D target (red curves in Figs. 10 and 4b, respectively) were notably suppressed at cue delays 150-500 ms; this suppression was stronger for DIM (Fig. 10b) than for BRIGHT targets (Fig. 10a), suggesting an asymmetry with stronger suppression from the brighter pattern. Such a delayed suppression was, however, not seen with DIM targets cued in the nonD eye (green curve in Fig. 10b). Here, brightness differences between the patterns caused an asymmetry in target detection that was not seen with equal-contrast patterns in Experiment 2. For delays up to 400 ms, the DIM target in the nonD eye was more often missed, and instead the BRIGHT target in the D eye seen (ratings below 50% in Fig. 10b), than when both patterns had equal contrast (all ratings >50% in Fig. 4b). Altogether, these variations would be consistent with a stronger suppression from the BRIGHT target and consequently poorer visibility of the DIM target, multiplexed into variations from ocular dominance, and would not be unexpected with the patterns used in Experiment 3. However, these differences were particularly strong immediately after stimulus onset and disappeared within 1-2 s; they thus cannot explain the expected reversal variations from reciprocal inhibition (Levelt, 1965; cf. Alais, 2012).

Is there any evidence that percept durations with the DIM pattern might have changed in Experiment 3 as proposed by Levelt? The individual data in Figure 8 show only gradual variations which are similar in amplitude to the modulations in Experiment 2 but now occur at levels that are already strongly biased for BRIGHT patterns. In fact, there were no preference shifts between targets at all, neither for monocular nor for binocular cues. BRIGHT targets were always better seen and predominated the perception of cued targets.

Altogether, the detection of cued targets has revealed the expected variations from the different pattern contrast in the two eyes, but did not reveal any variations that could be directly related to changes in perceptual reversal rates.

Experiment 4: Rivalry after adaption

In Experiment 4, one test pattern was shown three seconds earlier to adapt subjects, on one eye, to that stimulus.

Methods

Line luminance was set back to standard (18 cd/m^2) in both patterns, but one test pattern ("EARLY") was switched on 3 s before the other ("LATE"). The timing of cues and cue delays was synchronized to the onset of the second pattern. Both patterns were simultaneously switched off, for positive cue delays 250 ms after the cue onset, for negative cue delays 250 ms after the onset of the LATE pattern. The combination of EARLY and LATE patterns was applied to both eyes, in different test conditions. Tests were split in three blocks, as in Experiment 3. The same four subjects as in Experiments 2 and 3 also performed Experiment 4.

Results

Mean target preferences for EARLY and LATE patterns are plotted in Figure 11. Since cuing was synchronized to the onset of the LATE pattern (dotted vertical lines),

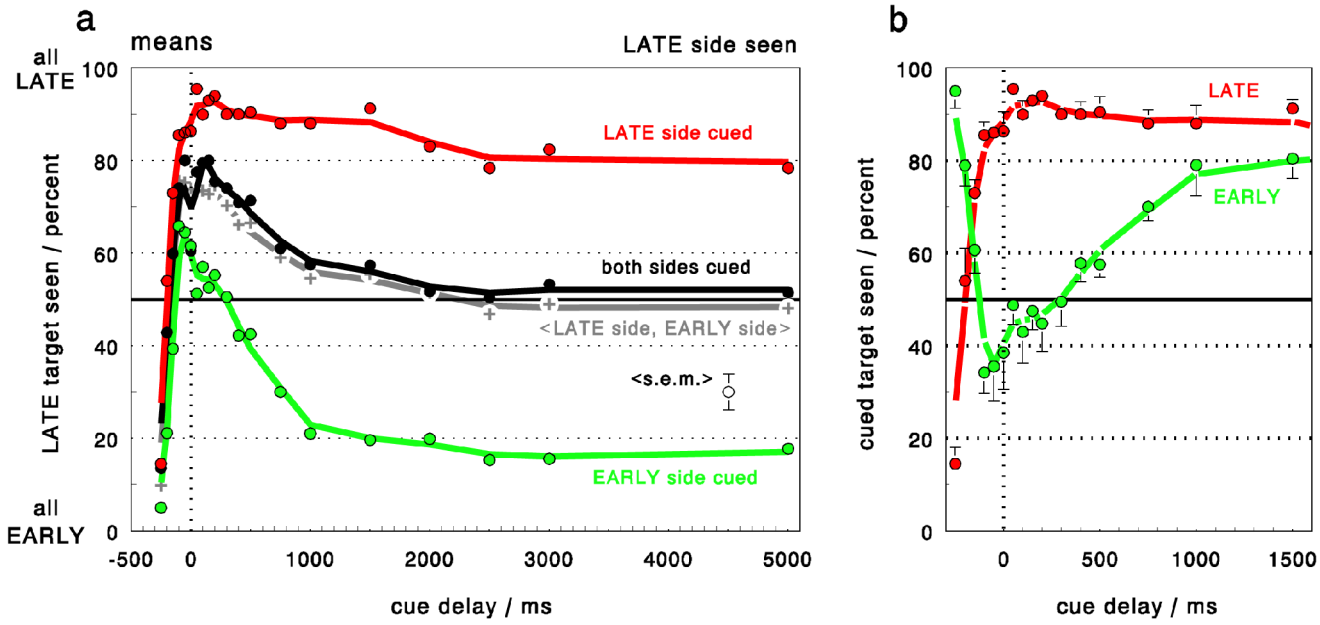

Figure 11. *Mean results of Experiment 4 (one pattern presented 3 s earlier).* Presentation as in Fig. 4. Measurements began shortly before the onset of the LATE pattern (dotted vertical lines). Test conditions from the dominant and non-dominant eyes are accumulated. ***a.*** Detection rates of LATE targets when the LATE targets (red), targets in the EARLY pattern (green), or both targets were cued. Cued targets in the new pattern (LATE) are much better seen than cued targets in the adapted pattern (EARLY). Adaptation has strongly reduced the number of detected targets on the adapted side (ratings above 50% in the green curves in *(a)*). Ratings of binocularly cued targets (black) closely matched the linear predictions from monocularly cued targets (gray). ***b.*** Performance differences between targets cued in the LATE and EARLY patterns, now plotted in percent of the cued targets seen. Curves are re-plotted from *(a)* and the green curve is inverted. While previous adaptation has strongly reduced the detection rates of cued EARLY side targets for more than 1000 ms, performance in cued EARLY target detection later exceeded that of cued targets on the LATE side *(a)*. Original data with smoothed curves.

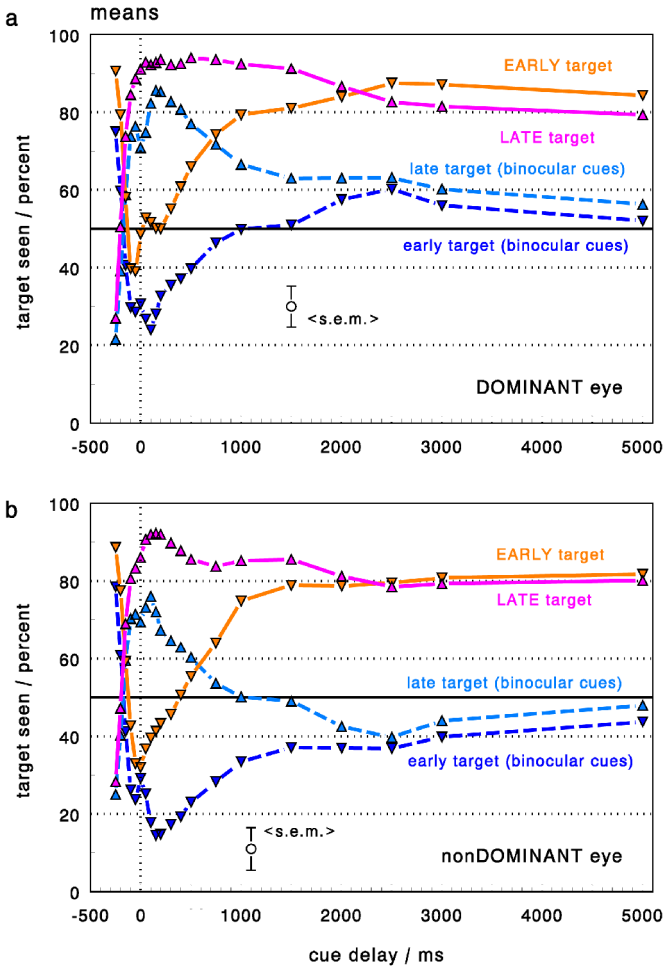

Figure 12. *Mean data of Experiment 4, now split for* ***a.*** *the dominant and* ***b.*** *the non-dominant eye.* In both eyes, LATE targets were initially much better seen than EARLY targets both in monocular and binocular cuing conditions. At around 2500 ms, rating preferences for monocular cues switch in the dominant eye. Across eyes, performances with the dominant eye *(a)* were generally better than performances in the non-dominant eye *(b)*. Due to stimulus conditions, curves with binocular cues are pairwise complementary. Smoothed data.

subjects still saw the EARLY target at negative cue delays. But when cues were presented shortly before or together with the LATE pattern onset, the LATE target became predominant and was reliably seen (red curve) even when the EARLY pattern was cued (green data points above 50%). With increasing cue delays, cued targets on the EARLY side were seen increasingly better and reached an intermediate rating plateau of about 20% (corresponding to 80% of the cued EARLY targets seen) 1000 ms after stimulus onset. This is best seen when the two monocular cuing conditions are directly compared (Fig. 11b). At the same time, ratings with the LATE side cued slightly diminished. With further increasing delays (cf. Fig. 11a), ratings of cued targets on the EARLY side even exceeded the ratings of cued targets on the LATE side at about 2500 ms (green curve is farer off from 50% than the red curve). Thus, although observers had adapted to the EARLY pattern before each measurement and therefore primarily saw the new LATE pattern when it was switched on, the EARLY pattern was again perfectly seen, and even better than the LATE pattern, after longer presentations. Since in Figure 11 ratings from the D and nonD eyes are averaged, the two ratings should likely equalize at even longer delays, which was however not tested. Ratings with binocular cues (black) laid in the middle between the two monocular curves and were again closely predicted by averaging the two ratings in these conditions (gray crosses).

Again it is interesting to analyze the data for differences between the D and nonD eyes (Fig. 12). Due to the stimulus combinations in tests, the ratings with binocular cues are pairwise reversed in Figure 12a and b. For each tested target condition, ratings were generally better for the D than for the nonD eye. These ratings are directly compared in Figure 13. Interestingly, while differences between the eyes were pronounced with the EARLY target right from the onset of the (LATE) stimulus (Fig. 13b), D vs. nonD differences were almost absent in the initial onset of the LATE target ratings (Fig. 13a). Apparently, after 3 s adaptation to the EARLY pattern, cued responses to the non-adapted new (LATE) target were so strong that they had masked any differences from ocular dominance. Figure 12 also shows that the preference crossing of EARLY over LATE targets about 2.5 s after stimulus onset was more pronounced in the D than in the nonD eye (cf. rose and violet curves in Fig. 12a and b).

Individual ratings from all four subjects (Fig. 14) showed even less variations at long cuing delays than in the previous experiments. All subjects were initially biased for the new (LATE) pattern, even when a target in the EARLY pattern was cued. With ongoing presentation time however, this bias was reduced and rating performance became more equal between patterns (Fig. 14b). Almost all subjects (not HCN, however) showed an overshooting of rating performances at later cue delays; the initially poorly detected EARLY targets were then better seen than the initially better detected LATE targets (green curves

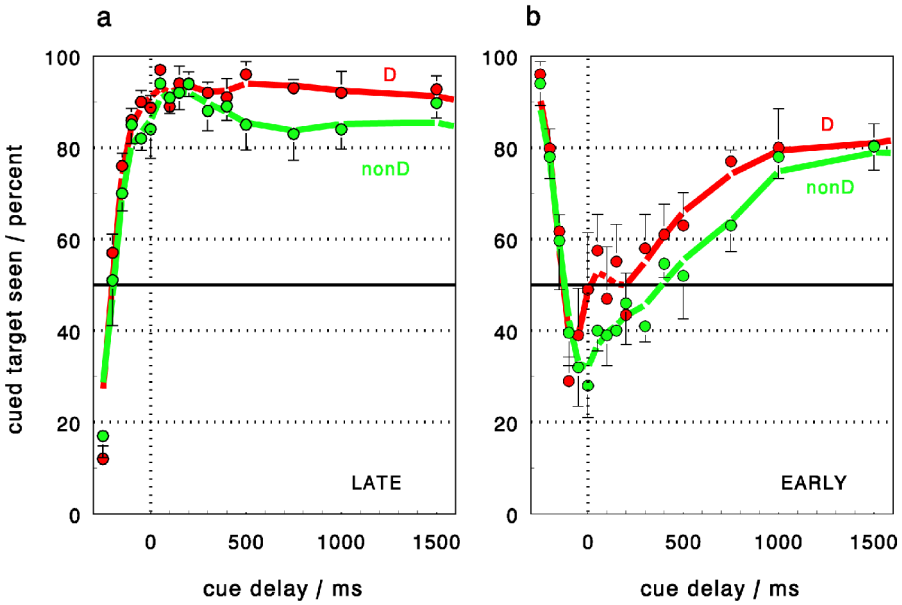

Figure 13. *Re-plot of ocular differences with **a.** LATE and **b.** EARLY targets in Experiment 4.* The differences document a generally better performance with the dominant eye, which did however not manifest in the initial ratings with the LATE patterns.

above red curves, marked by asterisks in Fig. 14b). In two subjects (not MM), this was accompanied by a similar (and rather small) shift of rating preferences with binocularly cued targets (black curves) across the 50% level (Fig. 14a). The initial bias towards LATE targets is clearly seen with all cued targets, including the binocularly cued ones; a similarly strong rating modulation was not nearly reached again during the ongoing pattern presentation during which perceptual reversals should have occurred.

Statistical analysis revealed significant differences in Figures 11 and 12 [$F(2,135)=629.16$, $p<0.0001$, and $F(3,135)\geq170.42$, $p<0.0001$, respectively], even on the basis of individual subjects [$F(2,28)>45.28$, $p<0.0001$, and $F(3,42)>10.3$, $p<0.0001$, respectively]. Ratings obtained with binocularly cues (Fig. 11, black curve) and predictions obtained by averaging the ratings from the two monocular cuing conditions (gray crosses) were not significantly different [$F(1,90)=3.92$, $p>0.05$], also in the data of two subjects [$F(1,14)<0.22$, $p>0.64$]; two subjects, however, did show significant differences [$F(1,14)=6.36$, $p<0.05$, and $F(1,14)=13.78$, $p<0.005$]. In the comparisons of D and nonD targets (Fig. 13) rating differences of LATE targets were only just significant [$F(1,90)=6.48$, $p<0.05$] but rating differences of EARLY targets were significant [$F(1,90)=13.05$, $p<0.005$]. This corresponds to the small and stronger differences seen in Figure 13a and b.

Discussion

First of all, rating performances reveal exactly the asymmetries that are expected to be seen in neural responses with and without previous adaptation. While responses to the EARLY stimulus should decay from adaptation, responses to the LATE stimulus should be strong immediately after stimulus onset. This was closely revealed in the rating performances with cued targets. With ongoing stimulus presentation however, this asymmetry weakens when neurons also begin to adapt to the LATE side stimulus. Interestingly, rating performances showed a small overshooting of adaptation effects at about 2.5 s after the LATE pattern onset; the cued EARLY target was then (after a total adaptation time of 5.5 s) seen slightly better than the cued LATE target (after an adaptation time of only 2.5 s). This suggests that rating performance was not only affected by the decaying activity of neurons but perhaps also by ocular interactions, like reciprocal inhibition.

By and large the data are in good agreement with Wolfe (1984) who found in analogue (but slightly different) experiments, that monocular adaptation had first (up to 200 ms) completely deleted the adapted stimulus from the binocular percept and then still had reduced it up to 1 s later. In my experiment, adaptation effects lasted even longer, up to 2.5 s. However, *perceptual* rivalry as

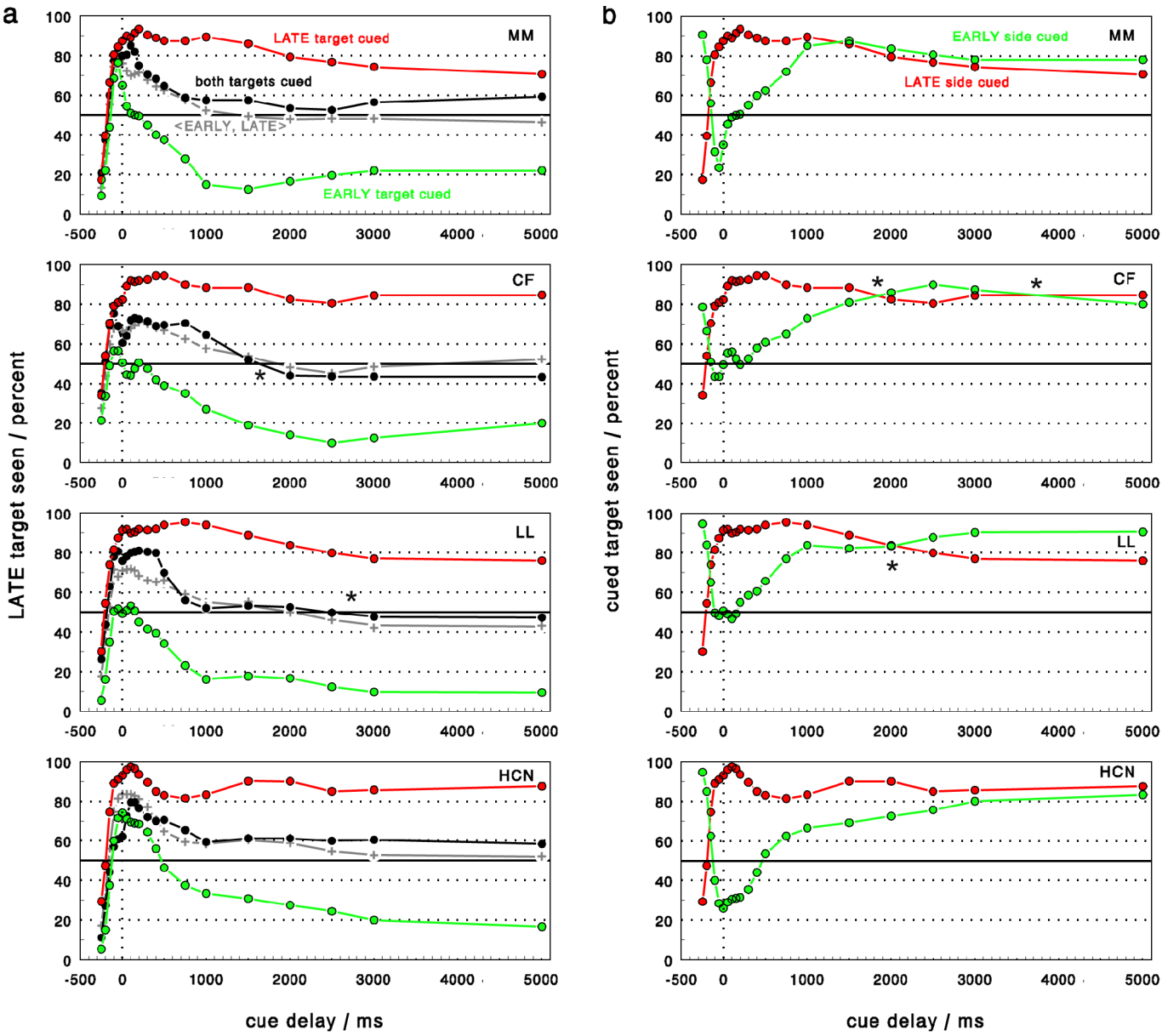

Figure 14. *Individual performances in Experiment 4.* Presentation as in Fig. 11 but separate for each subject. Target detection in the EARLY pattern was strongly reduced after adaptation and was predominated by the targets in the new LATE pattern. Strong modulations outside the first 2 s are rare but target preferences might have changed in some observers (*). Smoothed data.

reported by Wolfe was not tested in the present experiment. Neither the almost constant (and high) performance ratings in the mean data (Fig. 11), nor the rather small modulations in the data of individual observers (Fig. 14) provide reliably evidence of perceptual reversals, which however should have occurred in these experiments. This discrepancy will be further addressed in the General Discussion below.

Experiment 5:
Synchronization to perceived reversals

In all previous experiments, the detection rate of cued targets was measured irrespectively of what the observers saw just before the cue occurred. This was changed in the last experiment in which cued selection was synchronized to the individual percepts of observers.

Methods

To relate cued visual selection to the current percept of the observer but nevertheless keep control of the ocular side that was perceived, the experimental setup was modified in the following way. At the beginning of a trial, after 1 s with the (green) binocular fusion pattern, test patterns as in Experiment 2 were shown (simultaneous onset, equal luminance contrast, orthogonal lines at corresponding locations in the two eyes) and remained then visible until the end of the trial. One second later, a binocular four-dot cue with *red* dots (18 cd/m^2) was presented, for half a second, to mark a particular line pair. Subjects were asked to concentrate on this line and quickly report all subsequent changes in perceived orientation by pressing certain keys on the computer keyboard. When the line seemed to disappear and later reappear at the same orientation, subjects had to press the according orientation key again. In other words, during this part of each trial *("reversal phase")* subjects were requested to give a continuous report of changes in the perceived line orientation, with particular emphasis on the onset of new orientation percepts ("reversals"). After a certain (variable) number of reversals, the report of the correct orientation for a selected eye was taken as a trigger, which then started the usual cuing procedure *("cuing phase")* with one of three cue delays. After the delay, a single test line in the pattern was cued using the standard *white* four-dot cues. The three tested cue delays were 50 ms, 500 ms, and 1500 ms. Cuing was always monocular, on the L or R eye. Four different cuing conditions were tested in random sequence in each run. In condition A, cues were applied to the currently perceived target in the momentarily "leading" eye. In condition B, cues were applied to the (orthogonal) target at the same location in the opposite eye. In conditions C and D, cues were applied to a distant raster location in the line pattern on the opposite side of the fixation point in either the momentarily leading (C) or the other, non-leading eye (D). The distance between targets currently seen and distant targets varied between 2.2 deg (for targets vertically or horizontally displaced from the fixation point) and 3.1 deg (for targets in oblique directions from the fixation point). Subjects then had to enter the perceived orientation of the cued target, as in all previous experiments. Test patterns were continuously presented during the entire period of the trial and disappeared 250 ms after the onset of the final cue, as in the experiments before. Possible target locations were restricted to raster cells next to the fixation cross (eight possible locations), and response keys were changed. For the indication of perceived line orientations during the *reversal phase* of each trial, subjects used their left hands and the '<' and 'y' keys (QWERT layout) for lines tilted to the left and right, respectively. For reports in the *cuing task* (with white cues) they used their right hands, and the '.' and '-' keys for left- and right-tilted lines. Subjects were given an initial training run, for exercise, and were regularly reminded to enter line reversals quickly after they appeared. One short run for exercise was sufficient to let subjects become familiar with the task. In addition, they always could reject a trial and pause if they felt confused or stressed; rejected trials were returned to the pool of trials still to be performed and were repeated, with a new line pattern and a new target location, at a later time of the run.

Six subjects (three female) including all subjects from Experiments 2-4 participated in Experiment 5; two of them were R eye dominant. A third subject (NMB), originally classified as L dominant with the Porta sighting test, gave slightly better ratings with the R eye (cf- Fig. 3d) and was here also included as R eye dominant.

Results

Since, by the early selection of a single target, percepts could be related to the selected target location and one particular eye, it was possible to relate the rating performance with the later cued target to these parameters.

Figure 15 shows the percentage of cued targets seen, after the last reported line reversal. Ratings are shown for the three tested cue delays (adjacent bars) and for the four cuing conditions (groups of bars; A-D). Cues were presented at the location of the currently perceived target in the momentarily leading eye (A), at the same location in the other (momentarily not leading) eye (B), and at

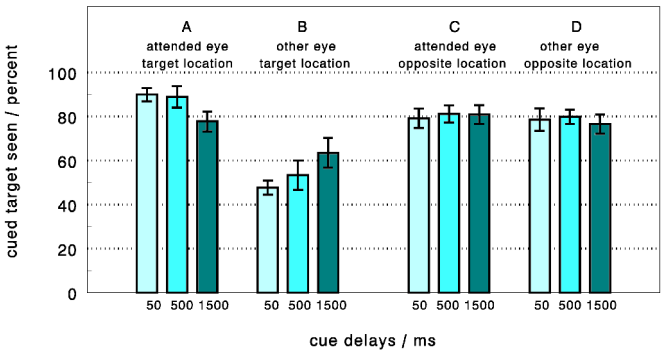

Figure 15. *Cued target detection in Experiment 5.* In the previous *reversal phase* of each trial, subjects had attended to one particular line location and reported all changes of perceived line orientation. When, after several reversals, the report indicated that the line in one particular eye was seen, the *cuing test* began, in which a certain line in one of four conditions (A-D) was cued at one of three delays after the reversal report (50 ms, 500 ms, 1500 ms). The graph plots only the mean results of this cuing test (six subjects). Target detection rates were increased when the currently seen target was cued (condition A) and strongly diminished when the corresponding target in the other eye was cued (condition B). Target locations 2-3 deg off the attended location produced intermediate responses (conditions C and D). Error bars indicate the s.e.m.

locations 2-3 deg away from the currently attended target location, on the opposite side of the line raster, in the momentarily leading (C) and non-leading eye (D). The means of all subjects (Fig. 15) reveal two intermingled modulations, a difference between cuing conditions A-D and a modulation over the different cue delays (50-1500 ms) in some of these conditions. Apparently, when the currently perceived target was cued (condition A), it was much better seen (reported more often) than when the rivaling target at the same location in the non-leading eye was cued (B). The difference was strongest right after the last reversal report (cue delay 50 ms) and diminished in time (delays 500 ms and 1500 ms). Ratings varied between 90% (A) and 48% (B), at the 50 ms delay, and 78% and 63%, respectively, at delay 1500 ms. However, when cues were applied to distant locations in the patterns on the other side of the fixation point (groups C and D), target ratings were in between, with only small differences between the momentarily leading (C) and the momentarily non-leading eye (D). The overall rating differences in Figure 15 are statistically significant between test conditions [two-factor ANOVA with replication, $F(3,60)=25.98$, $p<0.0001$] but not between cue delays [$F(2,60)=0.19$, $p>0.82$]. Detailed analysis, however, showed that the differences between conditions A and B are significant at the 50 ms and 500 ms delays ($p<0.0005$ and $p<0.01$, respectively; paired two-sided t-tests across subjects) but not at the 1500 ms delay ($p>0.23$). This is also true for the differences between B and C ($p<0.01$, $p<0.05$, $p>0.09$, respectively) and B and D ($p<0.005$, $p<0.05$, $p>0.18$, respectively) but generally not for differences between A and C, or C and D.

Note however that there was a stimulus difference between conditions A, B and C, D. While the orientation of the cued target was identical (A) or orthogonal (B) to the orientation of the previously attended target, target orientation was random in conditions C and D. To see whether ratings at the latter (non-attended) locations were improved when the cued target there had the same orientation as the previously attended target, test conditions C and D were later distinguished for the tested target orientation (which reduced the number of tests in each individual sample). In test conditions C1 and D1 (Fig. 16), cued targets had the same orientation as the attended target (for which reversals had been reported); in conditions C2 and D2, they were orthogonal. Indeed, data show a small but reliable difference. In the currently leading eye, targets in the attended orientation were slightly better seen than targets orthogonal to it (C1 vs. C2). The rating difference over all three cue delays (horizontal lines in Fig. 16) was 11.7% and is significant [$F(1,30)=7.88$, $p<0.01$]. Also in the opposite eye, there was a small (5.0%) difference between targets in the attended orientation (D1) and orthogonal targets (D2); this

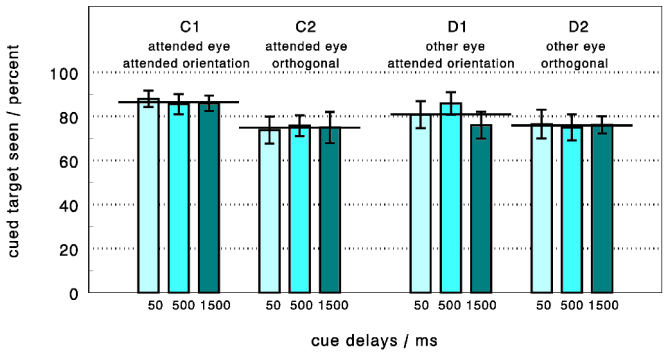

Figure 16. *Data from conditions C and D in Figure 15 split for the attended (C1, D1) and orthogonal line orientations (C2, D2).* Particularly targets in the attended eye (C) generated rating differences depending on the current orientation. Horizontal lines represent the means of all three delays. Error bars show s.e.m.

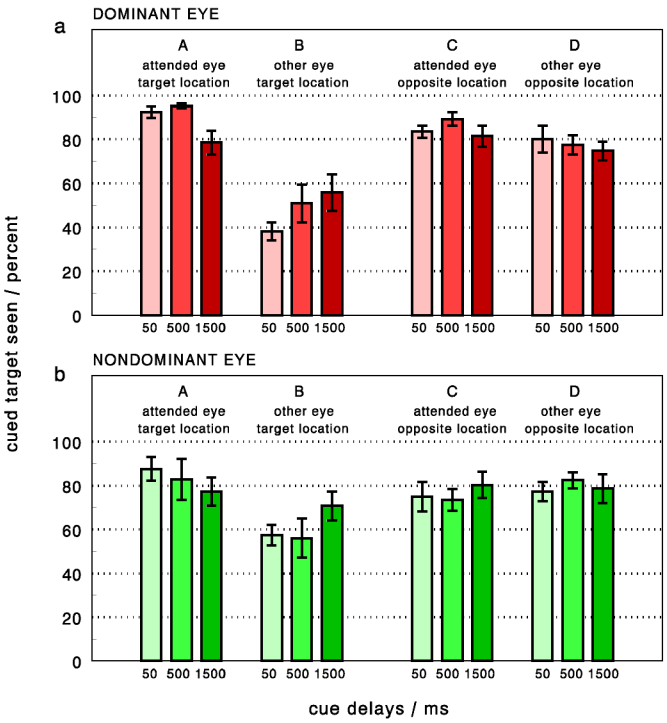

Figure 17. *Data from Figure 15 split for* ***a.*** *the dominant and* ***b.*** *the non-dominant eye.* Performance differences between A and B were more pronounced for the dominant *(a)* than for the non-dominant eye *(b)*. Note however that conditions B and D refer to the "other" eye, i.e. the non-dominant eye in *(a)*, and the dominant eye in *(b)*. With this in mind, responses were generally larger in the dominant than in the non-dominant eye.

difference, however, is not significant [$F(1,30)=1.13$, $p>0.29$]. Further analysis (paired two-sided t-tests across subjects, from all delays) revealed that also the ratings in conditions A and C2 are just statistically significant ($p<0.05$).

In Figure 17 data are split for the D and nonD eye. While the general response characteristics are the same, the differences between conditions A and B are even increased for the D eye, and slightly diminished for the nonD eye. Note however, that groups were defined in relation to the selected leading eye in the reversal phase; that is, conditions B and D with cues in the "opposite" eye were, in fact, evoked from the nonD (Fig. 17a) and the D eyes (Fig. 17b), respectively. With this in mind, the differences between cuing conditions A-D in Figure 17a and b are consistent with generally increased responses to the D eye, as was found in all previous experiments. The rating differences between cuing conditions in Figure 17 are statistically significant both for the D and the nonD eye [$F(3,60)=37.88$, $p<0.0001$, and $F(3,60)=6.27$, $p<0.001$, respectively; two-factor ANOVA with replication] but generally not between the different delays and not for every single observer. Differences between cuing conditions C1 (targets in attended orientation) vs. C2 (targets orthogonal) and D1 vs. D2 (Fig. 16) were generally smaller and were not separately analyzed for the D and nonD eye.

Reversal rates. The *reversal phases* in each trial allowed me to analyze the dynamics of perceptual reversals in the four subjects of Experiments 2-4, in particular the durations of predominance periods between reversals. Since the starting time of reversal reports was not well defined (the pattern was shown before one target was selected), the first reversal in each trial was ignored and analysis was restricted to subsequent reversals. Repeated reports of the same orientation, without an orientation change in-between, were not counted. The distribution of predominance durations between orientation reversals from all trials are shown in Figure 18. They reveal typical distribution patterns, with medians below 3 s for three subjects; only HCN showed much slower reversal rates, with a median of more than 7 s. There were no significant differences between percept durations in the D vs. the nonD eye.

Discussion

Reversal characteristics and durations of ocular predominance periods in the tested subjects were similar to those reported in literature. In a large population study on more than 1000 observers (Bosten *et al.*, 2015) medians of duration distributions peak around 2.5 s which was also found with three subjects of the present study (Fig. 18). Subject HCN showed notably increased perceptual durations, with a median of 7.3 s. This is likely due to the higher age of this observer; even in the population study with observers up to 40 years of age, the older adults were reported to show significantly larger medians than the younger adults (Bosten *et al.*, 2015). We can thus assume that the tested subjects behaved "normally". At least three of the four subjects should have regularly seen reversals in Experiments 2-4, in which presentation time was extended up to 5 s, and even subject

HCN should likely have seen one orientation switch during that time in quite a few trials.

But this reveals a discrepancy between the previous experiments and Experiment 5. While in Experiments 2 to 4, monocularly cued targets were detected with rather constant rates from cue delays of about 1 s onwards, the detection of monocularly cued targets in Experiment 5 differed strongly between the momentarily seen target and the target in the opposite eye (cf. Fig. 15). Here, ratings differed by more than 40% between trials in which the momentarily seen target was cued and trials in which the target in the opposite eye was cued (conditions A and B). With increasing delays after the last reversal report (not after stimulus onset which was long before), the differences diminished. Except during the initial 500 ms after stimulus onset, such a big difference was not seen in Experiments 2-4, where ratings of cued targets were constantly high for both eyes.

One explanation of this discrepancy might be attention. In Experiment 5 subjects attended to the location and current orientation of the target (to report line reversals), but they had never attended to a particular target or target location in Experiments 2-4 before the cue occurred. When, in Experiment 5, the cued target was orthogonal to the attended line orientation, like in condition B, target detection rates were strongly reduced. Even at other, non-attended locations (conditions C and D) targets in the attended orientation were better seen than targets orthogonal to it (conditions C1 vs. C2 and D1 vs. D2). Thus, although the role of attention in binocular rivalry is still under dispute (cf. Dieter, Brascamp, Tadin, & Blake, 2016), Experiment 5 might have revealed quite strong effects in the detection of cued targets. The strong suppression of targets in the other eye (condition B) however, indicates that attention would then not only enhance attended features and locations but would also enhance the suppression evoked from the attended lines to the orthogonal lines in the other eye.

If attention were exclusively spatial and were directed to the selected target location (where reversals had to be reported), we might have seen an increased preference for the attended target (which we do; condition A) and perhaps also an increased suppression of the orthogonal target at the same location in the other eye (which we also see; condition B) but not an enhanced response to a target farther away (which we do however; conditions C and D). On the other hand, if attention had modulated the two ocular inputs, thus producing generally better target ratings in the attended eye and an overall reduced performance in the non-attended eye (which we only see at the attended location), then we should have also seen significant *ocular* differences at other target locations (which we didn't; conditions C and D). (Note however that this latter case is partly hypothetic as the ocular origin of different patterns never reached the awareness of an observer.) Altogether, this seems to suggest that attention

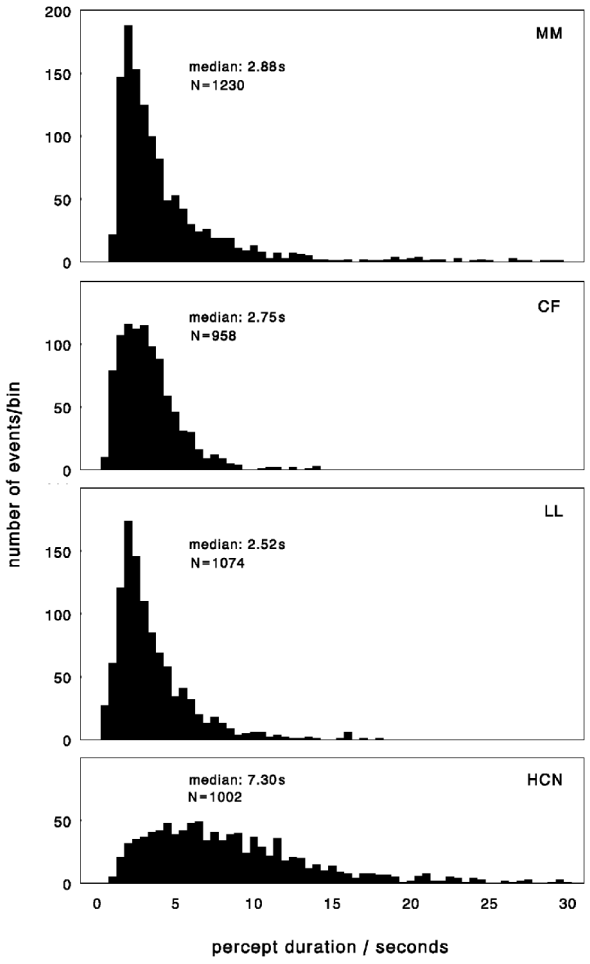

Figure 18. *Percept durations measured in the "reversal phase" of Experiment 5; data are only shown for the subjects of Experiments 2-4.* Distributions show the typical characteristics of young observers (except HCN) with medians below 3 s. This indicates that at least three subjects should have frequently seen complete target reversals in the long lasting trials of Experiments 2-4. Subject HCN revealed a speed-reduced distribution (median above 7 s) which is typical for older observers. Even he should have seen quite a few line reversals in long-lasting stimulus presentations of Experiments 2-4.

was paid to both the *location and orientation* of the currently perceived target, and that this selection was then partly generalized over different targets and target locations (conditions C1 vs. C2 and D1 vs. D2). Effectively, this would then represent a combination of spatial and feature-based attentional selection.

GENERAL DISCUSSION

In altogether five experiments, the method of *cued visual selection* (CVS) was used to evaluate the sensitivity of the visual system to monocularly or binocularly cued targets. Since binocular rivalry is, in principle, a highly competitive selection process, the CVS method might be particularly well suited to analyze and elucidate the steps of perceptual selection in binocular rivalry. Surprisingly, however, in none of the five experiments, cued selection has uncovered a selection process that was nearly as exclusive as that reported for the rivaling percepts in binocular rivalry.

In the following I will discuss three aspects of these findings. I will first look at the method and compare it with some previous work. I will then emphasize the consequences for localizing the neural mechanisms underlying binocular rivalry and discuss supportive and controversial findings from the literature. Finally, I will briefly underline the role of ocular dominance that was observed in the present experiments but seems to be often ignored in studies on binocular rivalry.

Cued visual selection

While perceptual reversals in binocular rivalry are known to start locally and eventually spread over from single locations to larger regions or even the entire pattern (Blake, O'Shea, & Mueller, 1992; Wilson, Blake, & Lee, 2001; Lee, Blake, & Heeger, 2005), only relatively few studies have indeed used discontinuous, patchy patterns when testing binocular rivalry. One of the first studies was by Kovacs and colleagues (Kovács, Papathomas, Yang, & Fehér, 1996) who reported that patches from different patterns can be grouped and perceptually combined even across eyes. This has started several studies that studied grouping processes in binocular rivalry and found that the ocular distribution of pattern information could be irrelevant for the synthesis of global percepts (e.g., Bonneh, Sagi, & Karni, 2001; Lee & Blake, 2004; Stuit, Paffen, van der Smagt, & Verstraten, 2011). The line raster used in the present experiments might have been particularly helpful, as it allowed me a much better timing in estimating perceptual reversals than had been possible with a large pattern, in which reversals must be distinguished between beginning piecemeal and the full global perception changes. With fairly densely arranged lines as in the present study, however, one must take care that lines do not binocularly fuse under false disparities. This was avoided by an added frame, a fixation cross, and several dots within the pattern, which all together provided a strong binocular fusion signal.

Cuing and the organization of patterns in the present study have put the weight on monocular and hence early processing stages, which however has made it possible to study the contribution of these processes, in particular. In principle, we do not know where cues and targets reach awareness, and subjects could not tell us which eye was cued nor which target had been presented to which eye. The ocular origin of the stimuli was unknown and irrelevant for the observers. Thus, modulations of cued target detection might have been generated at any processing level, from early levels where the two eyes are separately represented, to higher perceptual levels where the ocular information is combined and information about the eye-of-origin is lost. But the method was sensitive enough to measure early modulations like the strong and likely ocular interactions immediately after stimulus onset (which do not enter awareness), as well as later and much weaker modulations, which might be one source of ocular competition but did not reflect the strong suppression between exclusive percepts associated with binocular rivalry. The origin of these modulations, however, remains hidden; it might have been modulations from reciprocal inhibition between ocular representations (cf. Alais, 2012), as well as feedback from higher processing stages with pattern-organized representations. It is mainly the discrepancy between observations in the CVS data (strong vs. small modulations) and the lack of correlations with reported perceptual analogies, that led to the following arguments about the role of ocular suppression in binocular rivalry.

How ocular is binocular rivalry?

The surprising observation in the present experiments is that modulations in cued target detection are not related to the strong percepts of pattern competition and reversals. Strong modulations right after onset of the stimulus do not

lead to rivaling percepts. Strong perceptual reversals, on the other hand, that are seen under prolonged pattern inspection, are not accompanied by similarly strong modulations of cued target sensitivity. Furthermore, durations of perceptual predominance between reversals were generally not different between the D and the nonD eye, whereas there was a considerable bias towards the D eye in all cued target ratings of the present study. Given the many studies that seem to confirm a direct link between binocular interactions and perceptual variations (cf. Alais, 2012) and others that have questioned it (e.g., Logothetis, 1998), the issue deserves a more detailed analysis.

First of all, we cannot exclude that the monocular cues applied in the present experiments did not change the percept and made targets visible that were momentarily suppressed and had not been seen without the cue. In that case, the detection rate of cued targets might have been constant *despite* rivaling percepts from the ocular input. While attention is generally not necessary to see alternating percepts in binocular rivalry (Pastukhov & Braun, 2007), the four-dot cues in my experiments might have attracted attention to the cued stimulus and thus might have reduced any suppression of a momentarily unseen stimulus (cf. Walker & Powell, 1979). Although such processes should take time, it may thus be possible that the constant detection rates with monocularly cued targets above 1000 ms presentation time are merely an effect of cuing. However, the same (constant) bias and asymmetry in preferences was seen with *binocular* cues, which should not have evoked perceptual predominance of one or the other eye. It is also remarkable that the same cuing effects could not override the strong interocular modulations right after stimulus onset which lasted up to 1 s. These variations were highly reproducible, differed between observers and seem to represent an early phase of perceptual competition (Carter & Cavanagh, 2007).

How do the present results relate to the convincing reports of ocular suppression in binocular rivalry? Several studies have demonstrated strong interocular suppression (e.g., Stuit, Cass, Paffen, & Alais, 2009; for a detailed discussion, see Alais, 2012) which is, however, not necessarily and not directly responsible for perceived reversals. The strongest evidence that interocular suppression might be causally related to perceived reversals comes from Alais and colleagues (Alais, Cass, O'Shea, & Blake, 2010). By linking perceived patterns and reversals to the observers' momentary sensitivity to eventually applied probes, they could demonstrate decreasing and increasing sensitivity to the probes during predominant and suppressed perceptual periods, respectively, until percepts reversed at the moment when probe sensitivities were equal. In several aspects, their findings are similar to the present data. But also in their data, probe sensitivities vary only by 20-25%, indicating that probe sensitivity is *modulated* with the perceptual variations but does not itself reflect the strong alterations associated with exclusive percepts in binocular rivalry. Other studies have questioned a too close link of perceived alternations and ocular activities. Logothetis and colleagues, for example, found that only 20% of the neurons in V1 (where interocular suppression is strong and input from the two eyes is partly still separated) respond in correlation to the alternating percept of a rivaling stimulus (Keliris, Logothetis, & Tolias, 2010), while neural activity variations in higher levels were better correlated with the perceived reversals (Logothetis, 1998). Thus, it may well be that ocular interactions seen at early processing stages in the visual system and carefully demonstrated in elegant and sophisticated experiments, would initiate more central competitions which then may lead to exclusive percepts and perceptual reversals. Binocular interactions might be one cause of these processes, as would also be noise (Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006) or other variations. But the same competitions might then also be started with stimuli that are not statically separated between the eyes (Logothetis, Leopold, & Sheinberg, 1996; Bhardwaj, O'Shea, Alais, & Parker, 2008).

Subjects were generally not aware through which eye the cues and line patterns were shown. The eye-of-origin is not an attribute that can be recognized or selectively be attended to. However, if the ocular information is ignored and perceptually not available, why should perceptual competition then mainly be based on ocular differences? Why should we become aware of ocular activity variations but not of their ocular origin? It may rather be that ocular interactions modulate neural activity in subsequent stages, which then may cause perceptual reversals—perhaps initiated by interocular processes but not necessarily highly correlated with them. The fact, that rivaling patterns evoke similar perceptual reversals when presented in conventional (static) binocular rivalry conditions or when exchanged between the eyes three times per second, although only the former condition evokes strong interocular suppression (Bhardwaj, O'Shea, Alais, &

Parker, 2008), indicates that the interocular suppression cannot be the only driving factor. Maybe the ease of separate stimulation has simply biased our look upon possibly underlying mechanisms of "binocular" rivalry.

Ocular dominance

Given the many reports on perceptual processes in binocular rivalry, which do not seem to pay particular attention to the sighting ocular dominance of observers, I was surprised that ocular dominance had been a distinguishing parameter in all results of the present study. While in the present work, predominance durations between perceptual reversals did not reliably differ between the D and the nonD eye and this difference was also small (51.6% : 48.4%) in the large population study (Bosten *et al.*, 2015), the sensitivity to cued targets differed notably between D and nonD eyes. Cued targets were generally faster and better detected in the D eye than in the nonD eye. Differences were particularly pronounced during the first 500-1000 ms after stimulus onset, when interocular processes were apparently most active. Mainly during this initial interval, also strong individual differences between observers were seen. But in all experiments modulations finally settled in a constant bias in favor of the D eye. In almost all subjects, this bias was correlated with the ocular dominance measured with the Porta sighting test

CONCLUSIONS

The study has three messages. First, although stimulus variations (e.g., onset, contrast, adaptation) have strong effects on the initial modulation of ocular sensitivity for cued targets, the modulations diminish within one second and sensitivity then remains rather constant. Thus, variations in ocular sensitivity alone cannot be directly responsible for the ongoing perceptual variations in binocular rivalry. Second, there are notable differences associated with the ocular dominance of observers; after stimulus onset, sensitivity increases faster and reaches higher levels in the dominant than in the non-dominant eye. Third, cued visual selection has again been a useful method for studying neural processes in the perceiving brain.

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