



Very few exclusive percepts for contrast-modulated stimuli during binocular rivalry



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ABSTRACT

Binocular rivalry properties for contrast-modulated (CM) gratings were examined to gain insight into their locus of processing. Two orthogonally orientated gratings were presented, one to each eye. Perceptual change rates, proportions of exclusivity and mixed percepts, and mean durations were calculated. Stimuli were noiseless luminance-defined (L), luminance-modulated noise (LM) and contrast-modulated noise (CM) gratings with sizes of 1, 2 and 4 deg and spatial frequencies of 4, 2 and 1 c/deg, respectively. For the LM and CM gratings, binary noise was fully correlated between eyes. Maximum producible modulations were used (1.0 for CM, 0.78 for LM and 0.98 for L stimuli). In a control experiment, contrasts of LM gratings were reduced until the multiples over detection threshold were similar to those of CM stimuli. Trial durations of 120 s were analyzed. Exclusive visibility decreased with increasing stimulus size regardless of the stimulus type. Even with visibilities at similar multiples above detection threshold, significantly lower proportions of exclusive percepts and perceptual changes were found for CM, compared to LM gratings. The results obtained with dichoptically presented orthogonal CM gratings are significantly different from those obtained for orthogonal gratings presented to one eye. CM stimuli therefore do engage in binocular rivalry but with different characteristics to those found for LM stimuli. These results suggest that CM stimuli are processed by a mechanism that promotes binocular combination rather than rivalry, and therefore may involve cells in a higher visual area than those that initially process LM information.

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1. Introduction

Incompatible stimuli presented dichoptically can provoke competition between visual percepts, known as binocular rivalry (e.g. Breese, 1899, 1909; Levelt, 1965; Wheatstone, 1838). As a result of conflict during binocular rivalry, for a few seconds just one image will be perceived exclusively, whilst the other is suppressed. The dominance phases alternate between the two eyes over time. Different states of mixed percepts can also occur and can be categorized into piecemeal, when the perceived image is made up of portions of each stimulus (e.g. Blake, 1989), superimposition in which both stimuli are perceived in their entirety, overlapping each other (e.g. Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006; and see also Liu, Tyler, & Schor, 1992), and transparency superimposition, where rival stimuli with very different spatial frequencies are seen at the same time, overlapping each other, but with one appearing in front of the other (Yang, Rose, & Blake, 1992).

It has been suggested that competition between mainly monocular neurons is involved in the processing of exclusively visible percepts during traditional binocular rivalry (see review Tong, Meng, & Blake, 2006). In contrast, mixed states might represent the integration of two images at areas receiving predominantly binocular input along the visual pathway (Brascamp et al., 2006; Klink, Brascamp, Blake, & van Wezel, 2010; see also Liu et al., 1992).

Both early and later stages of the visual pathway are involved in binocular rivalry and sometimes stimulus rivalry overcomes binocular rivalry. For example, two rivalrous images shown to the two eyes, but with each containing parts of two stimuli, generate visual exclusivity of whole stimuli as a result of interocular grouping (Diaz-Caneja's, 1928 translated by Alais et al. (2000); Kovács, Papathomas, Yang, & Feher, 1996), suggesting that binocular rivalry can lead to competition between percepts, rather than between eyes. Results of neuro-imaging studies also support the engagement of both low (Lee & Blake, 2002; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005) and high visual areas (Tong, Nakayama, Vaughan, & Kanwisher, 1998; Buckthorpe, Jessula, &

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Mendola, 2011), as do results from a study using single-unit recordings from monkey (Leopold & Logothetis, 1996). Visual attention, a higher cortical process, also contributes to binocular rivalry (for review, see Paffen & Alais, 2011) and eye movements might influence alternation of perception as saccades occur with high probability, just before an alternation during rivalry (Van Dam & van Ee, 2006b). Nonetheless, traditional psychophysical studies have demonstrated that characteristics of binocular rivalry strongly depend on stimulus properties, such as contrast (Bossink, Stalmeier, & De Weert, 1993; Levelt, 1965) and size (Blake, O'Shea, & Mueller, 1992; Breese, 1909; O'Shea, Sims, & Govan, 1997), which are first encoded at a low-level of the visual system.

Previous studies have predominantly used stimuli that contained elements differentiated from their background by luminance differences, called first-order or luminance-defined (L) stimuli. The visual system is also capable of distinguishing between visual stimuli that differ from their background by changes in contrast, called second-order, or contrast-modulated (CM) stimuli. CM stimuli can be constructed by modulating visual noise. To examine the effects of noise per se on stimulus processing, the same noise characteristics used to create CM stimuli, can be added to luminance-defined stimuli, to create luminance-modulated (LM) stimuli. Both L and LM stimuli are in fact “luminance-defined”, but in this context, the luminance-defined (L) stimuli modulate the noiseless background luminance, whereas luminance-modulated (LM) stimuli modulate the background that contains noise. The ability to locate and identify second-order information can be explained by a “filter-rectify-filter” model (e.g. Landy & Graham, 2004; Mareschal & Baker, 1999; and see also Zhou & Baker, 1993). In this model, a linear spatiotemporal filter gives an orientation- and spatial frequency-selective response to luminance. Then, the rectified output of the first filter is passed to a second linear filter that responds selectively to variations in the outputs of the first-order filters and represents this variation across regions of an image.

Strong psychophysical evidence for separate mechanisms for the monocular processing of first- and second-order information was presented by Schofield and Georgeson (1999). The participant had to detect LM or CM test gratings superimposed on weak LM and CM grating backgrounds. The results showed that LM background gratings facilitate the detection of LM test gratings, and CM background gratings also facilitate the detection of CM test gratings. However, only very slight or no facilitation was found for the detection of LM gratings on a CM background, or vice versa.

Psychophysical support for differently sized processing mechanisms of LM and CM stimuli comes from a study by Sukumar and Waugh (2007) who made spatial summation estimates at the fovea and at various eccentricities (up to 10 deg) for blob detection. Participants had to detect dynamic binary noise LM and CM Gaussian blobs of various sizes. Spatial summation areas for the processing of CM blobs were bigger than those of LM blobs at all eccentricities. The authors speculated that this finding may be explained by a V2 site of second-order processing.

Human cortical electric activity in the brain evoked with LM and CM dynamic binary noise gratings (Calvert, Manahilov, Simpson, & Parker, 2005) has also been investigated. Visual evoked potential measurements were carried out whilst the participant gave responses to a psychophysical detection task for L, LM, and CM gratings. A significantly longer latency for CM gratings compared to LM gratings was found in the occipital area. Being in line with the “filter-rectify-filter” model, the authors speculated that the longer latency for second-order stimuli was due to additional processing in higher cortical areas for CM, than for LM stimuli. Larsson and collaborators presented first- and second-order texture defined grating stimuli and measured the metabolic activity in a wide range of lower and higher cortical visual areas

(Larsson, Landy, & Heeger, 2006). Both LM and CM stimuli generate activity in various areas (V1, V2, V3, V3 A/B, and in the visual areas anterior to dorsal V3 called L01, hV4, and V01). Whilst for LM stimuli the activity in extrastriate areas was the same as in V1, CM stimuli generated larger activity in areas beyond V1 (e.g. V01).

The involvement of areas receiving predominantly binocular input, i.e. beyond the entry level of V1, in the visual processing of CM stimuli was also suggested by Wong, Levi, and McGraw (2001). Detection thresholds for LM and CM stimuli were measured monocularly in individuals with amblyopia (a disorder of binocularity), and for the dominant eyes of healthy individuals. In almost all amblyopic, and in some preferred eyes of amblyopes, a relatively greater detection loss for CM, compared to LM stimuli was found. Visual sensitivity loss for amblyopic and preferred eyes in amblyopes to second-order information in particular, led Wong and collaborators to suggest that neurons involved are substantially more binocular, than those that process first-order information. In a study of inter-ocular blur suppression of first- and second-order stimuli by Chima, Formankiewicz, and Waugh (2015), binocularity of the visual system was disturbed by blurring one eye. Use of CM rather than LM stimuli resulted in deeper measures of inter-ocular suppression. This suggests that CM envelope extraction and combination across the two eyes occurs at a later stage of visual processing, than where binocular combination of the LM stimuli would first take place.

The evidence presented above suggests that the initial site for processing of CM stimuli lies further along the visual pathway than for LM stimuli. However, we know very little about the perception of CM stimuli under binocular rivalry conditions. An investigation of CM perception during binocular rivalry will help to enhance the understanding of the processing mechanisms of CM stimuli in the early visual cortex. In addition, the different processing sites that have been proposed for CM and LM stimuli might give rise to different characteristics of binocular rivalry for the two types of stimuli.

2. Methods

2.1. Observers

Six male and five female participants with an average age of 25.8 (\pm 5.4 standard deviation) years completed the study. One participant was excluded because of ongoing lack of concentration during the experimental task. Four of the ten remaining participants were experienced observers in binocular rivalry experiments (including one of the authors, J.S.) whilst the other six were inexperienced psychophysical observers. All observers except author J.S. were naïve to the purpose of the study. All observers had normal or corrected-to-normal vision with visual acuity of at least 6/6 and normal binocular vision as indicated by random-dot-stereopsis of at least 60 arcsec when measured with the Dutch Organization for Applied Scientific Research (TNO) stereo test (Lameris Ootech, Ede, Netherlands).

2.2. Stimuli

Three different stimulus types were used for the experiment (see Fig. 1):

The three stimulus types, illustrated in Fig. 1 can be mathematically described by the following equations (Calvert et al., 2005; Schofield et al., 1999).

Sinusoidal luminance (L) grating:

$$l_0(x, y) = l_0[1 + l \sin(2\pi x f_x)]$$

$l_0(x, y)$ is the luminance at position (x, y) , l_0 is the mean luminance, l is the luminance modulation and f_x is the spatial frequency.

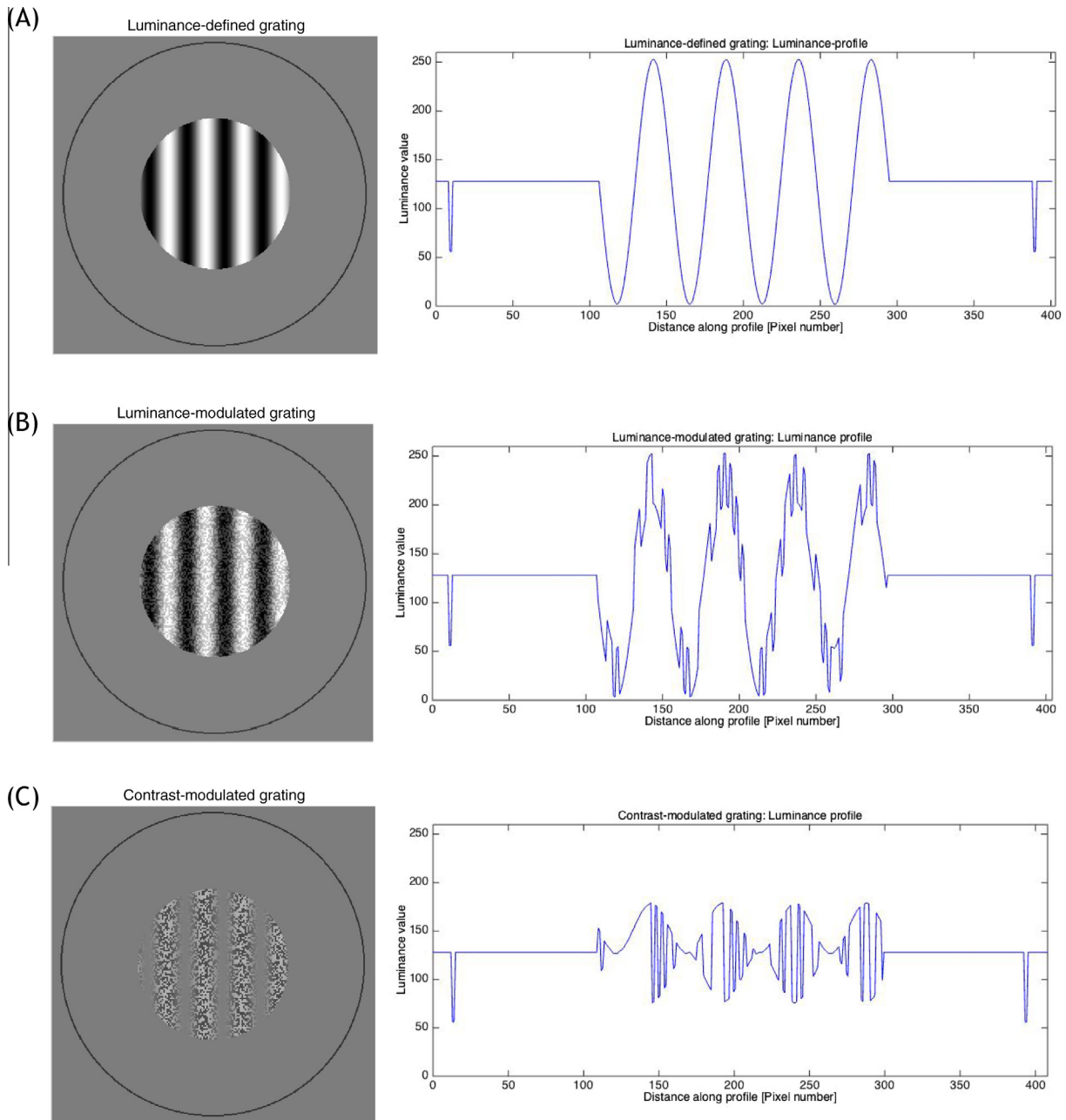


Fig. 1. Illustration of vertical first- and second-order gratings with luminance profiles for a horizontal line of pixels through the centre of the stimulus. (A) Luminance-defined sinusoidal grating with high contrast of 0.98. (B) Luminance-modulated sinusoidal grating with contrast of 0.78 and added two-dimensional binary noise with a contrast of 0.2. (C) Contrast-modulated sinusoidal grating with a two-dimensional binary noise carrier which had its contrast modulated by the grating (modulation 1.0).

Sinusoidal luminance-modulated (LM) grating:

$$l_0(x, y) = l_0[1 + nN(x, y) + l \sin(2\pi x f_x)]$$

Two-dimensional binary white noise added to a vertical sinusoidal luminance grating. N is the binary noise at position (x, y) (either black (-1) or white (1)) and n is contrast of 0.2.

Sinusoidal contrast-modulated (CM) grating:

$$l_0(x, y) = l_0[1 + nN(x, y) + nN(x, y)m \sin(2\pi x f_x)]$$

Contrast modulation is m . The mathematical term $nN(x, y)m \sin(2\pi x f_x)$ expresses the contrast-modulated grating that results from the multiplying random noise sample by a sinusoid.

For all three stimulus types, horizontal and vertical sinusoidal gratings in circular windows, and sizes of 1, 2, 4 deg containing spatial frequencies of 4, 2, 1 c/deg, respectively, were used. The

sizes and spatial frequencies of the gratings were co-varied to maintain a constant bandwidth for all stimuli. LM gratings were created by adding dynamic binary noise with an amplitude of 0.2 to the sine wave. The same noise amplitude was multiplied by the sine wave to create the CM gratings. For each stimulus type, close to maximum producible modulation was used, i.e. 1.0 for CM, 0.78 for LM and 0.98 for L stimuli. The stimuli were presented on a gray background with a mean luminance of 60.50 cd/m². The effective viewing distance was 100 cm and the screen pixel size at this distance was 1.3 arcmin.

The stimuli were presented dichoptically, such that the right eye saw the horizontal grating and the left eye, the vertical grating. A fusion lock seen by both eyes, here a surrounding annulus, was used to aid fusion and had a width of 2.6 arcmin or 2 pixels and its diameter was twice that of the grating (see Fig. 1). Dynamic

noise carriers are useful for the creation of CM stimuli (e.g. Georgeson & Schofield, 2011; Hairol & Waugh, 2010a, 2010b; Schofield & Georgeson, 2000; Zhou, Liu, Zhou, & Hess, 2014) since static noise carriers can result in clusters of first-order artefacts (Smith & Ledgeway, 1997). Therefore, in the current study, dynamic noise carriers were created by random presentation of ten stimulus pages, which were created using the equations described above with randomly generated noise patterns. The noise patterns were always the same in the two eyes, i.e. correlated. The noise check size was 2×2 pixels and each noise page was displayed for 14.28 ms (2 monitor frames with the monitor running at 140 Hz).

2.3. Apparatus and calibration

A Dell Precision 3500 with an operating system of Microsoft Windows XP Professional (Version 2002) was used to run the experiment and store the data. Stimuli were generated using the Cambridge Research Systems Visual Stimulus Generator, which was run by a custom written Matlab program (Version R2010b). A Mitsubishi Diamond Pro 2070SB CRT Monitor (with a resolution of 1027×769 pixels) was used for presenting the stimuli. Gamma correction was carried out periodically using the Cambridge Research Systems ColorCal and software to produce lookup tables and ensure the output of the intended luminance. Before each experiment began, the monitor was warmed-up for 30 min to achieve consistency of mean luminance.

It is important to ensure that second-order stimuli do not contain first-order artefacts. The use of dynamic noise (as described above) helps to eliminate luminance clumping. However, adjacent pixel non-linearity (APNL) (Klein, Hu, & Carney, 1996), which occurs when luminance levels of adjacent pixels cannot be reliably created, can lead to variation of local mean luminance. Manahilov, Calvert, and Simpson (2003) reported that dynamic noise of at least 2×2 pixels does not give rise to APNL artefacts. Our stimuli satisfied this criterion. We also made photometric measurements of our stimuli. The mean luminance of CM vertical and horizontal gratings did not vary with a change in contrast confirming that these did not contain luminance artefacts.

A four mirror stereoscope composed of optical components by OptoSigma (OptoSigma Corporation, California, USA) was used to present a horizontal grating to the right eye and a vertical grating to the left eye. The mirrors were carefully aligned prior to beginning the experiments to ensure that only one stimulus was visible to each eye.

2.4. Procedure

The experiment followed the ethical procedures of the Helsinki declaration of 1975. All participants gave informed consent and were reimbursed for time spent. The experiment was approved by the appropriate Anglia Ruskin University Ethics Committee.

All experiments were performed in a dark room. Participants sat on a comfortable chair and placed their heads in a chinrest. Before the actual experiment was initiated, the stimuli were aligned for each individual by adjusting the position of a left and right nonious marker on the screen. This was done to ensure comfortable viewing with both eyes during the experiment.

The participant's task was to press and hold the left button on a response box when only the vertical grating (left eye image) was visible, or the right button when only the horizontal grating (right eye image) was visible. If the percepts began to intermingle with each other or if the two percepts were superimposed, the participants were instructed to press and hold both buttons. No button presses indicated invalid responses. Participants were permitted to view any part of the image patch throughout the trial.

Blocks of L, LM or CM stimuli in different order of sizes were presented in a counterbalanced order. One trial lasted at least 120 s. Each stimulus condition was repeated 8 times. Instructions and practice trials were given before the data collection of the main experiment started. Breaks in-between trials were permitted if needed. A long break after half of the trials in a session were completed was enforced. Therefore, one full session lasted between 60 min and 90 min, depending on the breaks for each individual. Four sessions were carried out on separate days for each participant.

2.5. Data analysis

During each trial, a key or key combination was pressed and held as long as the participant perceived the actual perceptual state. This was recorded and stored in data files. Then, the number of perceptual changes, total duration of visual exclusivity (sum of horizontal (H) and vertical (V) percepts) as well as mixed (M) percepts were calculated across 120 s. The mean duration of each percept was also analyzed. The last perceptual response of a trial was not included in these calculations, as its duration would have been reduced by the termination of the trial at 120 s. When a percept did not occur during a trial (e.g. the observer never reported a vertical grating), a duration of 0 s was used in calculating the mean across trials to reflect the absence of a certain percept.

Binocular rivalry is often described as an ongoing perceptual change between two rival stimuli. In fact, that is not entirely true. The following perceptual changes were therefore also analyzed (see Fig. 2). Full flips are changes from one exclusive percept to another (button presses from H to V or V to H) without a mixed percept in-between. Half flips are perceptual changes that occur from an exclusive to a mixed percept, and vice versa (H to M, M to H, V to M, M to V). Reversions represent a change from one exclusive percept to a mixed one and back again to the same exclusive percept (e.g. Mueller & Blake, 1989; Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013) (button presses from H to M to H or from V to M to V).

If one visually exclusive percept followed on directly after the other (i.e. a vertical grating was seen and then a horizontal one, or vice versa as indicated by a change in pressing button from V to H or H to V), an invalid or mixed response may have occurred because of the possibility that for a short time either no button (invalid response) or both buttons (mixed response) were pressed. Also, inaccurate button pressings may confound the data with

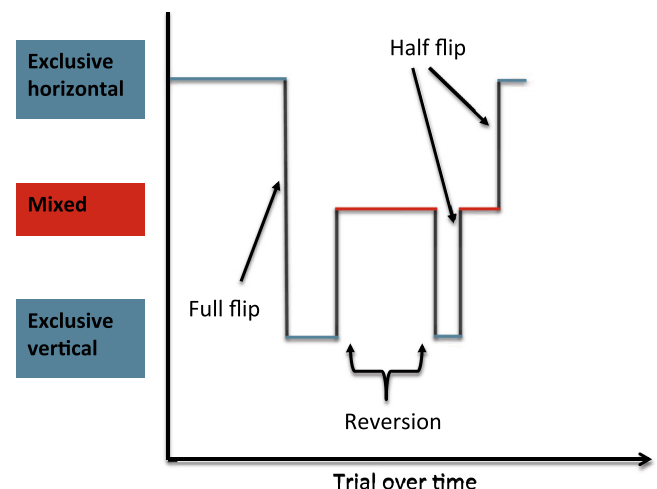


Fig. 2. Illustration of a response track and the perceptual changes that were analyzed in this experiment.

extremely short responses during a trial. Hence, a reaction time control experiment was carried out to extract these unwanted responses in the following way. Vertical and horizontal CM gratings with a size of 1 deg and spatial frequency of 4 c/deg were presented monocularly through the stereoscope. The vertical grating was presented to the left eye for a specific amount of time and then the horizontal grating was presented to the right eye. Each presentation lasted for a duration that was picked from a normal distribution with a mean of 3 s and a standard deviation of 1 s. In a trial, the presentation of horizontal and vertical grating alternated and each grating was presented 20 times. Four participants were instructed to indicate the physical changes of the percept with the same button presses as were used for the main experiment. After extracting the duration of invalid and mixed responses during these real “full” perceptual changes, the mean and standard deviation for each participant was calculated. The mean summed with two standard deviations was calculated individually and was finally averaged across participants to serve as a threshold. Based on the results of this control experiment, all perceptual durations ≤ 180 ms were excluded from the data analysis.

2.5.1. Statistical analysis

A customized Matlab program was used to analyze the raw data generated from this study. The final data were analyzed using SPSS, in which a repeated measure ANOVA with Greenhouse-Geisser correction was carried out. For post hoc pairwise comparisons, a Bonferroni correction was used. Planned comparisons were also carried out using Statistica to analyze interactions between various levels.

3. Results: effect of stimulus type and size

Fig. 3A shows exclusive visibility, i.e. the proportion of time during which either the horizontal or vertical gratings only were perceived for the three stimulus sizes and types used in the experiment, averaged across participants. In this section, we refer to stimulus size, but since size and spatial frequency co-varied (see Section 2.2), the reported effects of size, could also represent effects of spatial frequency. Averaged across size, exclusive visibility was 56.7 ± 5.43 (standard error), 57.3 ± 5.40 , $14.6 \pm 4.48\%$, for L, LM and CM-stimuli, respectively. A repeated measures ANOVA investigating the effects of stimulus type (L, LM and CM) and size (1, 2 and 4 deg) on exclusive visibility was carried out. A very highly significant main effect of type was found [$F(1.09, 9.85) = 69.73$, $p < 0.001$]. Post-hoc analysis indicated that there was no significant difference in exclusive visibility between L and LM stimuli [$p > 0.05$] whereas CM stimuli produced significantly less exclusive visibility than L and LM stimuli [$p < 0.001$]. A significant effect of stimulus size on exclusive visibility could also be demonstrated [$F(1.62, 14.54) = 23.35$, $p < 0.001$]. All three sizes were significantly different from each other [$p < 0.05$, post hoc analysis] with a reduction in exclusive visibility as the stimulus size increased.

Visual exclusivity represents the proportion of time in a trial during which responses indicate perception based on the right-eye only, or on the left-eye only. When the percept is not exclusive, it is mixed. The proportion of time during which mixed perception in a trial occurs is greater for CM than LM stimuli. Both of these (i.e. relative proportion of exclusive and mixed perceptions) take into account the mean duration of each percept and their frequency.

Mean dominance and mixed durations are shown in Fig. 3B and C, respectively. The statistical significance of the effects of stimulus size and type was assessed in separate ANOVAs for dominance and for mixed duration. Averaged across size, mean dominance duration was 1.54 ± 0.11 , 2.00 ± 0.20 , 1.56 ± 0.44 s, for

L, LM and CM-stimuli, respectively. Dominance duration reduced with an increase in stimulus size for all types of stimuli [$F(1.75, 15.75) = 12.85$, $p < 0.001$] and was not affected by stimulus type [$F(1.10, 9.90) = 1.50$, $p > 0.05$]. Averaged across size, mean mixed duration was 2.68 ± 1.29 , 2.82 ± 1.01 , 18.44 ± 3.88 s, for L, LM and CM-stimuli, respectively. Mixed duration increased with an increase in size [$F(1.69, 15.17) = 8.72$, $p < 0.01$] and was also affected significantly by stimulus type [$F(1.03, 9.23) = 34.96$, $p < 0.001$], being longer for CM than LM and L stimuli [$p < 0.01$, post hoc].

More perceptual changes were also observed for L and LM stimuli, than for CM stimuli (Fig. 4). The full flip rate (a perceptual change between two exclusive percepts without a mixed percept in-between) averaged across participants and stimulus size was 8.6 ± 2.5 , 5.8 ± 1.6 and 0.3 ± 0.1 flips/120 s trial for L, LM, and CM stimuli, respectively. There were more half flips (perceptual change from an exclusive to a mixed percept, and vice versa) than full flips in a trial. L and LM stimuli produced more half flips than CM stimuli (L: 64.5 ± 7.3 , LM: 54.4 ± 6.3 , CM: 14.9 ± 5.2). An analysis of the reversion rate (perceptual change from an exclusive percept to a mixed one and back again to the same exclusive percept) showed again a similar pattern, however, the number of reversions for L (6.9 ± 1.2) and LM (6.0 ± 0.9) was only twice that for CM (3.5 ± 1.2) stimuli.

The statistical significance of the effects of stimulus type and size were assessed in a separate repeated-measures ANOVA for each type of perceptual change.

An interaction between size and stimulus type for full flips could be shown [$F(1.55, 13.98) = 6.92$, $p < 0.05$]. A planned comparison showed that L stimuli varied throughout all sizes [$p < 0.05$] and LM stimuli varied between 2 and 4 deg stimuli sizes [$p < 0.05$], but not between 1 and 2 deg [$p > 0.05$]. In contrast to that, full flips occurred very rarely for CM stimuli and were not affected by changes in stimulus size [$p > 0.05$, planned comparison]. The numbers of full flips were significantly different between all types of stimuli [$p < 0.05$].

The analysis of half flips revealed a main effect for the type [$F(1.08, 9.73) = 40.73$, $p < 0.001$], but not for the size [$p > 0.05$]. All types differed significantly from each other [$p < 0.05$, post hoc].

For reversions, an interaction between stimulus type and size [$F(2.58, 23.24) = 4.08$, $p < 0.05$] was found. The number of CM reversions was significantly different from the numbers of L [$p < 0.05$]; and almost significantly different from the number of LM reversions [$p = 0.05$]. The effect of size was significant only for CM stimuli [$p < 0.05$].

4. Control experiment: effect of visibility levels

After we demonstrated that CM stimuli show significantly lower proportions of visual exclusivity and a lower rate of full flips, half flips and reversions than L and LM stimuli, it was necessary to determine whether the differences between the results are due to the differences in perceived visibility of the L, LM, and CM gratings. This is a possibility because it is known that the alternation rate increases with an increase in stimulus visibility level (or contrast for L stimuli) (Levelt's fourth proposition) (Brascamp, Klink, & Levelt, 2015; Levelt, 1965).

4.1. Methods

4.1.1. Detection threshold measurement

Detection thresholds for LM and CM stimuli were measured using a method of constant stimuli. Stimuli with a size of 2 deg and a spatial frequency of 2 c/deg, and the same noise characteristics as in the main experiment, were used. A two-alternative tem-

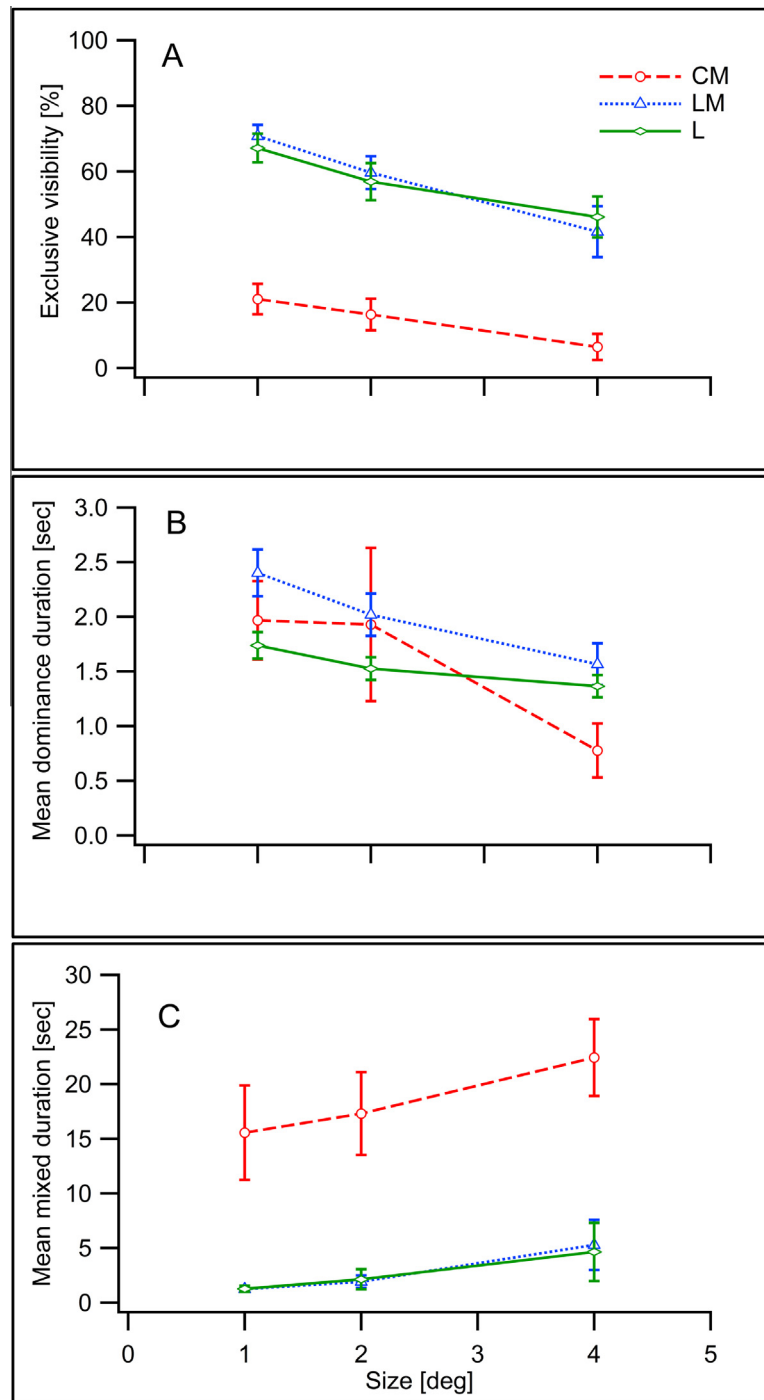


Fig. 3. Average of all participants' (A) exclusive visibility, (B) dominance duration, and (C) mixed duration for three sizes of L (diamond symbols, solid lines), LM (triangle symbols, dotted lines) and CM stimuli (circle symbols, dashed lines). Vertical bars represent ± 1 standard error.

poral forced choice task in which participants had to indicate whether the first or second interval contained the grating was used. Dichoptic presentation was achieved with a stereoscope (as in the first experiment) but only one stimulus was presented briefly (500 ms) to one eye whilst the other eye saw a mean luminance screen. The time interval from one presentation to the next was 500 ms. Eleven contrast levels, separated by 1.5 dB (0.075 log) steps, were used. These were chosen to span the full psychometric function for each condition and participant, i.e. from guess rate (50%) to 100% correct responses. Five subjects from the first experiment participated. One hundred and twenty-five trials were

presented in each run and four runs were performed. A baseline contrast value for each eye was determined in a short run using 70 trials.

4.1.2. Binocular rivalry using four different modulation levels for LM stimuli

LM stimuli were presented using four different modulations (0.78, 0.40, 0.20 and 0.10) and were compared with CM results of the main experiment (modulation 1.0). Stimulus size was 2 deg diameter containing a 2 c/deg spatial frequency. Noise conditions and the experimental procedures were the same as in the main

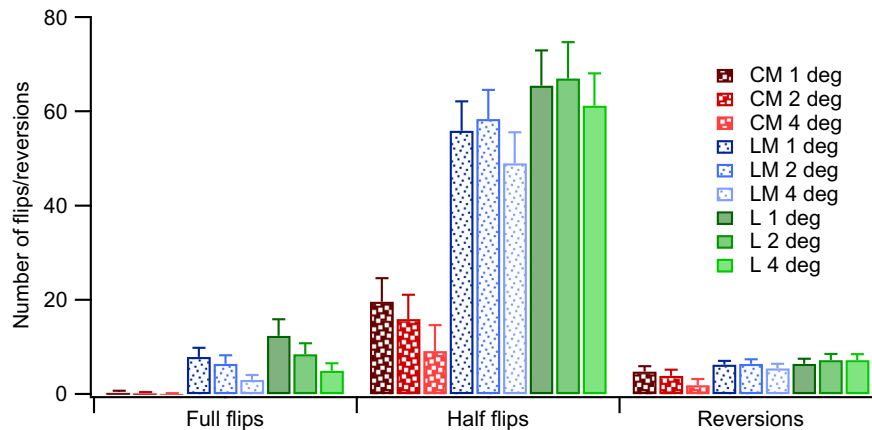


Fig. 4. Number of full flips, half flips, and reversions for L (green, solid bars), LM (blue, bars with small dots), and CM (red, bars with big dots) stimuli, averaged across participants. The different hues of the specific stimuli types represent the various stimuli sizes (dark 1 deg, medium 2 deg, light 4 deg). Vertical bars represent +1 standard error.

experiment. Thirty-two trials (4 modulations \times 8 repeats) in a counterbalanced order were carried out in two sessions; one session per day.

4.2. Analysis

4.2.1. Detection threshold measurement

Performance data for the 11 different contrast levels were calculated for each condition and participant. These data were fit with a Weibull function using Igor Pro software to obtain contrast threshold for 75% correct performance, the slope of the function and the chi-square. The function fits were weighted by the inverse standard errors. The mathematical expression for the Weibull formula is:

$$P_{\text{correct}}(c) = 1 - 0.5 * 2^{-(c/th)^{\beta}}$$

c is the target contrast, th is the estimated threshold at 75% correct response and β is the slope of the function (Hairol & Waugh, 2010a, 2010b; Yu, Klein, & Levi, 2002).

4.2.2. Binocular rivalry using 4 different modulation levels for LM stimuli

Data analysis followed the analysis of the main experiment. In addition, exclusive visibility over trial time was also calculated as follows. A trial was separated into 3-s bins. The sum of exclusive and mixed percepts provided the total perceptual time (invalid responses were excluded). Then, the relative amounts of exclusive and mixed percepts were calculated for every 3-s interval, which provided a sufficiently fine time scale to show changes over time, (i.e. the mean dominance duration averaged across stimuli type, contrast level and participants was 2.2 s). The averages across trials were calculated for each individual and these were then averaged across participants.

Since the individual detection thresholds for LM and CM stimuli were known, it was possible to determine and compare visibility levels of LM and CM gratings. The visibility level was calculated by dividing the modulation level used in the experiment by the detection threshold of each eye.

Right and left visibility levels were then averaged to a visibility level for each individual. Finally, visibility levels were averaged across participants to get an average visibility value for LM and CM stimuli.

4.3. Results

For the modulation used in the main experiment, visibility levels (as determined by multiples of detection threshold) averaged across participants and both eyes were $7x \pm 0.96$ (standard error) for CM stimuli (modulation of 1.0) and $43x \pm 6.49$ for LM stimuli (modulation of 0.78). For the LM stimuli used in the control experiment, visibility levels were $22x \pm 3.33$ for modulation of 0.40, $11x \pm 1.66$ for modulation of 0.20, and $5x \pm 0.83$ for modulation of 0.10. A similar level of visibility for LM and CM stimuli is therefore achieved when the luminance modulation is 0.1 (and CM modulation is 1.0).

In this section, statistical analyses were performed firstly to investigate the effects of luminance modulation (or visibility as multiples of detection threshold) on characteristics of binocular rivalry. To compare the characteristics for LM and CM stimuli, a separate ANOVA was carried out using the data generated by stimuli with similar levels over the detection threshold, i.e. a modulation of 0.1 for LM and 1.0 for CM.

The exclusive visibility levels for the LM stimuli (Fig. 5) are stable regardless of the modulation [$F(1.35, 5.39) = 0.07, p > 0.05$]. CM stimuli generated a significantly lower proportion of exclusively visible percepts ($10.1 \pm 4.15\%$) than LM stimuli ($53.5 \pm 6.35\%$) when both were presented at similar multiples of detection threshold [$F(1, 4) = 29.65, p < 0.01$]. In a subsequent control experiment on 2 participants, it was found that even near detection threshold (approximately 2x above), LM stimuli generate more exclusively visible percepts than CM stimuli (see gray bar in Fig. 5 and Section 6).

Fig. 6 shows visual exclusivity analyzed across the trial time, in 3-s intervals. An unambiguous difference in exclusive visibility over time is observed between LM and CM stimuli: visual exclusivity is always lower for CM than LM stimuli.

Statistical analysis of visual exclusivity over 120 s for LM stimuli could not demonstrate any significant effects of contrast [$F(1.30, 5.18) = 0.04, p > 0.05$] or time [$F(2.63, 10.53) = 3.17, p > 0.05$]. Visual exclusivity for CM stimuli also did not show a significant change over 120 s [$F(2.20, 8.80) = 0.80, p > 0.05$]. A planned comparison was carried out to compare exclusive visibility over the first seconds after initiating of binocular rivalry. A comparison of all LM stimuli with different contrast levels showed that exclusive visibility increases significantly between the first '3-s bin' and the second '3-s bin' [$F(1, 4) = 9.66, p < 0.05$], but there was no further significant increase between the second and third '3-s bins' [$p > 0.05$]. CM stimuli on the contrary showed no significant change over the first 9 s (i.e. the first three 3-s bins) [$p > 0.05$].

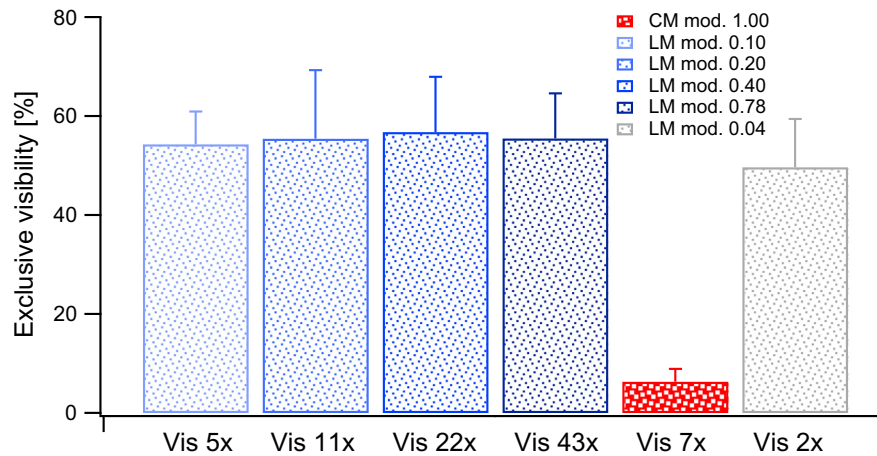


Fig. 5. Exclusive visibility, in percent, for different LM (blue, bars with small dots) and CM (red, bars with big dots) stimuli. The blue hues represent the different modulation levels (shown in the legend) and therefore the different visibility levels (multiples over detection threshold). The gray bar with small dots on the right side of the graph represents results averaged for 2 participants for LM stimuli presented near detection threshold. Vertical bars represent ± 1 standard error.

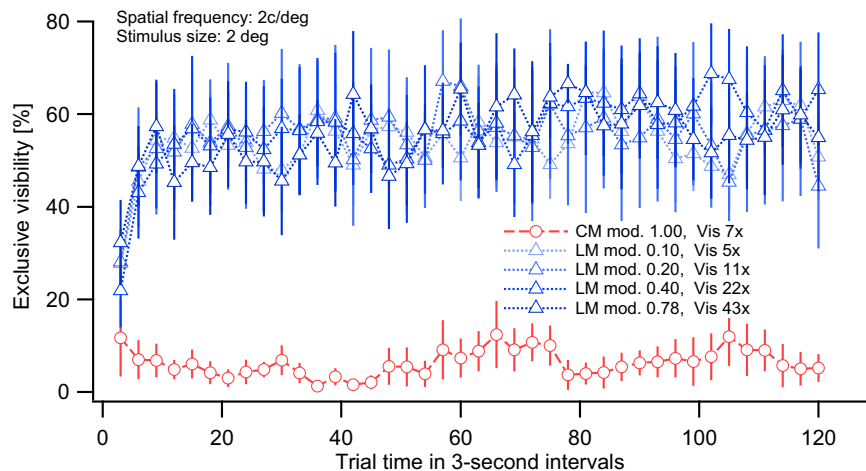


Fig. 6. Average exclusive visibility for all participants in percent calculated every 3 s over 120 s in total. The various blue, dotted functions represent the LM stimuli (triangle symbols) with luminance contrast of 0.10, 0.20, 0.40 and 0.78. CM stimulus (circle symbol) is plotted in red with a dashed line. Visibility levels (Vis) for the different stimuli (multiples of detection threshold, averaged across participants and eyes) are depicted in the legend. Vertical bars represent ± 1 standard error.

Numbers of full flips, half flips and reversions are plotted in Fig. 7. The increase in modulation (and visibility) for LM stimuli significantly increased the number of full flips [$F(1.81, 7.25) = 4.87, p < 0.05$] and half-flips [$F(1.67, 6.70) = 11.36, p < 0.01$]. The number of reversions was not affected by changing the LM visibility [$F(1.77, 7.08) = 0.84, p > 0.05$]. A statistical comparison of the number of perceptual changes for similarly visible LM and CM stimuli (LM with a modulation of 0.1 and the CM with a modulation of 1.0) showed significantly fewer full flips [$F(1, 4) = 11.03, p < 0.05$], half flips [$F(1, 4) = 28.93, p < 0.01$] and reversions [$F(1, 4) = 37.45, p < 0.01$] for CM compared to LM stimuli.

Fig. 8 shows that the mean dominance duration (representing exclusive percepts) of LM stimuli with a modulation of 0.1 ($3.13 \text{ s} \pm 0.76$) is significantly longer than that of similarly visible CM stimuli ($1.14 \text{ s} \pm 0.60$) [$F(1, 4) = 9.88, p < 0.05$]. Mean mixed duration for CM stimuli ($24.27 \text{ s} \pm 5.85$) is significantly greater than for comparable LM stimuli ($3.03 \text{ s} \pm 0.38$) [$F(1, 4) = 13.13, p < 0.05$]. Increasing the visibility of LM stimuli reduced the mean dominance duration slightly but not significantly [$F(1.60, 6.41) = 4.13, p > 0.05$] and did not affect the mean mixed duration [$F(1.03, 4.10) = 0.58, p > 0.05$]. As can be seen in Fig. 8, the variance for

the longest duration (CM mixed) is greater than for the other conditions and percepts. In order to homogenize the variance, data were transformed by taking a square root. Statistical analyses of the transformed data revealed the same significance of results as reported above for the original data.

The differences in the relative amounts of visually exclusive percepts for CM compared to LM stimuli are also depicted in Fig. 9, which shows example rivalry sequences. The higher occurrence of perceptual changes for LM compared to CM stimuli, and longer mixed phases for CM than LM stimuli, can be observed.

5. Control experiment: monocular grid versus binocular rivalry

The results of the current study show low perceptual change rates, very little visual exclusivity and long mixed periods for CM stimuli. With such results, one could ask, whether binocular rivalry actually occurs for CM stimuli or whether the brief periods of exclusivity are the result of other factors such as attention shifts, eye movements and blinks, criterion shifts, local adaptation and contrast adaptation. These other effects would also influence the

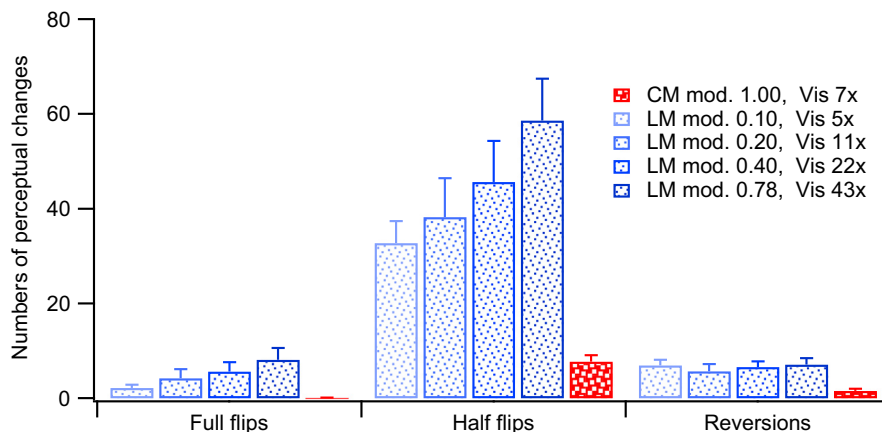


Fig. 7. Perceptual changes subdivided into full flips, half flips, and reversions. The different blue bars containing small dots indicate the LM stimuli with contrast of 0.10, 0.20, 0.40 and 0.78. The red bars containing big dots represent CM stimulus result from the first experiment. Visibility levels (Vis) for the different stimuli (multiples of detection threshold, averaged across participants and eyes) are depicted in the legend. Vertical bars represent +1 standard error.

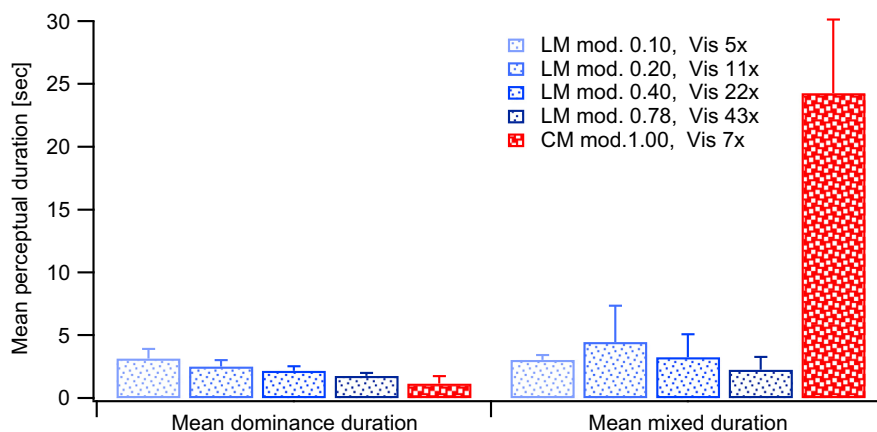


Fig. 8. Mean durations for LM and CM stimuli. The different blue bars with small dots indicate the LM stimuli with contrast of 0.10, 0.20, 0.40, and 0.78. The red bars with big dots represent CM stimulus result from the first experiment. Visibility levels (Vis) for the different stimuli (multiples of detection threshold, averaged across participants and eyes) are depicted in the legend. Vertical bars represent +1 standard error.

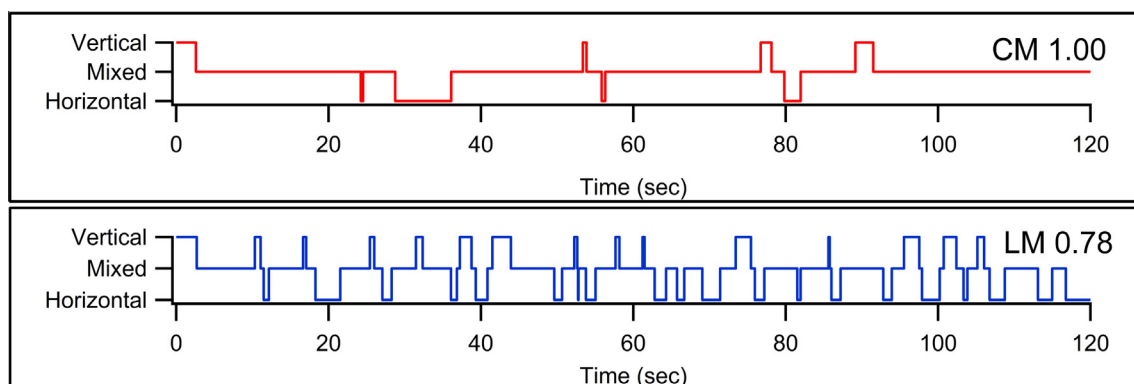


Fig. 9. Examples of rivalry sequences for single trials of CM stimuli (at a modulation of 1.0) (red) and LM stimuli (at the highest modulation of 0.78) (blue), both at a size of 2 deg and a spatial frequency of 2 c/deg. Exclusive horizontal and vertical percept as well as mixed percept responses are plotted over time.

perception of a grid presented monocularly. We therefore carried out a subsequent experiment to compare the perception of orthogonally presented gratings separately to the two eyes (binocular rivalry condition described in the main experiments) to the perception of these two orthogonal gratings presented to one eye to form a grid.

5.1. Methods

Five new participants were recruited for the experiment; all were naïve to the purpose of the study. The inclusion criteria for the participants as well as the instructions for the task were the same as in the previous experiments. One session included CM

and LM binocular rivalry trials, as well as CM and LM monocular grid trials, presented in random order. Eight trials, each lasting at least 120 s, were carried out per condition.

5.1.1. Binocular rivalry stimuli

The sizes for all stimuli were 2 deg with a spatial frequency of 2 c/deg. The contrast for LM stimuli was 0.10 and the modulation depth for CM stimuli 1.00, which represent similar visibility levels. All other conditions were the same as in the other experiments.

5.1.2. Monocular grid stimuli

The vertical and horizontal gratings were added to produce a grid, and presented to one eye, whilst the carrier noise (with an amplitude of 0.20) was presented to the other eye. Since the horizontal and vertical gratings needed to be (physically) added to create the grid, the modulation depth of each individual grating was half of the one used for the dichoptic presentation, at 0.50 for the CM grating and 0.05 for the LM grating. This ensured that the modulation of the grid at the intersections was the same as the modulation used for each component grating contributing to the dichoptic combination. We checked from our previously obtained (unpublished) data, that if we had also used the lower modulation for the dichoptic CM gratings, our result would still hold. In this control experiment LM stimuli were presented at a visibility level comparable to those of CM stimuli. For each stimulus type, the grid was presented 4 times to the right eye and 4 times to the left eye, in random order.

5.1.3. Analysis

Exclusive visibility was calculated for each subject for 120 s in percent and then averaged across individuals.

5.2. Results

The results are shown in Fig. 10. The CM binocular rivalry condition produced significantly more exclusive percepts, at $13.4 \pm 0.5\%$, than the CM grid condition, at $2.7 \pm 1.1\%$ [$F(1, 4) = 112.07$ $p < 0.001$]. The difference between LM binocular rivalry condition ($39.8 \pm 8\%$) and LM grid condition ($5.4 \pm 0.9\%$) was also significant [$F(1, 4) = 16.45$ $p < 0.05$]. Visual exclusivity reported during the presentation of the LM grid was not significantly different from that for the CM grids [$F(1, 4) = 3.52$ $p > 0.05$].

6. Discussion

Our experiments reveal that binocular rivalry alternation for CM gratings is very infrequent compared with that for L and LM gratings (Fig. 4). Exclusive visibility occurs very rarely for CM stimuli and generates significantly longer mixed periods, 15–24 s or more, compared to L and LM stimuli (Figs. 3 and 8).

6.1. Effect of stimulus size on the characteristics of binocular rivalry

The mild decrease found in exclusive visibility with increasing size for luminance-defined (L) stimuli revealed in Fig. 3A has been previously demonstrated (Blake et al., 1992; Breese, 1909; O'Shea et al., 1997). The same pattern was found for luminance-modulated (LM) noise stimuli, which contained added dynamic binary noise, and contrast-modulated (CM) noise stimuli. The reduction in exclusive visibility with an increase of size can be explained by the accompanying reduction of mean dominance duration previously demonstrated for L stimuli (Breese, 1909), and an increase in mean mixed duration for all types of stimuli (Fig. 3C). This is the first study to show that the same relationship holds for CM stimuli. Although strong evidence exists to support separate processing mechanisms for LM and CM stimuli (e.g. Calvert et al., 2005; Chima et al., 2015; Schofield et al., 1999), the results described above show that similarities between the two can be observed.

In this study, a full flip represents a change from one exclusive percept to another without a mixed state in-between. The demonstrated decrease of full flips with increasing size for L stimuli (Fig. 4) is in line with previous experimental results (O'Shea et al., 1997). The same result is shown for LM stimuli in the current experiments. CM stimuli rarely provoked a full flip.

6.2. Effect of visibility levels on binocular rivalry

The differences in perceptual changes for L and LM compared to CM stimuli could have resulted from their very different contrasts and therefore visibility levels. According to Levelt's fourth law, reducing the contrast of both rival stimuli reduces the expected rate of perceptual alternation (Levelt, 1965), however this effect may reverse when both stimuli are at the same near-threshold level (Brascamp et al., 2015). Hence, we investigated whether the differences were due to a simple difference in visibility levels between LM and CM stimuli or due to a higher, more binocular processing mechanism for CM, compared to LM stimuli.

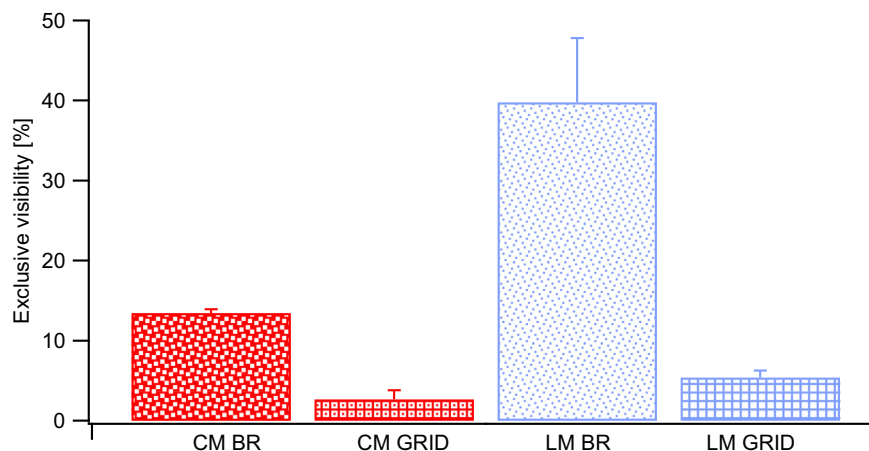


Fig. 10. Exclusive visibility results in percent for CM (red bar with big dots) and LM (blue bar with small dots) binocular rivalry (BR) and monocular grid conditions (GRID) for CM (red grid pattern with dots) and LM (blue grid pattern) stimuli. Vertical bars represent +1 standard error.

The increase in contrast for LM stimuli leads to an increase in the number of full flips (in agreement with Levelt's fourth law (Brascamp et al., 2015; Levelt, 1965)), and half flips (Fig. 7), and thus to a decrease of the mean dominance duration (Fig. 8).

Exclusive percepts for all LM stimuli tend to increase in proportion, over the first 6 s and then stabilize (see Fig. 6). The visual system is accustomed to combining monocular information to a binocular percept. Under binocular rivalry conditions however, neurons are unable to combine different monocular inputs. Instead, the binocular neurons may feedback to the monocular neuronal columns and gradually activate mutual inhibition. Said and Heeger (2013) suggested that this feedback could involve opponency neurons, which receive excitatory input from one eye and inhibitory input from the other eye for each orientation and compute differences between the signals from the two eyes. According to the idea of mutual inhibition as an underlying mediating force of perceptual alternations during binocular rivalry (e.g. Seely & Chow, 2011) and the possible role of opponency neurons (Said & Heeger, 2013), we speculate that 6 s are necessary to gain sufficient neuronal excitation and inhibition in columns of monocular neurons to reach exclusive visibility (or absolute suppression). CM stimuli do not demonstrate a significant change of perception over time and are mainly perceived as a mixed percept. At a similar visibility level (LM at $\sim 5\times$ detection threshold and CM at $\sim 7\times$ detection threshold) LM stimuli trigger significantly more perceptual changes than CM stimuli.

6.3. Why is second-order rivalry different than first-order rivalry?

The most striking finding of the present study is the much lower rate of all types of perceptual change as well as the higher proportion of mixed percepts for CM compared to LM stimuli, at a similar visibility level (Figs. 5 and 7). Differences in the relative proportion of visual exclusivity between similarly visible LM and CM stimuli result from longer mean mixed durations for CM stimuli (see Fig. 9).

Psychophysical estimates of spatial summation areas are larger, and visual acuity is worse, for CM than for LM stimuli suggesting underlying CM processing mechanisms are larger (Sukumar & Waugh, 2007; Hairol, Formankiewicz, & Waugh, 2013). A stimulus presented to the 'CM system', would seem relatively smaller than the same size stimulus presented to the 'LM system'. Blake et al. (1992) showed that exclusive visibility increases as stimulus size decreases. On this basis more exclusivity should be reported for CM, than for LM stimuli, the opposite of what we found. Therefore, the difference in our results for CM and LM stimuli cannot be explained by the two systems operating at different spatial scales.

It has been suggested that binocular rivalry of luminance-defined stimuli might be a result of mutual inhibition of orientation specific monocular neurones (e.g. Blake, 1989; Scocchia, Valsecchi, & Triesch, 2014; Seely & Chow, 2011). The processing of second-order information may require an additional stage to the processing of first-order stimuli. This has been reflected in the "filter-rectify-filter" model proposed for the processing of second-order information (e.g. Baker & Mareschal, 2001; Schofield et al., 1999). Results of single cell (Li et al., 2014), neuroimaging (Kim, Kim, Chung, & Wilson, 2007; Larsson et al., 2006), electrophysiological (Calvert et al., 2005) and psychophysical (e.g. Sukumar & Waugh, 2007; Wong et al., 2001) studies have suggested that the site for this processing of second-order information is beyond V1 and that the neurones involved are binocular (e.g. Hairol & Waugh, 2010a, 2010b; Tanaka & Ohzawa, 2006; Wong et al., 2001). Of particular significance to the current study, is an abstract of a neuro-imaging study by Kim et al. (2007) where the authors used uncorrelated CM dynamic random-dot fields to generate binocular rivalry. Kim and collaborators suggested that

area V2 is specialized in processing second-order stimuli after they found fluctuations in the metabolic activity in V2 but not in V1 during perceptual alternations in binocular rivalry.

One could speculate that the low perceptual change rates and exclusive visibility for CM stimuli are due to the involvement of binocular neurones, in an area beyond V1, that are not orientationally selective and therefore promote mixed perception of orthogonal gratings. However, two single-cell studies in macaques' area V1 and V2 showed that these neurones display orientation tuning to CM stimuli (An et al., 2014; Li et al., 2014). Therefore, different neurones process information from the horizontal and the vertical CM grating, but our results indicate that they do not engage in binocular rivalry in the same fashion as neurones that initially process LM information.

In fact, our results of the 'binocular rivalry' experiments could mean that orthogonal CM gratings do not rival at all, and any exclusivity reported is the effect of other factors such as eye movements or blinks, attention shifts or adaptation, that have disrupted the perception of the grid formed by the two gratings. However, the results of the 'monocular control' experiment (Fig. 10) show that exclusivity measured during dichoptic presentations is higher than that measured when both gratings are presented to one eye to form a grid. Hence, when orthogonal CM gratings are presented dichoptically to the two eyes, the observed binocular rivalry is very likely to be a result of competition of cortical units. The competition occurs infrequently, which implies that the neurones involved promote combination rather than competition between each other. This is plausible if the neurones that process CM stimuli are binocular. Additional support comes from preliminary results, in which we showed that the high proportions of mixed perception for CM stimuli are greatly due to superimposed (fully combined percepts), rather than piecemeal perception (local rivalry) (Skerswetat, Formankiewicz, & Waugh, 2015, ECV abstract). Neurones that combine information from the two eyes can rival as shown in studies where interocularly grouped percepts created from images presented to the two eyes undergo binocular rivalry (e.g. Diaz-Caneja's, 1928 translated by Alais et al. (2000); Kovács et al., 1996). We suggest that our results differ from those of interocularly grouped rivalry because of the simple, non-object like, nature of our CM gratings.

Like has been proposed for luminance stimuli (Brascamp et al., 2006; Lehky, 1995), CM stimuli may sometimes generate exclusivity during binocular rivalry as a result of intrinsic noise. Noise in this context refers to the stochastic variation of system components in the cortex such as vesicular (local neurotransmitter) release variations, spiking variations, and fluctuations in global neurotransmitter level (Moreno-Bote, Rinzel, & Rubin, 2007). After the first-order noise is filtered (Schofield et al., 1999), the second-order grating component needs an additional processing stage, which could also be disrupted because of intrinsic noise (Brascamp et al., 2006; Lehky, 1995) and therefore trigger perceptual alternation. Visual attention (e.g. Lack, 1974; Scocchia et al., 2014), and eye movements (Van Dam & van Ee, 2006a, 2006b) may also play a crucial role in driving perceptual change during binocular rivalry.

The result of low perceptual change rates for CM stimuli is akin to the results obtained for monocular rivalry (e.g. Andrews & Purves, 1997; Breese, 1899; O'Shea, Parker, La, & Alais, 2009). In the case of monocular rivalry, a stimulus composed of competing elements e.g. orthogonally oriented red and green gratings, will trigger perceptual change when it is viewed monocularly or binocularly. O'Shea et al. (2009) suggested that monocular rivalry is a form of perceptual ambiguity that is mediated by a high-level mechanism (O'Shea et al., 2009). Low rates of CM half and full flips could point to a similar processing site beyond the level of monocular neurones.

During the experimental design and stimulus calibration process, we took steps to ensure that our second-order stimuli did not contain luminance artefacts (see Methods), (also see Scott-Samuel & Georgeson, 1999). However, it is possible that a first-order signal may arise from the visual processing of a second-order stimulus. For example, psychophysical responses show an imbalance for black and white luminance processing within second-order stimuli (Lu & Sperling, 2012). This imbalance may introduce a first-order signal into the visual processing of a second-order stimulus. In fact, the low levels of exclusive visibility and flip rate that we report for CM stimuli might be expected for low visibility LM stimuli. We therefore presented LM stimuli near to their detection-threshold and even for these LM stimuli, exclusive visibility was much higher than for CM stimuli (see Fig. 5).

Our results imply that CM stimuli do engage in binocular rivalry but with different characteristics to those found for LM stimuli. Our results would agree with suggestions made in previous studies that initial stages for processing of CM-stimuli involve a more binocular neuronal population than those engaged in the initial processing of LM stimuli (e.g. Chima et al., 2015; Hairol & Waugh, 2010a, 2010b; Wong, Levi, & McGraw, 2005; Wong et al., 2001).

6.4. Role of binary noise in CM stimuli

The current study uses correlated binary luminance noise for stimuli presented to both eyes, i.e. noise checks correspond in space, time and luminance in right and left eyes. Studies that investigated the role of noise in the binocular combination of second-order stimuli have reported no significant differences in results obtained with correlated, uncorrelated or anti-correlated noise. Wilcox and Hess (1996) reported no significant differences between stereo-acuity results for uncorrelated and correlated one dimensional noise. Binocular summation of contrast detection thresholds for LM and CM sinusoidal gratings using correlated, uncorrelated and anti-correlated noise produced the same results (Georgeson & Schofield, 2011). Zhou and collaborators measured the perceived phase of binocularly combined LM and CM gratings with correlated, uncorrelated, and anti-correlated noise (Zhou et al., 2014). Again, no significant differences were found between those noise conditions.

However, binocular rivalry occurs because the two monocular images differ (e.g. in their orientation). It is possible to increase the difference between the two monocular gratings currently used in the study by removing the binocular correspondence of the noise checks, i.e. by un- or anti-correlating the noise. Orthogonal gratings that contain uncorrelated and, in particular, anti-correlated noise would provide higher “potential for binocular rivalry” than when the noise is correlated. The difference in luminance between left and right stimulus would provide an additional difference in the first-order input. Kim and collaborators reported in an abstract, that binocular rivalry for CM stimuli can be successfully generated using uncorrelated noise (Kim, Buckthought, & Wilson, 2006). It remains unclear, however, whether this alternation was due to the first-order input of the uncorrelated noise, the second-order component, or perhaps both.

7. Conclusion

Binocular rivalry can be triggered by both LM and CM grating stimuli using correlated binary noise. Our study demonstrated that orthogonal CM gratings presented dichoptically tend to combine with each other for much longer periods than do L and LM stimuli. The results provide further evidence for a different processing

mechanism for CM stimuli that tends to encourage binocular combination rather than rivalry.

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