1 **More superimposition for contrast-modulated than luminance-modulated stimuli during binocular rivalry**

Authors: Jan Skerswetat [a], Monika A. Formankiewicz [a] & Sarah J. Waugh [a]

Affiliation: [a] Anglia Vision Research, Department of Vision and Hearing Sciences, Anglia Ruskin University, East Road, CB1 1PT, Cambridge, UK

Corresponding Author: Jan Skerswetat
Email address: jan.skerswetat@anglia.ac.uk

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25   Abstract
26

27   Luminance-modulated noise (LM) and contrast-modulated noise (CM) gratings were presented
28   with interocularly correlated, uncorrelated and anti-correlated binary noise to investigate their
29   contributions to mixed percepts, specifically piecemeal and superimposition, during binocular
30   rivalry. Stimuli were sine-wave gratings of 2c/deg presented within 2 deg circular apertures.
31   The LM stimulus contrast was 0.1 and the CM stimulus modulation depth was 1.0, equating to
32   approximately 5 and 7 times detection threshold, respectively. Twelve 45s trials, per noise
33   configuration, were carried out. Fifteen participants with normal vision indicated via button
34   presses whether an exclusive, piecemeal or superimposed percept was seen. For all noise
35   conditions LM stimuli generated more exclusive visibility, and lower proportions of
36   superimposition. CM stimuli led to greater proportions and longer periods of superimposition.
37   For both stimulus types, correlated interocular noise generated more superimposition than did
38   anti- or uncorrelated interocular noise. No significant effect of stimulus type (LM vs CM) or
39   noise configuration (correlated, uncorrelated, anti-correlated) on piecemeal perception was
40   found. Exclusive visibility was greater in proportion, and perceptual changes more numerous,
41   during binocular rivalry for CM stimuli when interocular noise was not correlated. This
42   suggests that mutual inhibition, initiated by non-correlated noise CM gratings, occurs between
43   neurons processing luminance noise (first-order component), as well as those processing
44   gratings (second-order component). Therefore, first- and second-order components can
45   contribute to overall binocular rivalry responses. We suggest the addition of a new well to the
46   current energy landscape model for binocular rivalry that takes superimposition into account.
47

48   **Keywords:** Binocular rivalry, piecemeal percepts, superimposition, interocular noise, second-
49   order, first-order

50
51
52
53
54
55
56
57
58

1. Introduction

Binocular rivalry refers to visual competition that arises when different images are presented separately to each eye (e.g. Brascamp, Klink, & Levelt, 2015; Helmholtz, 1867; Levelt, 1965; Wheatstone, 1838). Visual stimuli such as gratings presented at orthogonal orientations, e.g. a horizontal grating to the left eye and a vertical grating to the right eye, generate perceptual alternations from one exclusively visible grating to the other. However, mixed states of both gratings in one percept can occur in the form of piecemeal rivalry in zones, so that a percept contains portions of each grating (e.g. Blake, O'Shea, & Mueller, 1992). Near contrast detection threshold, orthogonally orientated grating stimuli can appear to overlap, a percept referred to as a 'dichoptic plaid' (Liu, Tyler, & Schor, 1992) or 'superimposition' (e.g. Brascamp, van Ee, Noest, Jacobs, & van den Berg, 2006). If rivalling stimuli with very different spatial frequencies are presented, they can begin to superimpose and can be perceived in different depth planes (Yang, Rose, & Blake, 1992).

Piecemeal percepts are suggested to represent rivalry within small spatial zones throughout the visual field. They occur for larger stimuli, but have been described for stimulus sizes as small as 10 arcmin (Blake et al., 1992). Blake and collaborators (1992) designed a model in which rivalry develops via independent, adjacent, non-overlapping interacting retinal areas. Spatial concatenations of multiple zones in different exclusivity states were thought to result in piecemeal percepts during binocular rivalry. Whereas superimposition is thought to be an indicator of binocular fusion (Brascamp et al., 2006; Liu et al., 1992).

Whether an exclusive or a mixed percept occurs during binocular rivalry can depend on low-level stimulus characteristics (i.e. those initially processed in early stages of the visual cortex) such as size (e.g. Blake et al., 1992; Breese, 1899; O'Shea, Sims, & Govan, 1997), contrast (e.g. Bossink, Stalmeier, & De Weert, 1993; Brascamp, Klink, & Levelt, 2015; Levelt, 1965), orientation (e.g. Schor, 1977; Wade, 1974) and spatial frequency (e.g. Kitterle & Thomas, 1980; O'Shea, Sims, & Govan, 1997). The level of stimulus complexity also influences the course of binocular rivalry alternation (e.g. Alais & Melcher, 2007; Nguyen, Freeman, & Alais, 2003; but see also Kovács, Papathomas, Yang, & Feher, 1996). Gratings or circles are considered to have low complexity, whereas houses or faces are thought to be complex stimuli in this context, as they require more cognitive or semantic computation (see Lumer et al. (1998) but also Blake & Logothetis, 2002).

93

All of the studies described above used luminance-based or coloured gratings or objects (so-called first-order spatial stimuli), which are differentiated from their backgrounds by a change of mean luminance or colour. Contrast-modulated noise (CM) stimuli (i.e. a type of second-order stimulus) can be perceived even though they do not show variations of mean luminance across a stimulus but only variations in contrast (e.g. Chubb & Sperling, 1988; Landy & Graham, 2004; Mareschal & Baker, 1999; Schofield & Georgeson, 1999; Zhou & Baker, 1993). Results from a number of psychophysical studies (e.g. Chima, Formankiewicz, & Waugh, 2015; Hairol & Waugh, 2010; Schofield & Georgeson, 1999), an electrophysiological study (Calvert, Manahilov, Simpson, & Parker, 2005), a neuro-imaging study (Larsson, Landy, & Heeger, 2006), and neurophysiological studies in cats (Mareschal & Baker, 1998; Tanaka & Ohzawa, 2006) and macaques (An et al., 2014; Li et al., 2014) have led to suggestions that additional computation is necessary in order for second-order stimuli to be perceived, compared to first-order stimuli (e.g. Baker, 1999; Landy & Graham, 2004; Schofield & Georgeson, 1999). Results from studies on amblyopia and interocular suppression suggest that this extra computation occurs in an area that involves binocular neurons (Wong, Levi, & McGraw, 2001, 2005; Chima, Formankiewicz, & Waugh, 2016). Dynamics of binocular rivalry are affected by a number of stimulus attributes (as outlined above), but in the present study, we are specifically concerned with differences that arise as the result of using LM and CM stimuli whilst keeping all other stimulus properties the same. Any differences in the characteristics of rivalry should therefore reflect the different processing sites for the two stimulus types.

In a recent study, we investigated binocular rivalry characteristics for orthogonally oriented gratings created using sinusoidal modulations of luminance (L), luminance modulated noise (LM) and contrast modulated noise (CM) (Skerswetat, Formankiewicz, & Waugh, 2016). We demonstrated that even under comparable visibility levels (multiples above detection threshold), a greater proportion of "mixed" percepts was evident for rivalling CM, than LM stimuli. This result in normal vision provides further support for the suggestion that more binocular areas are engaged in the processing of CM, than LM stimuli. However, as noted above, "mixed" percepts likely consist of both piecemeal and superimposition.

The first aim of the current study is to quantify the proportions of piecemeal and superimposition that occur during binocular rivalry for LM and CM stimuli. If CM stimuli are first processed by units involved in binocular fusion (e.g. Chima et al., 2015; Hairol & Waugh,

125 2010a; Wong et al., 2001; Wong, Levi, & McGraw, 2005), then significantly greater
126 proportions of superimposition would be found for CM, than for LM stimuli. The second aim
127 of the current study is to investigate the effects that different interocular luminance noise
128 correlations have on binocular rivalry characteristics. If rivalry is initiated when luminance
129 information is extracted, both LM and CM rivalry dynamics should change in a similar way
130 only when noise is not fully correlated.

131 **2. Methods**

132

133 **2.1 Participants**

134

135 Eight male and seven female participants with an average age of 25.7 ± 5.2 years carried out
136 the experiment. Three were experienced in binocular rivalry experiments. All except one
137 participant (author J.S.) were naïve to the purpose of the study. All participants had normal or
138 corrected-to-normal visual acuity of at least 6/6 and normal binocular vision as indicated by
139 random-dot-stereopsis of at least 60 arcsec when measured with the Dutch Organization for
140 Applied Scientific Research (TNO) stereo test (Lameris Ootech, Ede, Netherlands).

141

142

143

144 **2.2 Stimuli**

145

146 All stimuli were presented in a circular aperture of 2 deg diameter and contained a 2c/deg
147 sinusoidal grating. The left eye's stimulus contained a horizontal grating, and the right eye's, a
148 vertical grating. LM gratings were created by adding dynamic two-dimensional binary noise
149 with an amplitude of 0.2 to a sine-wave with luminance modulation of 0.1. The same noise
150 amplitude was multiplied by the sine-wave to create the CM gratings with a modulation of
151 1.00. It is important to consider the visibility of stimuli used to generate binocular rivalry since
152 luminance contrast (and therefore visibility) of first-order stimuli influences the course of
153 rivalry (e.g. Brascamp et al., 2015; Levelt, 1965). In a previous study, we measured detection
154 thresholds for CM and LM stimuli of the same size, spatial frequency as used in the current
155 study (Skerswetat et al., 2016). Based on these detection thresholds (averaged across
156 participants), for the modulations used in this experiment, the visibilities for the two types of

157   stimuli are similar, at 7 ± 1 (standard error) times and 5 ± 1 times for CM and LM stimuli,
158   respectively.

159

160   The stimulus types can be mathematically described as follows.

161

162   Sinusoidal luminance-modulated (LM) grating:

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

164   Two-dimensional binary white noise added to a sinusoidal luminance grating. *N* is the binary

165   noise at position (x,y) (either black (-1) or white (1)) and *n* is contrast of 0.2.

166

167   Sinusoidal contrast-modulated (CM) grating:

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

169   Contrast modulation is m. The mathematical term $nN(x,y)msin(2\pi x f_x)$ expresses the

170   contrast-modulated grating that results from the multiplying random noise sample by a sinusoid

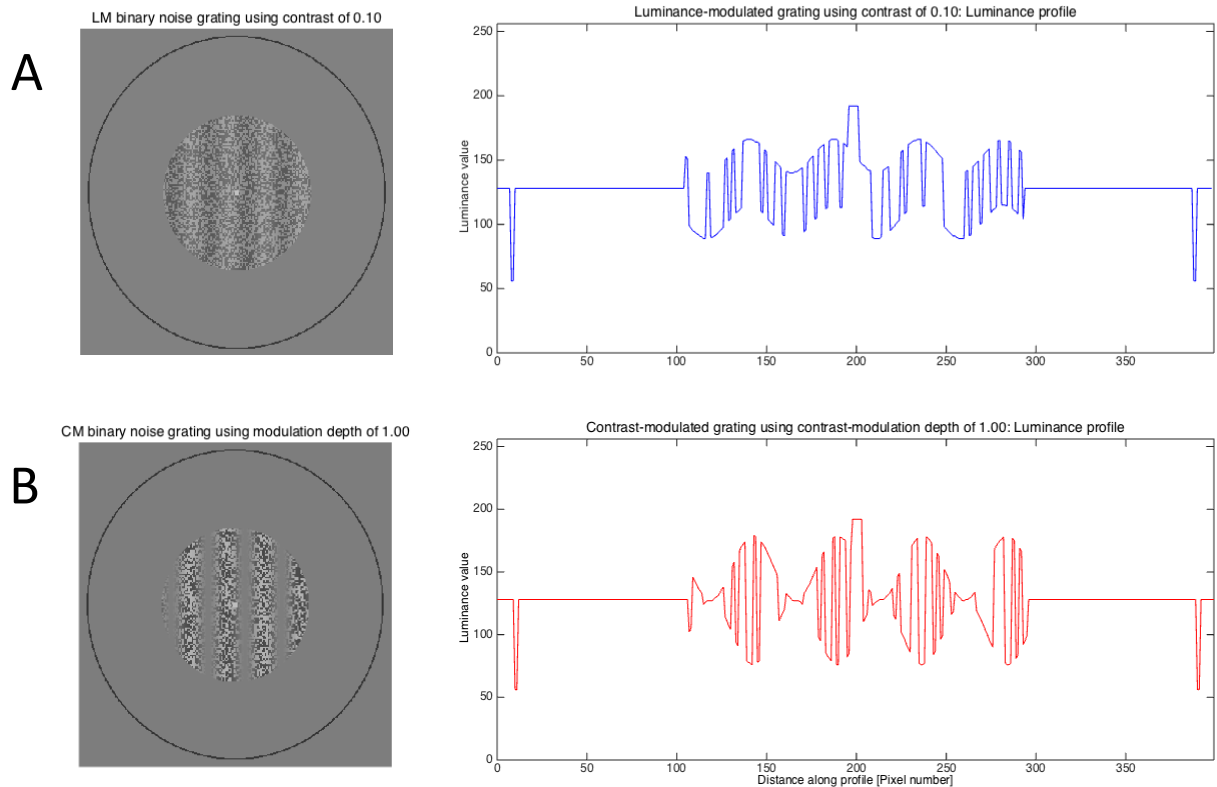171   (Calvert et al., 2005; Schofield & Georgeson, 1999).

172

173

174

175   *Figure 1: Illustration of vertical LM and CM gratings with luminance profiles taken through*

176   *the centre of the stimulus. A) Luminance-modulated (LM) sinusoidal grating with contrast of*

177   *0.10 and added binary noise with a contrast of 0.20. B) Contrast-modulated (CM) sinusoidal*

178 *grating modulating the binary noise carrier (modulation 1.00). Both stimuli were surrounded*

179 *by a circular fusion lock (4 deg diameter) and contained a static fixation spot (6x6 pixels) in*

180 *the centre with a luminance contrast of 0.20.*

181

182

183 Stimuli were presented on a grey background with a mean luminance of 48.55 cd/m^2. The

184 stimuli were viewed through a stereoscope. The optical distance from the participant's eyes

185 through the mirrors to the monitor was 100 cm. The pixel size at this distance was 1.3 arcmin.

186 A surrounding annulus with a diameter of 4 deg and a width of 2.6 arcmin (2 pixels) was used

187 as a fusion lock (See Figure 1).

188

189 Three different noise configurations were used. 'Correlated noise' refers to noise checks that

190 correspond interocularly in space, time and luminance. 'Anti-correlated noise' refers to noise

191 checks that correspond interocularly in space and time, but with opposite luminance values.

192 'Uncorrelated noise' refers to noise checks that randomly correspond interocularly in space and

193 time, thus, there is a 50 % chance that a particular check in one eye also corresponds in

194 luminance with the same check in the other eye. At 100cm, each noise check subtended 2.6

195 arcmin (or 2x2 pixels).

196

197 To avoid any first-order artefacts in the second-order stimuli due to pixel clumping of static

198 noise, dynamic noise was used (e.g. Ellemberg, Allen, & Hess, 2004; Georgeson & Schofield,

199 2016; Hairol & Waugh, 2010; Schofield & Georgeson, 1999, 2000; Zhou, Liu, Zhou, & Hess,

200 2014). Ten stimulus pages were created using the equations above, each with a different,

201 random noise pattern. These ten pages were cycled in random order for the duration of the trial

202 to generate dynamic noise. Each page was displayed for two monitor frames with the monitor

203 running at 140 Hz. Consequently, the noise checks across the stimulus changed every 14.28ms

204 in both stimuli.

205

206

207

208 **2.3 Apparatus and monitor calibration**

209

210 The stimuli were presented on a Mitsubishi Diamond Pro 2070SB CRT Monitor with a

211 resolution of 1027 x 769 pixels. Dell Precision 3500 hardware and Microsoft Windows XP

212 Professional (Version 2002) software were used to run the experiment and store the data. A
213 customised MatLab program (Version R2010b) in combination with the Cambridge Research
214 Systems Visual Stimulus Generator (ViSaGe) was used to create and present the stimuli.
215
216 Careful preparation prior to stimulus presentation and monitor calibration are essential for the
217 investigations of second-order stimulus properties. Gamma correction was carried out, using a
218 Cambridge Research Systems (CRS) ColorCal and software to produce lookup tables, to
219 correct the monitor's inherent nonlinear luminance intensities. Prior to each experimental
220 session, the monitor needed a warm-up time of 30 minutes to reach a consistent mean
221 luminance level. Adjacent pixel non-linearity may confound a second-order signal with local
222 first-order input (Klein, Hu, & Carney, 1996). Photometric measures for the luminance and
223 contrast modulated stimuli were carefully checked. A four mirror stereoscope composed of
224 optical components by OptoSigma (OptoSigma Corporation, California, USA) was used for
225 stimulus presentation. The mirrors were carefully aligned prior to beginning the experiments to
226 ensure that only one stimulus was visible to each eye.
227
228

229 **2.4 Procedure**
230
231 The experiment followed the ethical principles of the Helsinki declaration of 1975. All
232 participants were provided with written and verbal information about the project in advance
233 and gave written informed consent before taking part. Participants were reimbursed at a
234 minimal rate for time spent. Ethics approval to conduct the experiments on human participants
235 was obtained from the Faculty of Science and Technology Research Ethics Panel
236 (FST/FREP/12/327) at Anglia Ruskin University. All experiments were performed in a dark
237 room. Participants sat on a comfortable chair and placed their heads in a chinrest. The stimuli
238 were aligned by adjusting the position of a left and right nonious marker on the screen to ensure
239 comfortable binocular viewing for each participant. The task for the participant was to press
240 and hold various button configurations on a response box (Figure 2). The alternatives were, 1)
241 only the horizontal grating (left eye's image) was visible, 2) only the vertical grating (right
242 eye's image) was visible, 3) the percept contained portions of both stimuli (piecemeal), or 4)
243 both stimuli appeared to completely overlap (superimposition). No button press, or any other
244 button combination indicated invalid responses. Three experimental sessions were carried out,
245 in which different noise configurations were used. Each session included 12 trials for LM and

246   12 trials for CM stimuli in randomised order. One trial lasted at least 45 s. Instructions and
247   practice trials were given before formal data collection started. Breaks between trials were
248   permitted if needed. A complete session lasted between 25 and 45 mins, depending on the
249   breaks for each participant. For each participant, the three sessions were carried out on
250   separate days.
251

252   **2.5 Data analysis**

253

254

255   The data were analysed to extract a number of rivalry parameters. Definitions of perceptual
256   change categories are provided in Figure 2 and Table 1. Perceptual durations of exclusive
257   visibility (sum of responses for the horizontal and the vertical grating), piecemeal and
258   superimposed perception across 45 s and their respective mean durations were calculated. The
259   last response of a trial was not included in these calculations as its duration would have been
260   reduced by the termination of the trial at 45 s. When a percept did not occur during a trial (e.g.
261   a participant never reported an exclusive visible horizontal percept), a duration of 0 s was used
262   in calculating the mean across trials. Perceptual state results for 3 s intervals ('3-s-bins') across
263   the trial duration were also calculated to investigate the effects of time on the course of rivalry.

264

265   As we used the same spatial frequency for both gratings, we did not expect that participants
266   would perceive a superimposed mixed state with a depth impression (see Yang et al., 1992).
267   Participants were asked orally whether they experienced that one grating was seen in front of
268   the other during pilot sessions and training trials. No participant reported superimposition with
269   depth impression. Fast changes of button presses could cause the recording of false perceptual
270   states of very short durations. Hence, responses smaller than 180 ms were excluded. More
271   details about the determination of this 'cut-off' time can be found in a previous publication
272   (Skerswetat et al., 2016). A customized Matlab program was used to analyse the raw data
273   generated from this study. Repeated measures ANOVAs with Greenhouse-Geisser correction
274   and planned comparisons were also carried out using Statistica (Stat Soft, Int., U.S.A.).

275

276

Perceptual change category	Perceptual changes
Full flips	H <->V
Half flips	H <->P V <->P

	H <->S V <->S P <->S
Reversion (total)	H ->P -> H P ->H ->P V ->P ->V P ->V ->P H ->S ->H S ->H ->S V ->S ->V S ->V ->S P ->S ->P S ->P ->S
Within mixed reversion	P ->S ->P S ->P ->S
Gradual (via piecemeal) flips	H <->P V <->P P <->S
Abrupt flips	Full flips H <->S V <->S

Table 1: Perceptual change categories and their respective responses. The perceptual states are indicated as follows: horizontal (H), vertical (V), piecemeal (P) and superimposed (S). The symbol <-> indicates flips between the indicated states whereas the symbol -> is used for all reversion types to indicate a change from one state to another.
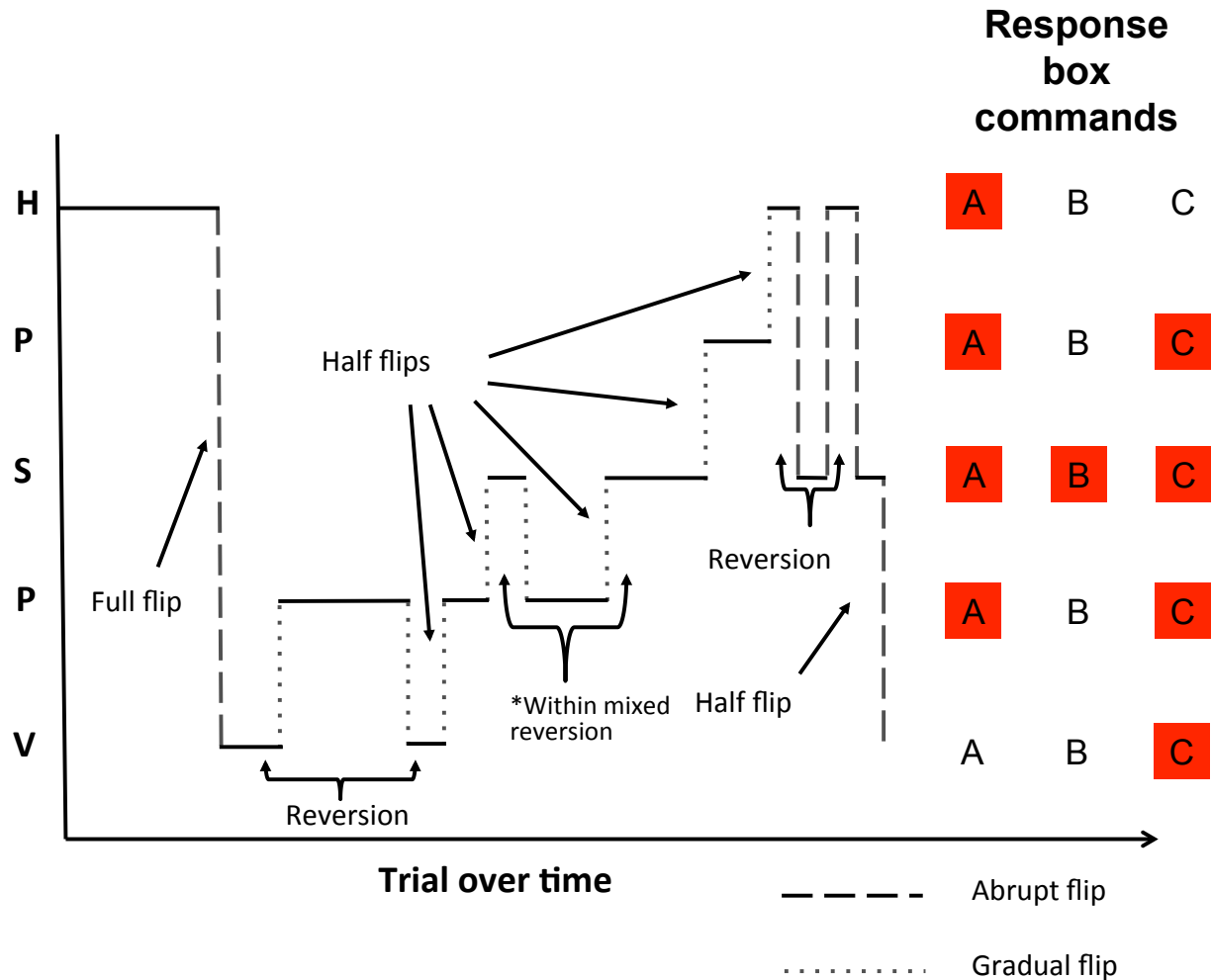

Figure 2: Illustration of a binocular rivalry sequence over time and description of the various perceptual change options. The y-axis shows the four response options: exclusive horizontal (H), exclusive vertical (V), piecemeal (P) and superimposed (S). The x-axis represents the trial

286 *duration. The letters "A", "B" and "C" marked in red on the right side of the illustration*
287 *represent the corresponding response box buttons. Pressing the button labelled "A" on the*
288 *response box signalled that an exclusive horizontal grating was perceived, "C", that an*
289 *exclusive vertical grating was perceived. Pressing both "A" and "C" referred to piecemeal*
290 *percepts. Pressing buttons "A", "B" and "C" together indicated that both gratings were*
291 *perceived completely superimposed. The dashed lines represent abrupt flips and the dotted*
292 *lines represent gradual flips.*

293
294
295
296

297 **2.5.1 Analysis of perceptual phase distributions**

298

299 The distributions of the various perceptual phase durations were fit with a gamma distribution
300 using Matlab (Version R2014b). For each condition and each participant, data was first
301 normalized by dividing the phase durations by the relevant mean. These normalised data were
302 then combined across participants. The perceptual phases are presented in the following form
303 using a gamma distribution:

304
305
306

$$f(x|\alpha,\beta) = \frac{1}{\beta^\alpha \Gamma(\alpha)} \, x^{\alpha-1} e^{\frac{-x}{\beta}} \; ; x > 0, \alpha > 0, \beta \geq 0$$

307
308
309

310 The gamma function is indicated with $\Gamma(\alpha)$, the "shape" parameter is α and represents the
311 skewness of the distribution, the "scale" parameter β scales the distribution along the abscissa
312 and the number of perceptual events x (e.g. Lev elt, 1965; O' Shea, Parker, La, & Alais, 2009;
313 Veser, O'Shea, Schröger, Trujillo-Barreto, & Roeber, 2008). The coefficient of determination
314 (R^2) has been used in previous studies (e.g. Logothetis, Leopold, & Sheinberg, 1996; Lunghi &
315 Burr, 2013; O' Shea et al., 2009) as an indicator of how well actual data fit a predicted model;
316 the closer R^2 is to 1, the better fit of the model to the actual data.

317

3. Results

Our aims were 1) to quantify the proportions of piecemeal and superimposition that occur during binocular rivalry for LM and CM stimuli, and 2) to investigate the effects that different interocular noise correlations have on binocular rivalry characteristics. To do this we analyse several aspects of binocular rivalry including proportions and mean durations of different perceptual states, rates of change in states, overall changes of rivalry across time and shapes of distributions of exclusive events.

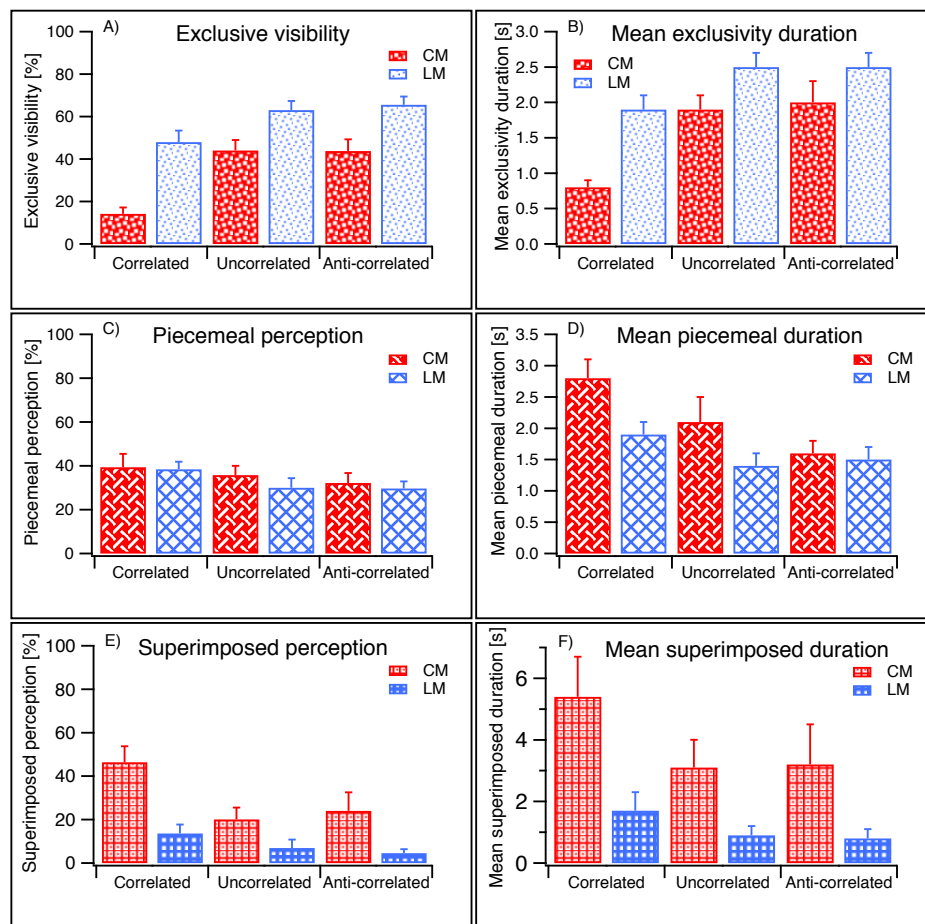### 3.1 Perceptual states and mean durations

Figure 3: Results for the relative proportions of exclusive visibility (A), piecemeal perception (C) and superimposed perception (E) in a trial and their respective mean durations (B), (D) and (F) using interocularly correlated, uncorrelated and anti-correlated noise, averaged across trials and participants. The blue bars with small dots (A,B), mosaic-pattern (C,D) and

339

340

341 The proportions of trial time during which exclusive visibility, piecemeal and superimposed

342 percepts were reported are depicted in Figure 3A, C and E, respectively. As our aim was to

343 investigate the effects of stimulus type and noise configuration on the characteristics of

344 binocular rivalry, we describe and statistically analyse the results for each percept separately.

345

346 The proportion of exclusive visibility ranges from 14 ± 3 (SE) % for CM correlated noise

347 stimuli to 63 ± 4 % and 66 ± 4 % for LM stimuli created using un- and anti-correlated noise,

348 respectively. For both types, but especially for CM stimuli, exclusive visibility is greater for

349 un- and anti-correlated than correlated noise. This differential effect of noise configuration on

350 stimulus type is confirmed by a statistically interaction [$F(1.9, 26.9) = 3.7$, $p < 0.05$]. All LM

351 stimuli generate significantly more exclusive visibility than CM stimuli [$p < 0.001$, planned

352 comparisons]. The differences in exclusive visibility are accompanied by significantly greater

353 proportions of superimposition for CM (from 20 ± 5 % for uncorrelated noise to 46 ± 7 % for

354 correlated noise) than for LM (4 ± 2 % to 14 ± 4 %) stimuli [$F(1,14) = 24.2$, $p < 0.001$]. The

355 proportions of superimposition are also affected by noise correlation [$F(1.7, 24.2) = 7.9$, $p <$

356 0.01] and are highest with correlated noise. The proportion of piecemeal perception is not

357 significantly different for the two types of stimuli [$F(1, 14) = 0.7$, $p > 0.05$] or three noise

358 configurations [$F(2.0, 27.3) = 1.9$, $p > 0.05$], ranging from 30 ± 4 % to 39 ± 6 %.

359

360 Figures 3 B, D and F show the mean percept durations. There was a reduction in mean

361 exclusivity duration for both stimulus types as the noise became correlated but again, this effect

362 was greater for CM than LM stimuli [$F(1.9, 26.7) = 3.8$, $p < 0.05$]. The greater proportions of

363 superimposition for CM than LM stimuli are due to the significantly longer mean durations

364 [$F(1, 14) = 15.2$, $p < 0.01$], which averaged across noise are 3.9 ± 1.2 s for CM and 1.2 ± 0.4 s

365 for LM stimuli. CM stimuli also generate longer piecemeal durations compared to LM stimuli

366 [$F(1, 14) = 18.3$, $p < 0.01$]. Duration of superimposed and piecemeal percepts was also

affected by noise type [$F_{(2.0, 27.3)} = 3.9$, $p < 0.05$ for superimposed; $F_{(1.5, 21.2)} = 4.4$, $p < 0.05$ for piecemeal] and was longer with correlated than anti- and uncorrelated noise.

In summary, CM stimuli generate significantly more superimposition than LM stimuli regardless of the noise configuration. Correlated noise engages in shorter moments of exclusive visibility, but longer phases of superimposed and piecemeal perception for both LM and CM stimuli compared to anti- and uncorrelated noise configurations.

3.2 Perceptual changes and reversions

In this section, we compare the effects of stimulus type and noise configuration separately for each of the perceptual changes described in Figure 2 and Table 1.
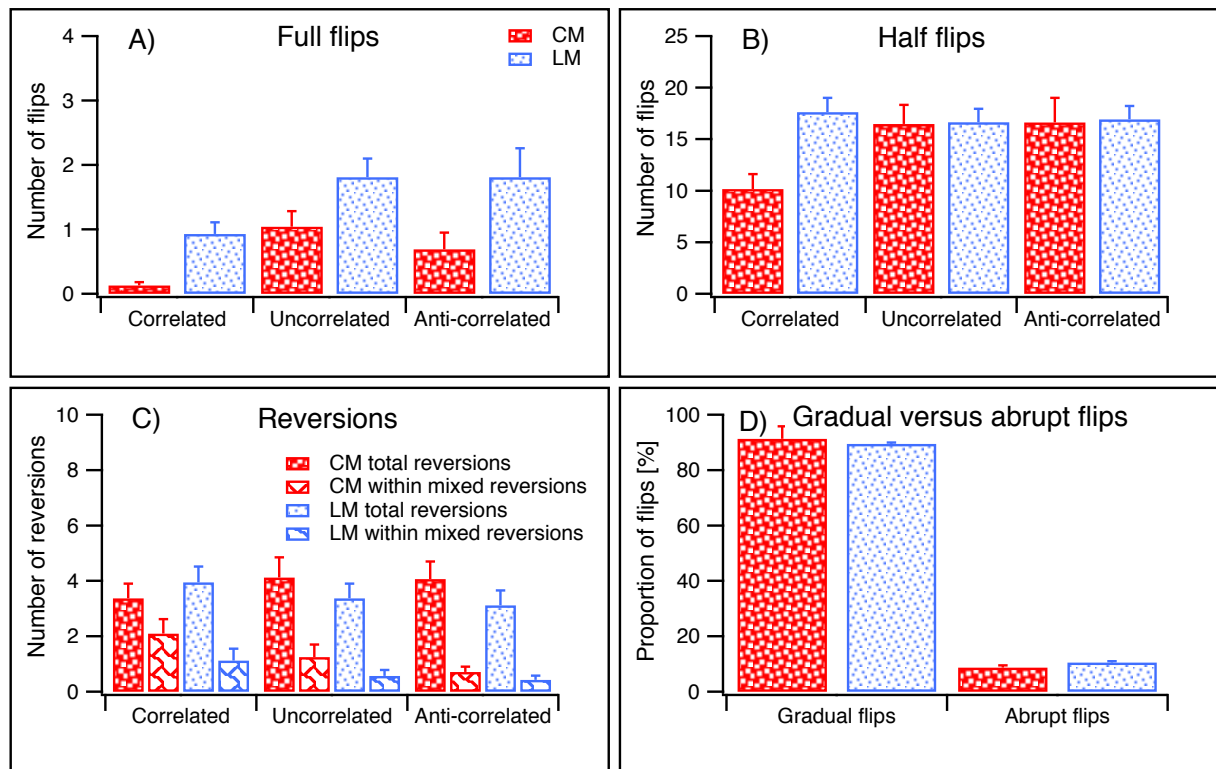

Figure 4: Results for number of full flips (A), half flips (B), reversions (C) using interocularly correlated, uncorrelated and anti-correlated noise, averaged across trials and participants. Note the different scale on the y-axes. Gradual versus abrupt flips (D) averaged across trials, participants and noise configurations. Red bars with big dots represent CM-stimuli, blue bars with small dots LM-stimuli. The scaled bars in graph C) are "within mixed reversions" between piecemeal and superimposition for CM and LM stimuli. Error bars indicate +1SEM.

387   Traditionally, binocular rivalry alternation has been described as a change of perception
388   between two exclusive states (e.g. Breese, 1899; Levelt, 1965; O'Shea et al., 1997), which in
389   the present study are referred to as full flips (Figure 4A). Full flips are thought to reflect
390   changes in the balance of monocular neural activity (e.g. Blake, 1989). All LM stimuli engage
391   in significantly more full flips than CM stimuli [$F(1, 14) = 12.8$, $p < 0.01$]. The effect of noise
392   configuration on full flips [$F(2.0, 27.9) = 9.1$, $p < 0.01$] is due to fewer full flips for correlated
393   noise compared to the other two noise configurations. Half flips always involve piecemeal or
394   superimposition (see Table 1). Half flips are thought to reflect changes between different
395   rivalry (exclusive and piecemeal) and fusion (superimposition), states.
396
397   A striking finding is the lower number of half flips for the correlated CM compared to all other
398   conditions (Figure 4B). This interaction of stimulus type and noise configuration is statistically
399   significant [$F(1.2, 17.0) = 15.2$, $p < 0.01$] as is the difference between LM and CM stimuli
400   under correlated noise configuration [$p < 0.001$, planned comparison].
401
402   During binocular rivalry, perceptual changes from an exclusive percept to a mixed state and
403   back again are referred to as reversions (e.g. Brascamp et al., 2006; Mueller & Blake, 1989;
404   Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013). In the paradigm used for the
405   current study, reversions within mixed perceptual states were computed and added to the total
406   number of reversions (Figure 4C). In correlated noise, there were slightly more reversions with
407   LM than CM stimuli, whereas the opposite pattern was observed with anti- and uncorrelated
408   noise. This difference is confirmed by a significant interaction between stimulus type and
409   noise [$F(1.9, 26.1) = 5.9$, $p < 0.01$], but the only statistical significance in the number of
410   reversions for LM and CM stimuli was for the anti-correlated noise [planned comparison, $p <$
411   0.05]. To the knowledge of the authors, we present here for the first time results for reversions
412   between piecemeal and superimposition (and vice versa). CM stimuli generate more within
413   mixed reversions than LM stimuli [$F(1, 14) = 8.3$, $p < 0.05$] and correlated noise conditions
414   trigger more of those reversions than anti- and uncorrelated noise [$F(1.8, 24.6) = 5.4$, $p < 0.05$].
415   We introduce gradual and abrupt flips as new perceptual change categories (see Figure 4D).
416   For both stimulus types, the majority of perceptual changes are gradual (90 % for CM and 91 %
417   for LM) rather than abrupt.
418
419

3.3 Results of perception across time

It is known that adaptation may change perception during rivalry across time (e.g. Hollins & Hudnell, 1980; Klink et al., 2010a, 2010b) for luminance-defined stimuli. We compared the effects of time on rivalry characteristics for LM versus CM stimuli. Figure 5 shows proportions of visual exclusivity, piecemeal and superimposition across 45s in 3s intervals for correlated, uncorrelated and anti-correlated noise, averaged across participants. Statistical analyses were performed separately for each perceptual state. Since a trial consists of fifteen '3-s-bins', effects between single intervals might not be revealed as a main effect using an ANOVA. Hence, we also performed planned comparisons between single '3-s-bins'.
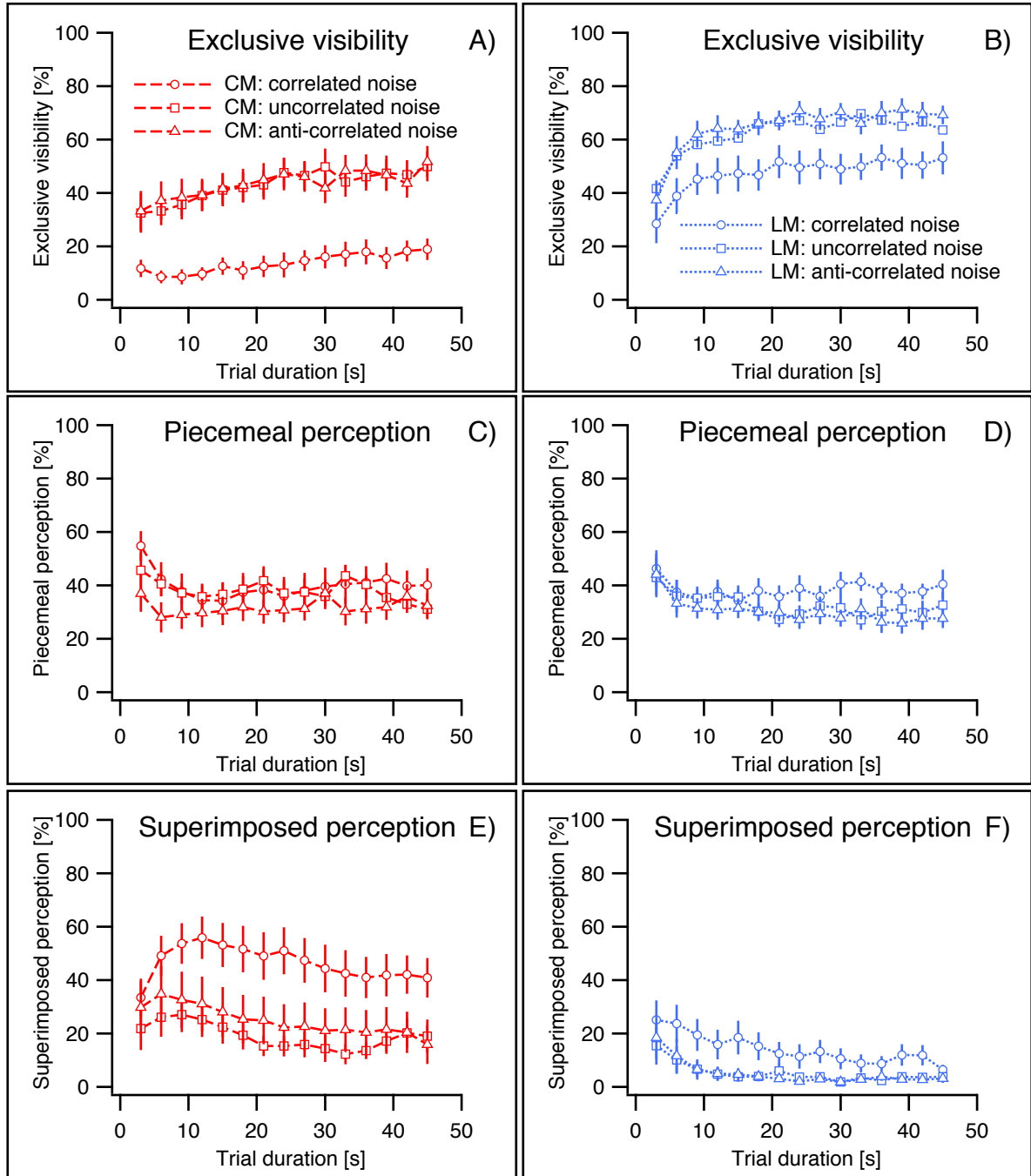
Figure 5: Proportions of perceptual states in 3 s intervals across the 45 s trial for CM (red dashed lines) and LM stimuli (blue dotted lines), and interocularly correlated (circles), uncorrelated (squares) and anti-correlated (triangles) noise. Error bars indicate ± 1SEM.

The red and blue functions of Figure 5 represent the perceptual states across trial time for CM and LM stimuli, respectively. The proportion of exclusive visibility for CM correlated noise stimuli does not show a definite trend across time whereas it increases gradually for CM un- and anti-correlated noise stimuli. A steep increase is seen over the first few seconds for all LM

442 stimuli. Statistical analysis shows a significant interaction between stimulus type and time
443 [$F(5.4, 75.9)=3.9$, $p < 0.01$], but not between noise configuration and time [$F(7.0, 98.5) = 0.78$,
444 $p > 0.05$].   Planned comparisons confirmed the trends observed in Figure 5A and B, i.e. there
445 is a statistically significant [planned comparisons, $p < 0.05$] increase in exclusive visibility
446 from the first to the second, and from the second to the third '3 s bin' for LM but not for CM
447 stimuli.

448

449 The proportion of piecemeal perception reduces at the beginning of the trial for all stimuli.
450 Although, overall there is no statistically significant main effect of time [$F(1.8, 25.8)=3.0$, $p >$
451 0.05], the first and second 3 s intervals are significantly different [planned comparisons, $p <$
452 0.05]. The trend across time for superimposition is different for LM and CM stimuli and this
453 difference is confirmed by a statistically significant interaction between stimulus type and time
454 [$F(3.2, 44.7) = 4.0$, $p < 0.05$]. Over the first 6 s of the trial, the proportion of perceptual
455 superimposition grows significantly [planned comparison, $p < 0.01$] from 28 ± 8 to 37 ± 8 %
456 for CM stimuli, whereas LM stimuli's perception decreased mildly but not significantly
457 [planned comparison, $p > 0.05$] from 20 ± 8 % to 15 ± 6 %.

458

459 **3.4 Distribution of exclusively visible phases**

460

461
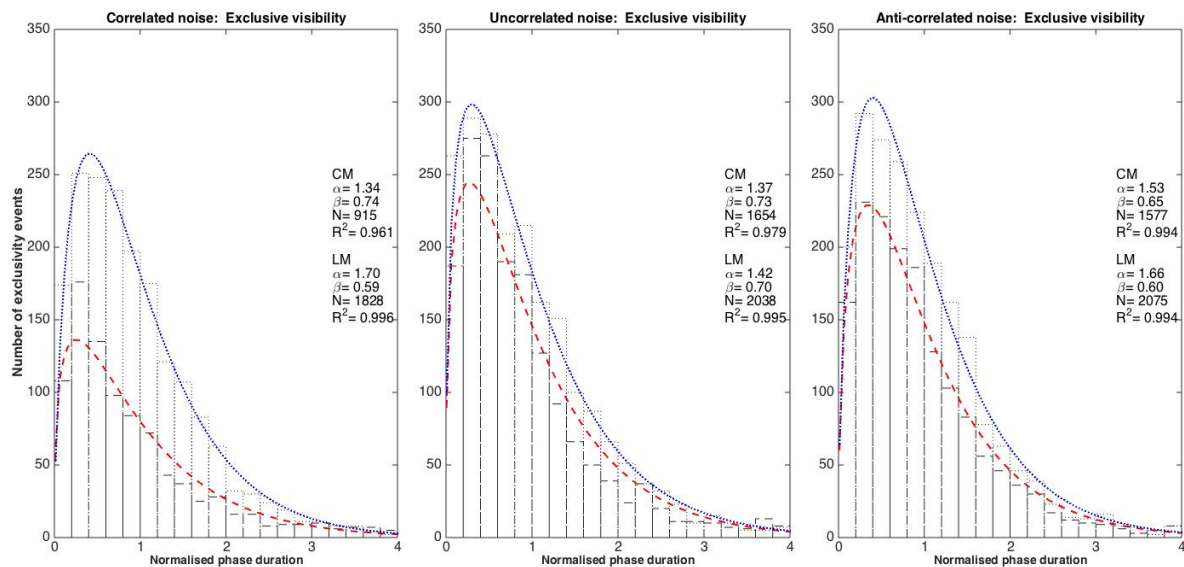
Figure 6: LM and CM phase distributions for exclusively visible percepts using interocularly correlated (left), uncorrelated (middle) and anti-correlated (right) noise. The x-axes depict normalised phase durations. The y-axes represent the number of perceptual events. The fitted gamma functions are shown together with parameters for LM (blue) and CM stimuli (red).

Both CM and LM phase distributions for exclusive visibility for all noise configurations show a typical gamma-shape, which has been described as a hallmark of binocular rivalry (see Alais & Blake, 2005; Levelt, 1965, 1967). As shown in Figure 6, LM stimuli show greater peak values than CM stimuli. Also, interocularly correlated noise CM stimuli generate fewer exclusive events than all other stimulus type/noise configurations. The coefficient of determination, indicated by R^2 values, is overall closer to 1 for LM compared to CM stimuli.

4. Discussion

Our experiments have shown that under all noise configurations, but in particular for correlated noise, rivalrous CM stimuli engage in significantly less exclusive visibility and more superimposition than LM stimuli do. Interocular anti- or uncorrelated noise checks increase the amount of exclusive visibility compared to correlated noise especially for CM, but also for LM stimuli. Piecemeal perception was unaffected by changes of stimulus type and noise configuration (Figure 3). This study has also demonstrated that the use of LM stimuli triggers significantly more full and half flips than the use of CM stimuli (Figure 4) and that regardless of the stimulus type or interocular noise configuration, more gradual than abrupt flips occur (Figure 4). In the following sections, we will discuss the findings of the current study and use them to establish a framework that aims to address the differences between first- and second-order binocular rivalry.

4.1 Mixed states during first- and second-order binocular rivalry

Previously, we reported that CM stimuli created with interocularly correlated noise generate many more mixed percepts (i.e. sum of superimposed and piecemeal percepts) than do LM stimuli (Skerswetat et al., 2016) when both are presented at comparable visibility levels. In the current study, we subdivided mixed states into "piecemeal" and "superimposed" perceptual

494 states. It has been suggested that piecemeal perception is rivalry in local zones (e.g. Blake et
495 al., 1992) whereas superimposition indicates binocular fusion (e.g. Brascamp et al., 2006; Liu
496 et al., 1992). Liu et al. (1992) suggested that non-oriented receptive fields may provide an
497 underlying neuronal substrate for superimposition. However, Brascamp and collaborators
498 (2006) showed that superimposition increases gradually as the stimulus contrast is reduced. If
499 superimposition involves a separate mechanism, the transition from piecemeal perception to
500 superimposition might be expected to be abrupt.
501
502 In the current study, we found significantly greater proportions of superimposition for CM than
503 LM stimuli for all noise configurations, due to longer mean superimposed durations (Figure 3E
504 and F). The trend of piecemeal perception across time is similar for LM and CM stimuli, in
505 that there is a mild decrease over the first 6 s of a trial. However, the results for the two types
506 of stimuli are different for superimposition: the proportion of superimposition increases at the
507 beginning of the trial for CM stimuli, but decreases for LM stimuli. These results might be
508 expected if superimposition has a more binocular processing site compared to piecemeal rivalry
509 (Brascamp et al., 2006; Klink, Brascamp, Blake, & van Wezel, 2010; Klink, Brascamp, Blake,
510 & Wezel, 2010a; Liu et al., 1992; but see also Blake et al., 1992) and if CM stimuli are
511 initially processed in areas of the cortex, which receive greater binocular input than those
512 processing LM stimuli (e.g. Hairol & Waugh, 2010; Skerswetat et al., 2016; Sukumar &
513 Waugh, 2007; Wong, Levi, & McGraw, 2001).
514

A

Can the results be explained by the 'blank vs. local contrast' effect?

Left eye's stimulus

Right eye's stimulus

Combining left and right eyes' stimuli

Local contrast vs. local contrast intersection

'Blank' vs. local contrast intersection

vs.

vs.

B

Correlated noise

Noise configuration

Anti-correlated and uncorrelated noise

Superimposition

Possible perception

Either piecemeal

Potential for mean luminance areas at the intersections due to summation

or superimposition

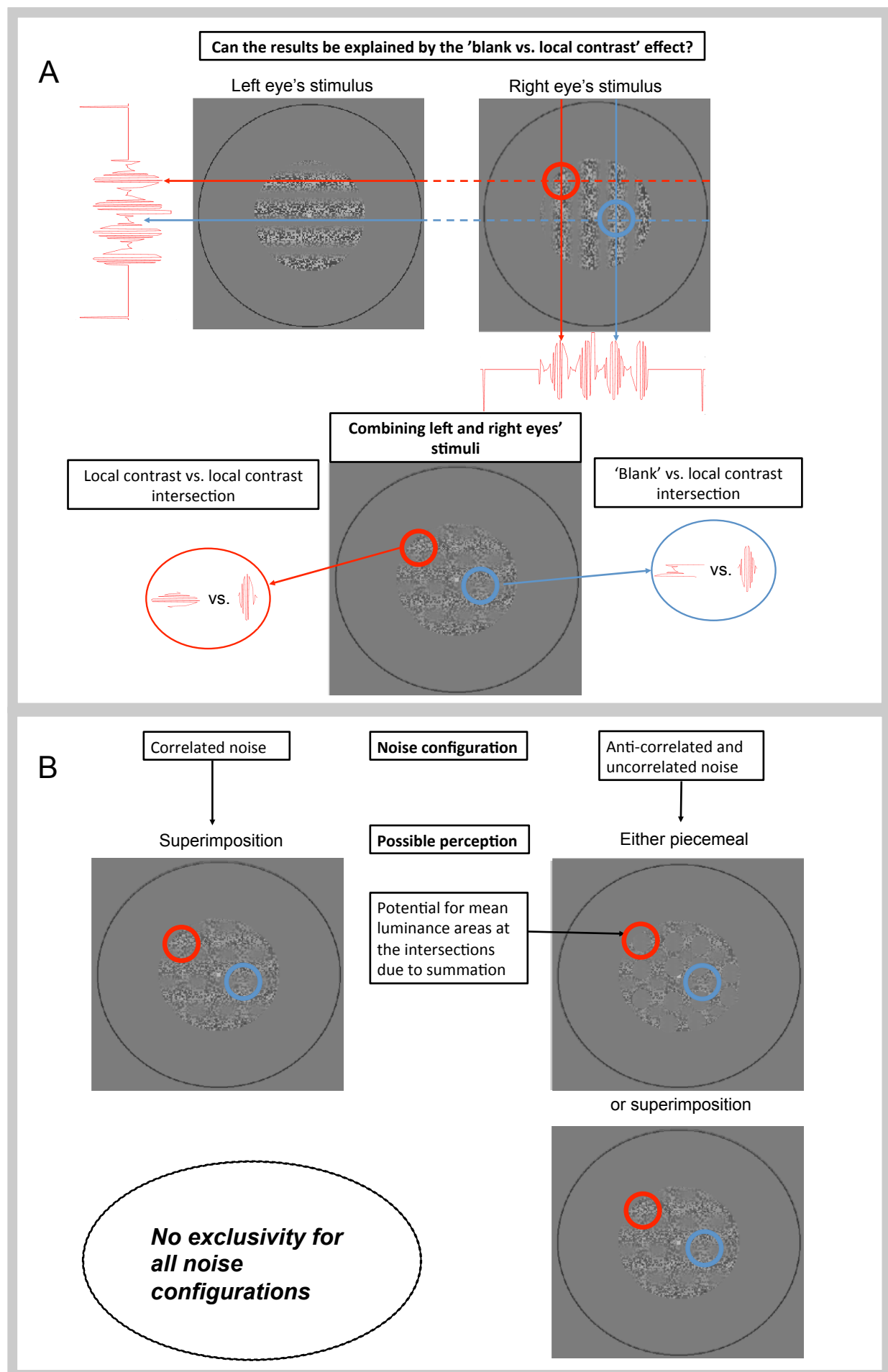*No exclusivity for all noise configurations*

515

Figure 7: Scheme of an alternative hypothesis discussed in text. A) When the left and right eye's stimuli are combined, two local percepts are depicted: Intersections of local contrast regions (red circles) and intersections of regions close to mean luminance ('blank') vs. local contrast regions (blue circles). B) Three possible perceptual states that can arise with different noise correlations. Note that this hypothesis cannot explain the existence of exclusive percepts.

4.2 Can the results be explained by the "blank vs. local contrast" effect?

An alternative explanation for our finding that higher proportions of superimposition are found for CM than LM stimuli, could be that for CM stimuli, local contrast-modulation areas in one eye, predominate over areas that are close to mean luminance in the other eye (see Figures 7A and B, blue circles). Whether a piecemeal percept or superimposition is reported would depend upon the regions of intersection where there is CM/CM combination (Figures 7A and B, red circles). For correlated noise, there would be no rivalry, so superimposition is likely to be reported (Figure 7B: left). The results of our study show a substantial proportion of superimposition (Figure 3E), but they also show a similar proportion of piecemeal (Figure 3C), which would not be expected by this alternative explanation.

For anti- and uncorrelated noise, if local rivalry occurs at the intersection, then superimposition or piecemeal could be reported (Figure 7B: right). If luminance averaging (summation) occurs at the intersection resulting in areas of mean luminance, piecemeal could be reported. In this case, the proportion of piecemeal perception should be higher for un- and anti-correlated than for correlated noise, but our results again do not support this (Figure 3C) as they show that proportions of piecemeal are roughly equal for all noise conditions.

If the pattern was interpreted as superimposition because of "filling-in" or local rivalry (resulting in some noise being perceived) at the intersections, then the same high proportion of superimposition should be reported for all noise conditions. However, our data (Figure 3E) show that the proportion of superimposition is greater for correlated, than anti- and uncorrelated noise. It is possible that rivalry at CM/CM intersections could lead to a pattern that is sometimes interpreted as superimposition and sometimes as piecemeal (Figure 7B: right). In this instance, the proportion of superimposition should be lower for anti- and uncorrelated noise than correlated noise. This is what we found (Figure 3E). However, this

549   reduction in the proportion of superimposition should be accompanied by an increase in the

550   proportion of piecemeal, but it is not (Figure 3C).

551

552   For both LM and CM stimuli, a reduction in superimposition is accompanied by an increase in

553   exclusivity for anti- and uncorrelated noise, compared to correlated noise. Exclusive visibility

554   for CM stimuli would be very difficult to achieve if local contrast-modulation areas in one eye

555   always predominated over areas that are close to mean luminance in the other eye. We report

556   exclusive visibility with all types of noise conditions and both types of stimuli (Figure 3A).

557   We showed that the exclusivity reported for correlated noise cannot be explained by stimulus

558   fading (Skerswetat et al., 2016).

559

560   Thus, rather than this alternative explanation being true, the greater proportions of

561   superimposition for CM stimuli are likely to be explained by binocular fusion.

562

563   **4.3 The effect of binary two-dimensional noise on the course of binocular rivalry**

564

565   Interocular noise configuration was varied in the current study. We used 1) correlated noise,

566   i.e. noise checks corresponded in time, space and luminance, 2) anti-correlated noise, i.e. noise

567   checks corresponded in time and space, but the luminance information was reversed and 3)

568   uncorrelated noise, i.e. noise checks corresponded in time and space, but luminance values

569   corresponded (correlated) or did not correspond (anti-correlated) with a chance of 50 %.

570

571   Other studies examining the effects of different interocular noise configurations on the

572   perception of second-order stimuli have been carried out. It has been reported that stereopsis

573   thresholds were not significantly different when one dimensional uncorrelated and correlated

574   noise was used (Wilcox & Hess, 1996). The binocular summation of contrast detection

575   thresholds for LM and CM sinusoidal gratings using correlated, uncorrelated and anti-

576   correlated noise were also not significantly different (Georgeson & Schofield, 2016). Studies

577   concerning the phase of binocularly combined LM and CM stimuli also showed no significant

578   differences in results obtained with correlated, uncorrelated and anti-correlated noise

579   configurations (Zhou, Georgeson, & Hess, 2014; Zhou, Liu, et al., 2014).

580

581   Our results show that binocular rivalry characteristics of CM stimuli are affected by the nature

582   of interocular noise correlation. When noise is fully correlated, changes in exclusive visibility

583   across time for CM stimuli are more gradual and reduced in magnitude compared to LM

584   stimuli (Figure 5A). The lack of change over time for the CM correlated noise condition makes

585   sense due to the greater magnitude of superimposition facilitated by fusion reducing the

586   influence of adaptation on rivalry alternation. In the context of the CM filter-rectify-filter

587   processing model, at the second stage, the envelope is filtered and either binocularly summed

588   (superimposition) or suppressed (piecemeal perception or exclusive visibility). When noise is

589   anti- or uncorrelated, greater proportions of exclusively visible percepts (Figure 3A) and

590   greater numbers of full and half flips (Figure 4) are likely to be due to competing carrier

591   information, which adds to the conflict of the competing envelopes.

592   **4.4 Distribution of exclusively visible phases**

593

594   The gamma distribution for CM stimuli using correlated noise showed much smaller peak

595   values than all other exclusive visibility gamma phase distributions due to the lowest number of

596   events. These results may support the suggestions of different processing mechanisms for first-

597   and second-order stimuli (e.g. Chima et al., 2015; Schofield & Georgeson, 1999; Waugh, Lalor,

598   & Hairol, 2009). We consider pure second-order rivalry to occur only in the correlated noise

599   condition. Our results show gamma distributions with R^2 values close to 1 for both exclusively

600   visible CM and LM stimuli (Figure 6). The poorest fit occurred when CM stimuli were

601   presented under correlated noise conditions, which is likely to be due to the low number of flips

602   (Figure 4A).

603

604   **4.5 Addition of a third well to current energy landscape models of binocular**

605   **rivalry dynamics**

606

607   The highlight of the current study is that CM stimuli generate significantly more

608   superimposition than do LM stimuli. But how does this result fit into the current view of

609   binocular rivalry? Double-well or energy landscape illustrations have been used to

610   metaphorically describe the dynamics of perceptual alternations during binocular rivalry (e.g.

611   Brascamp et al., 2006; Kang & Blake, 2011; Kim et al., 2006; Moreno-Bote et al., 2007; Rubén

612   Moreno-Bote, Shpiro, Rinzel, & Rubin, 2010; Pastukhov & Braun, 2011; Seely & Chow,

613   2011). Well-established models describe a mediator-mechanism often called mutual or

614   reciprocal inhibition (e.g. Blake, 1989; Kang & Blake, 2011; Seely & Chow, 2011). The

615   models are based on the assumption that different populations of neurons compete with each

616   other during binocular rivalry. During phases of exclusive visibility, dominant neural

617   populations are inhibiting neural populations of the other eye's stimulus completely, i.e.,

618   mutual inhibition. One idea is that neural adaptation weakens the dominant stimulus over time

619   and decreases its suppressive impact on the suppressed stimulus until a point of equality, which

620   leads to an abrupt change with short transient (mixed perceptual) phases (Blake, Tadin, Sobel,

621   Raissian, & Chong, 2006; Kalarickal & Marshall, 2000; Laing & Chow, 2002; Lankheet, 2006;

622   Lehky, 1988; Mueller, 1990; Seely & Chow, 2011; Wilson, 2003). This is illustrated in Figure

623   8A. The state potential changes as a result of adaptation and the perceptual state (red circle),

624   moves between the two exclusive states (the two minima).

625

626   Alternatively, random intrinsic noise within the visual system could be the driving force for

627   perceptual alternation (e.g. Brascamp et al., 2006; Kim et al., 2006; Rubén Moreno-Bote,

628   Rinzel, & Rubin, 2007; Webber & Bressloff, 2013). The noise model is illustrated in Figure

629   8B, where the potential remains constant, but intrinsic noise triggers perceptual alternation

630   between the two minima, i.e. the two exclusivity states.

631

632   The adaptation model also implies a rapid change between the two exclusive states, but the

633   existence of reversions and mixed periods argues against this idea (Brascamp et al., 2006).

634   Brascamp and collaborators suggested that intrinsic noise is a crucial factor necessary to

635   describe the results of binocular rivalry under low contrast conditions (Figure 8C). The minima

636   tend to be shallow and thus generate long mixed durations (e.g. Liu et al., 1992) when the

637   perceptual state (red circle) reaches the associated flat transition region. Our findings of many

638   more gradual than abrupt flips (Figure 4D) are in line with the idea of intrinsic noise as a

639   predominant cause for perceptual alternation during binocular rivalry.

640

641   Both adaptation and noise models do not address the fact that reversions occur between

642   piecemeal and superimposed percepts (Figure 4C). Therefore, we suggest in Figure 8D, adding

643   piecemeal (P) and superimposition (S) within the transient region. The minimum of S, a new

644   third well, within the transient region depends on various stimulus characteristics such as the

645   stimulus type reported here (CM or LM), but also on other stimulus characteristics such as size

646   (e.g. Blake et al., 1992; Breese, 1899; O'Shea, Sims, & Govan, 1997), contrast (e.g. Brascamp

647   et al., 2015; Brascamp et al., 2006; Liu et al., 1992), orientation (Schor, 1977; Wade, 1974),

648 stimulus complexity (e.g. Alais & Melcher, 2007) and spatial frequency (e.g. O'Shea et al.,

649 1997; Livingstone & Hubel, 1987).

650

651 The proposed addition of a third well can also address for the first time, binocular rivalry for

652 CM stimuli (Figure 8E). The greater proportions of superimposition under comparable

653 visibility levels (multiples of detection threshold) for CM stimuli is represented by a much

654 deeper minimum of the S region than for the LM counterpart (Figure 8D).

655

656
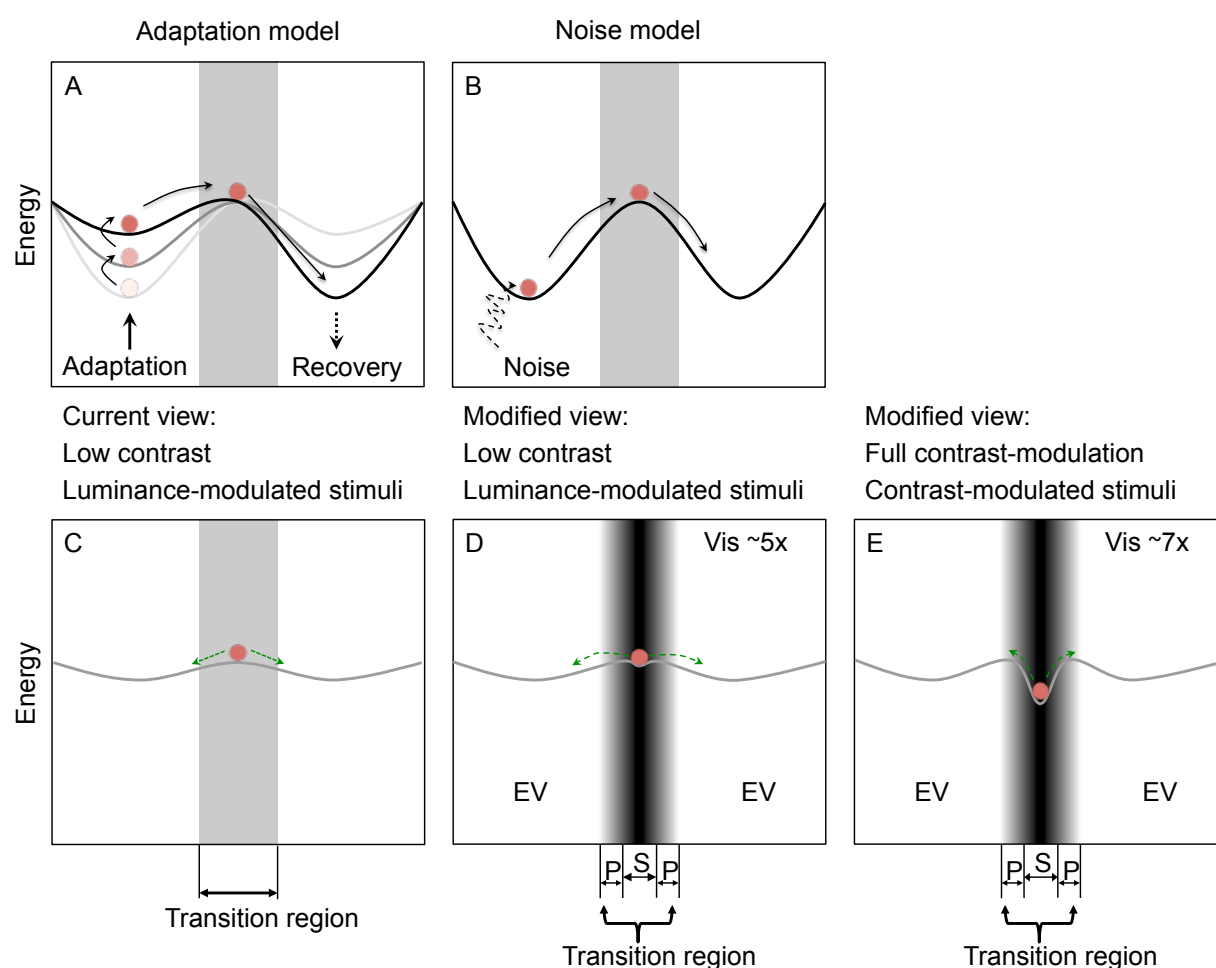
657 *Figure 8: First-and second-order binocular rivalry states predicted using a double well*

658 *potential model adapted from Brascamp et al. (2006) and Pastukhov & Braun (2011). The grey*

659 *zones in the centre of the boxes A-C depict the transient or mixed perceptual region. The black*

660 *wavy lines in the graphs A and B represent perceptual state potential; the minima of each*

661 *potential represents exclusive visibility. The red circle represents the actual system*

662 *(perceptual) state. A) Adaptation model: The landscape changes over time due to adaptation*

663 *(upward pointing arrow) of the current perceptual state and the simultaneous recovery*

664 *(downward pointing arrow) of the suppressed state. B) Noise model: The potential remains*

constant, however, intrinsic noise of the system (curved-dashed arrow) drives the red circle into the other state potential. C) Current view of binocular rivalry dynamics under low contrast conditions (see Brascamp et al., 2006; Pastukhov & Braun, 2011). The deterministic forces, due to intrinsic noise, are weak and the system state may develop in either direction (green dashed arrows). D) The gradation of grey levels to indicate different mixed states (piecemeal (P) to superimposition (S)) adds to the current view of first-order binocular rivalry (Brascamp et al.,2006). The minimum of S depends on various stimulus characteristics e.g. size, contrast, spatial frequency etc. Under the LM stimuli conditions of the current study, mixed perception occurred mainly in a piecemeal fashion, hence S minima level is relatively shallow compared to the CM stimuli condition illustrated in E) Using comparable visibility levels between CM and LM stimuli, the minimum of S is deeper for CM than for LM stimuli (Figure 3E)).

5. Conclusion

Regardless of noise configuration, CM stimuli generate fewer proportions of exclusivity and greater proportions of superimposition, than do LM stimuli. Interocular noise configuration affects binocular rivalry for both LM and CM stimuli. CM stimuli alternate less than LM stimuli as they trigger fewer full flips. Superimposition for CM stimuli develops differently over time, than for LM stimuli. The high proportions of superimposition for CM stimuli suggest that the envelope component is processed by neurons that compute initially binocular, rather than monocular, information. Orthogonally presented CM envelopes engage in stronger binocular rivalry if interocular carrier noise is not correlated. We propose the addition of a new well to the current qualitative energy landscape model for binocular rivalry alternation, to take our findings into account.

References

Alais, D., & Blake, R. (2005). *Binocular Rivalry*. Cambridge/USA: MIT press.

Alais, D., & Melcher, D. (2007). Strength and coherence of binocular rivalry depends on shared stimulus complexity. *Vision Research*, *47*(2), 269–79. https://doi.org/10.1016/j.visres.2006.09.003

An, X., Gong, H., Yin, J., Wang, X., Pan, Y., Zhang, X., … Wang, W. (2014). Orientation-cue invariant population responses to contrast-modulated and phase-reversed contour stimuli in macaque v1 and v2. *PLOS ONE*, *9*(9), e106753. https://doi.org/10.1371/journal.pone.0106753

Baker, C. L. (1999). Central neural mechanisms for detecting second-order motion. *Current Opinion in Neurobiology*, *9*, 461–466.

Blake, R. (1989). A neural theory of binocular rivalry. *Psychological Review*, *96*(1), 145–67.

Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews Neuroscience*, *3*(1), 13–21. https://doi.org/10.1038/nrn701

Blake, R., O'Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Visual Neuroscience*, *8*(5), 469–78.

Blake, R., Tadin, D., Sobel, K. V, Raissian, T. a, & Chong, S. C. (2006). Strength of early visual adaptation depends on visual awareness. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(12), 4783–8. https://doi.org/10.1073/pnas.0509634103

Bossink, C. J. H., Stalmeier, P. F. M., & de Weert, C. M. M. (1993). A test of Levelt's second proposition for binocular rivalry. *Vision Research*, *33*(10), 1413–9.

Brascamp, J. W., Klink, P. C., & Levelt, W. J. M. (2015). The 'laws' of binocular rivalry: 50 years of Levelt's propositions. *Vision Research*, *109*, 20–37. https://doi.org/10.1016/j.visres.2015.02.019

Brascamp, J. W., van Ee, R., Noest, A. J., Jacobs, R. H. A. H., & van den berg, A. V. (2006). The time course of binocular rivalry reveals a fundamental role of noise. *Journal of Vision*, *6*(11), 1244–56. https://doi.org/10.1167/6.11.8

Breese. Burti B. (1899). On inhibition. *The Psychological Review*, *3*, 18–65.

Calvert, J., Manahilov, V., Simpson, W. a, & Parker, D. M. (2005). Human cortical responses to contrast modulations of visual noise. *Vision Research*, *45*(17), 2218–30.

726 https://doi.org/10.1016/j.visres.2005.02.012

727 Chima, A., Formankiewicz, M. A., & Waugh, S. (2015). Investigation of interocular blur
728 suppression using luminance-modulated and contrast-modulated noise stimuli. *Journal of*
729 *Vision*, *15*(22), 1–22. https://doi.org/10.1167/15.3.22.doi

730 Chima, A. S., Formankiewicz, M. A., & Waugh, S. J. (2016). Interocular suppression patterns
731 in binocularly abnormal observers using luminance- and contrast-modulated noise stimuli.
732 *Journal of Vision*, *16*(20), 1–28. https://doi.org/10.1167/16.10.20.doi

733 Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying
734 non-Fourier motion perception. *Journal of the Optical Society of America. A, Optics and*
735 *Image Science*, *5*(11), 1986–2007.

736 Ellemberg, D., Allen, H. A., & Hess, R. F. (2004). Investigating local network interactions
737 underlying first- and second-order processing. *Vision Research*, *44*(15), 1787–97.
738 https://doi.org/10.1016/j.visres.2004.02.012

739 Georgeson, M. A., & Schofield, A. J. (2016). Binocular functional architecture for detection of
740 contrast-modulated gratings. *Vision Research*, *128*, 68–82.
741 https://doi.org/10.1016/j.visres.2016.09.005

742 Hairol, M. I., & Waugh, S. J. (2010a). Lateral facilitation revealed dichoptically for luminance-
743 modulated and contrast-modulated stimuli. *Vision Research*, *50*(23), 2530–42.
744 https://doi.org/10.1016/j.visres.2010.08.026

745 Hairol, M. I., & Waugh, S. J. (2010b). Lateral interactions across space reveal links between
746 processing streams for luminance-modulated and contrast-modulated stimuli. *Vision*
747 *Research*, *50*(9), 889–903. https://doi.org/10.1016/j.visres.2010.02.012

748 Hollins, M., & Hudnell, K. (1980). Adaptation of the binocular rivalry mechanism.
749 *Investigative Ophthalmology & Visual Science*, *19*(9), 1117–1120.

750 Kalarickal, G. J., & Marshall, J. a. (2000). Neural model of temporal and stochastic properties
751 of binocular rivalry. *Neurocomputing*, *32–33*, 843–853. https://doi.org/10.1016/S0925-
752 2312(00)00252-6

753 Kang, M.-S., & Blake, R. (2011). An integrated framework of spatiotemporal dynamics of
754 binocular rivalry. *Frontiers in Human Neuroscience*, *5*(August), 88.
755 https://doi.org/10.3389/fnhum.2011.00088

756 Kim, Y.-J., Grabowecky, M., & Suzuki, S. (2006). Stochastic resonance in binocular rivalry.
757 *Vision Research*, *46*(3), 392–406. https://doi.org/10.1016/j.visres.2005.08.009

758   Kitterle, F. L., & Thomas, J. (1980). The effects of spatial frequency, orientation, and color

759   upon binocular rivalry and monocular pattern alternation. *Bulletin of the Psychonomic*

760   *Society*, *16*(5), 405–407. https://doi.org/10.3758/BF03329581

761   Klein, S. A., Hu, james Q., & Carney, T. (1996). The adjacent pixel nonlinearity: Problems

762   and solutions. *Vision Research*, *36*(19), 3167–3181.

763   Klink, P. C., Brascamp, J. W., Blake, R., & van Wezel, R. J. A. (2010a). Experience-driven

764   plasticity in binocular vision. *Current Biology*, *20*(16), 1464–9.

765   https://doi.org/10.1016/j.cub.2010.06.057

766   Klink, P. C., Brascamp, J. W., Blake, R., & van Wezel, R. J. A. (2010b). Supplemental

767   Information Experience-Driven Plasticity in Binocular Vision. *Current Biology*, *20*(16).

768   Kovács, I., Papathomas, T., Yang, M., & Feher, A. (1996). When the brain changes its mind:

769   Interocular grouping during binocular rivalry. *Proceedings of the National Academy of*

770   *Sciences of the United States of America*, *93*(December), 15508–15511.

771   Laing, C. R., & Chow, C. C. (2002). A spiking neuron model for binocular rivalry. *Journal of*

772   *Computational Neuroscience*, *12*(1), 39–53.

773   Landy, M., & Graham, N. (2004). Visual perception of texture. *The Visual Neurosciences*, 1–

774   43.

775   Lankheet, M. J. M. (2006). Unraveling adaptation and mutual inhibition in perceptual rivalry.

776   *Journal of Vision*, *6*(4), 304–10. https://doi.org/10.1167/6.4.1

777   Larsson, J., Landy, M. S., & Heeger, D. J. (2006). Orientation-selective adaptation to first- and

778   second-order patterns in human visual cortex. *Journal of Neurophysiology*, *95*(2), 862–81.

779   https://doi.org/10.1152/jn.00668.2005

780   Lehky, S. (1988). An astable multivibrator model of binocular rivalry. *Perception*, *17*, 215–

781   228.

782   Levelt, W. J. M. (1965). *On binocular rivalry*. Soesterberg/Netherlands.

783   Levelt, W. J. M. (1967). Note on the distribution of dominance times in binocular rivalry.

784   *British Journal of Psychology*, *58*(1–2), 143–145.

785   Li, G., Yao, Z., Wang, Z., Yuan, N., Talebi, V., Tan, J., … Baker, C. L. (2014). Form-cue

786   invariant second-order neuronal responses to contrast modulation in primate area V2. *The*

787   *Journal of Neuroscience*, *34*(36), 12081–92. https://doi.org/10.1523/JNEUROSCI.0211-

788   14.2014

789   Liu, L., Tyler, C. W., & Schor, C. M. (1992). Failure of Rivalry at low contrast: evidence of a

790   suprathreshold binocular rummation process. *Vision Research*, *32*(8), 1471–1479.

791   Livingstone, M. S., & Hubel, D. H. (1987). Psychophysical of Form , Color , Evidence

792   Movement , for Separate and Depth Channels for the Perception. *The Journal of*

793   *Neuroscience*, *7*(November), 3416–3468.

794   Logothetis, N., Leopold, D., & Sheinberg, D. (1996). What is rivalling during binocular

795   rivalry? *Nature Neuroscience*, *380*, 621–624.

796   Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the

797   human brain. *Science*, *280*(5371), 1930–4.

798   Lunghi, C., & Burr, D. C. (2013). Long-term effects of monocular deprivation revealed with

799   binocular rivalry gratings modulated in luminance and in color. *Journal of Vision*, *13*, 1–

800   15. https://doi.org/10.1167/13.6.1.doi

801   Mareschal, I., & Baker, C. L. (1998). Temporal and Spatial Response to Second-Order Stimuli

802   in Cat Area 18. *Journal of Neurophysiology*, 2811–2823.

803   Mareschal, I., & Baker, C. L. (1999). Cortical processing of second-order motion. *Visual*

804   *Neuroscience*, *16*(3), 527–40.

805   Moreno-Bote, R., Rinzel, J., & Rubin, N. (2007). Noise-induced alternations in an attractor

806   network model of perceptual bistability. *Journal of Neurophysiology*, *98*(3), 1125–39.

807   https://doi.org/10.1152/jn.00116.2007

808   Moreno-Bote, R., Shpiro, A., Rinzel, J., & Rubin, N. (2010). Alternation rate in perceptual

809   bistability is maximal at and symmetric around equi-dominance. *Journal of Vision*, *10*(11),

810   1. https://doi.org/10.1167/10.11.1

811   Mueller, T., & Blake, R. (1989). A fresh look at temporal dynamics of binocular rivalry.

812   *Biological Cybernetics*, *61*(3), 223–232.

813   Mueller, T. J. (1990). A physiological model of binocular rivalry. *Visual Neuroscience*, *4*(1),

814   63–73.

815   Nguyen, V. a., Freeman, A. W., & Alais, D. (2003). Increasing depth of binocular rivalry

816   suppression along two visual pathways. *Vision Research*, *43*(19), 2003–2008.

817   https://doi.org/10.1016/S0042-6989(03)00314-6

818   O' Shea, R. P., Parker, A., La, D., & Alais, D. (2009). Monocular rivalry exhibits three

819   hallmarks of binocular rivalry : Evidence for common processes. *Vision Research*, *49*(7),

820   671–681. https://doi.org/10.1016/j.visres.2009.01.020

821   O'Shea, R., Sims, J. H., & Govan, G. (1997). The Effect of Spatial Frequency and Field Size

822   on the Spread of Exclusive Visibility in Binocular Rivalry. *Vision Research*, *37*(2), 175–

823   183.

824   Pastukhov, A., & Braun, J. (2011). Cumulative history quantifies the role of neural adaptation

825   in multistable perception. *Journal of Vision*, *11*(12), 1–10.

826   https://doi.org/10.1167/11.10.12.

827   Robertson, C. E., Kravitz, D. J., Freyberg, J., Baron-Cohen, S., & Baker, C. I. (2013). Slower

828   rate of binocular rivalry in autism. *The Journal of Neuroscience*, *33*(43), 16983–91.

829   https://doi.org/10.1523/JNEUROSCI.0448-13.2013

830   Schofield, A. J., & Georgeson, M. A. (1999). Sensitivity to modulations of luminance and

831   contrast in visual white noise: separate mechanisms with similar behaviour. *Vision*

832   *Research*, *39*(16), 2697–716.

833   Schofield, A. J., & Georgeson, M. A. (2000). The temporal properties of first- and second-order

834   vision. *Vision Research*, *40*(18), 2475–87.

835   Schor, C. M. (1977). Visual stimuli for strabismic suppression. *Perception*, 583–593.

836   Seely, J., & Chow, C. C. (2011). Role of mutual inhibition in binocular rivalry. *Journal of*

837   *Neurophysiology*, *106*(5), 2136–50. https://doi.org/10.1152/jn.00228.2011

838   Skerswetat, J., Formankiewicz, M. A., & Waugh, S. J. (2016). Very few exclusive percepts for

839   contrast-modulated stimuli during binocular rivalry. *Vision Research*, *121*, 10–22.

840   https://doi.org/10.1016/j.visres.2016.01.002

841   Sukumar, S., & Waugh, S. J. (2007). Separate first- and second-order processing is supported

842   by spatial summation estimates at the fovea and eccentrically. *Vision Research*, *47*(5),

843   581–96. https://doi.org/10.1016/j.visres.2006.10.004

844   Tanaka, H., & Ohzawa, I. (2006). Neural Basis for Stereopsis from Second-Order Contrast

845   Cues. *Journal of Neuroscience*, *26*(16), 4370–4382.

846   https://doi.org/10.1523/JNEUROSCI.4379-05.2006

847   Veser, S., O'Shea, R. P., Schröger, E., Trujillo-Barreto, N. J., & Roeber, U. (2008). Early

848   correlates of visual awareness following orientation and colour rivalry. *Vision Research*,

849   *48*(22), 2359–69. https://doi.org/10.1016/j.visres.2008.07.024

850   von Helmholtz, H. (1867). Handbuch der physiologischen Optik. In *Encyklopädie der Physik*

851   (9th ed., p. 901). Leipzig: Gustav Karsten.

852   Wade, N. J. (1974). The effect of orientation in binocular contour rivalry of real images and

853   afterimages. *Perception & Psychophysics*, *15*(2), 227–232.

854   https://doi.org/10.3758/BF03213937

855   Waugh, S. J., Lalor, S., & Hairol, M. I. (2009). Binocular summation for luminance- and

856   contrast-modulated noise stimuli. *Journal of Vision*, *8*(9(8)), 1012.

857   https://doi.org/doi:10.1167/9.8.1012.

858   Webber, M., & Bressloff, P. (2013). The effects of noise on binocular rivalry waves: a

859   stochastic neural field model. *Journal of Statistical Mechanics: Theory and Experiment*,

860   *3*(12).

861   Wheatstone, C. (1838). Contributions to the physiology of vision.--Part the first. On some

862   remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical*

863   *Transactions of the Royal Society of London*, *128*, 371–394.

864   Wilcox, L. M., & Hess, R. F. (1996). Is the site of non-linear filtering in stereopsis before or

865   after binocular combination? *Vision Research*, *36*(3), 391–399.

866   Wilson, H. R. (2003). Computational evidence for a rivalry hierarchy in vision. *Proceedings of*

867   *the National Academy of Sciences of the United States of America*, *100*(24), 14499–503.

868   https://doi.org/10.1073/pnas.2333622100

869   Wong, E. H., Levi, D. M., & McGraw, P. V. (2001). Is second-order spatial loss in amblyopia

870   explained by the loss of first-order spatial input? *Vision Research*, *41*(23), 2951–60.

871   Wong, E. H., Levi, D. M., & McGraw, P. V. (2005). Spatial interactions reveal inhibitory

872   cortical networks in human amblyopia. *Vision Research*, *45*(21), 2810–9.

873   https://doi.org/10.1016/j.visres.2005.06.008

874   Yang, Y., Rose, D., & Blake, R. (1992). On the variety of percepts associated with dichoptic

875   viewing of monocular imuli. *Perception*, *21*, 47–62.

876   Zhou, J., Georgeson, M. A., & Hess, R. F. (2014). Linear binocular combination of responses

877   to contrast modulation: Contrast-weighted summation in first-and second-order vision.

878   *Journal of Vision*, *14*, 1–19. https://doi.org/10.1167/14.13.24.doi

879   Zhou, J., Liu, R., Zhou, Y., & Hess, R. F. (2014). Binocular combination of second-order

880   stimuli. *PLOS ONE*, *9*(1), e84632. https://doi.org/10.1371/journal.pone.0084632

881   Zhou, Y. H., & Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons

882   for non-Fourier responses. *Science, 261*, 98–101.

883